

Oceanography and Marine Biology

AN ANNUAL REVIEW

Volume 37

Founder Editor
HAROLD BARNES

Editors
A. D. ANSELL
R. N. GIBSON, MARGARET BARNES

Also available as a printed book
see title verso for ISBN details

OCEANOGRAPHY
and
MARINE BIOLOGY

AN ANNUAL REVIEW

Volume 37

OCEANOGRAPHY
and
MARINE BIOLOGY

AN ANNUAL REVIEW

Volume 37

Editors

A.D. Ansell

R.N. Gibson

Margaret Barnes

*The Dunstaffnage Marine Laboratory
Oban, Argyll, Scotland*

Founded by Harold Barnes



First published 1999 by Taylor & Francis
11 New Fetter Lane, London EC4P 4EE
Simultaneously published in the USA by Taylor & Francis
29 West 35th Street, New York, NY1001

Taylor & Francis is an imprint of the Taylor & Francis Group

This edition published in the Taylor & Francis e-Library, 2003.

© 1999 A.D.ANSELL, R.N.GIBSON, MARGARET BARNES

All rights reserved. No part of this book may be reprinted or reproduced or utilised in any form or by any electronic, mechanical, or other means, now known or hereafter invented, including photocopying and recording, or in any information storage or retrieval system, without permission in writing from the publishers.

Every effort has been made to ensure that the advice and information in this book is true and accurate at the time of going to press. However, neither the publisher nor the authors can accept any legal responsibility or liability for any errors or omissions that may be made. In the case of drug administration, any medical procedure or the use of technical equipment mentioned within this book, you are strongly advised to consult the manufacturer's guidelines.

British Library Cataloguing in Publication Data
A catalogue record for this book is available from the British Library

Library of Congress Cataloging in Publication Data
are available

ISBN 0-203-48482-7 Master e-book ISBN

ISBN 0-203-79306-4 (Adobe eReader Format)
ISBN 0-748-40919-X (Print Edition)

CONTENTS

Preface	vii
<i>Air-sea gas exchange into the millennium: progress and uncertainties</i> Thomas Frost & Robert C.Upstill-Goddard	1
<i>The role of benthic microalgae in neritic ecosystems</i> Lawrence B.Cahoon	47
<i>Mesoherbivore-macroalgal interactions: feeding ecology of sacoglossan sea slugs (Mollusca, Opisthobranchia) and their effects on their food algae</i> S.I.Williams & D.I.Walker	87
<i>Population structuring, gene dispersal and reproduction in the Actinia equina species group</i> M.C.Perrin, J.P.Thorpe & A.M.Solé-Cava	129
<i>The mortality of intertidal cirripedes</i> Margaret Barnes	153
<i>The biology of siphonariid limpets (Gastropoda: Pulmonata)</i> Alan N.Hodgson	245
Author index	315
Systematic index	337
Subject index	345

PREFACE

This, the thirty-seventh volume in the series, contains the usual broad mix of topics covering physical and biological aspects of marine science. As in the past the contents of the articles range widely from global ocean processes through the ecological importance of particular groups to detailed reviews of the biology of individual genera and species that are of worldwide interest. Reviews such as these provide a great service to the marine science community by summarizing and evaluating the literature but they are time consuming to write. Consequently, the incentive to produce such articles may be less strong at a time when publication rates are considered, rightly or wrongly, to be one measure of scientific achievement. Fortunately, the steady influx of high quality manuscripts indicates the willingness of authors to compile reviews and ensures the continuing success of the series.

As always, it is a pleasure for the editors to acknowledge the authors' patience and co-operation in responding to editorial requests and the efficiency of the publishers in maintaining the regular appearance of these volumes.

It is with great regret that we have to report the death of Dr A.D. Ansell during the final stages of the production of this volume. He was a long-standing colleague and friend and will be greatly missed. We dedicate this volume to his memory

RNG, MB

AIR-SEA GAS EXCHANGE INTO THE MILLENNIUM: PROGRESS AND UNCERTAINTIES

THOMAS FROST & ROBERT C. UPSTILL-GODDARD

*Department of Marine Sciences and Coastal Management, University of Newcastle,
Newcastle upon Tyne, NE1 7RU, UK.*

Abstract The current status of research into air-water gas exchange is reviewed. Some relevant basic concepts are re-examined within the context of current progress towards parameterization of the air-sea gas exchange process using models and data from wind-tunnels, and the interpretational difficulties that still persist with these approaches are identified and discussed. Subsequently, field measurements of air-water gas exchange are reviewed, with key developments highlighted, in particular, important recent advances in the use of micrometeorological and chemical tracer-based techniques of measurement. Results obtained with these methods are summarized and compared with laboratory wind-tunnel-based measurements, in order to identify some outstanding gas exchange issues still to be resolved. In the light of these, the potentially important roles played by a variety of physical, chemical and biological forcings are considered and some likely fruitful avenues for nature research are outlined for this important area of global science.

Introduction

The exchange of gases between oceans and atmosphere is a fundamentally important process in global biogeochemistry. For many gases of biogeochemical interest the oceans are a net atmospheric source; important examples include DMS (Charlson et al. 1987, Turner et al. 1996), N₂O (Law & Owens 1990, Nevison et al. 1995, Bange et al. 1996a,b), CH₄ (Crutzen 1991, Owens et al. 1991, Bange et al. 1994), non-methane hydrocarbons (Plass-Dülmer et al. 1993), CO (Johnson & Bates 1996), COS (Andreae & Ferek 1992, Uher & Andreae 1997), and CS₂ (Kim & Andreae 1992). These gases play important roles in atmospheric chemistry and climate regulation and for all of them, the gas exchange rate itself controls directly the sea-to-air flux. Consequently, knowledge of air-sea gas exchange rates is directly relevant to a range of global issues, including the role of marine-derived aerosols in climate regulation (Schwartz 1988, 1989, Wigley 1989), relative source strengths of natural and anthropogenic acid rain sulphur (Nriagu et al. 1987, Turner et al. 1988), the oceanic source strengths of N₂O, CH₄, CO, and COS (Bange et al. 1994, Nevison et al. 1995, Johnson & Bates 1996, Uher & Andreae 1997) and the role of the oceans in regulating atmospheric halocarbons (Butler 1994, Lobert et al. 1995, Nightingale et al. 1995).

In contrast, for CO₂, for which the oceans are a net atmospheric sink, the situation is somewhat more complex. The rate of CO₂ uptake by the deep ocean is ultimately dictated by the rate at which CO₂ in surface waters can be exchanged vertically downward across the thermocline; on average a doubling of the air-sea gas exchange rate only promotes an

approximately 10% increase in the overall rate of CO₂ absorption (Siegenthaler & Sarmiento 1993). Even so, accurate estimates of the air-sea exchange rate of CO₂ are nevertheless critical to our perception of the global carbon cycle, over which there is currently substantial uncertainty (e.g. Hesshaimer et al. 1994, Houghton et al. 1996, Schimel 1998). This situation principally arises because of conflicting conclusions regarding the magnitudes and geographical distributions of major global CO₂ source and sink regions, as derived from various ocean or terrestrial-atmosphere models combined with limited field measurements (e.g. Tans et al. 1990, Sarmiento & Sundquist 1992, Siegenthaler & Sarmiento 1993, Braziunas et al. 1995, Cao & Woodward 1998, Sarmiento et al. 1998). As an indication of the inherent model uncertainties, their predictions for the stabilization level of atmospheric CO₂ range from 350 μatm to 1000 μatm (Sarmiento et al. 1995, Schimel et al. 1996).

An important example which further highlights the role of gas exchange in the global carbon cycle refers to processes in the North Atlantic; subregions such as the Norwegian and Greenland Seas are currently important sites for CO₂ transport to the deep ocean via surface water downwelling. During its northerly transport driven by this downwelling, Atlantic surface sea water cools rapidly and its capacity for dissolved CO₂ increases. However, because re-equilibration of CO₂ via air-sea exchange is currently too slow to keep pace with the cooling rate, the downwelled water is significantly undersaturated in CO₂ (Keeling 1968). Therefore, changes in the local gas exchange rate have the potential to modify the atmospheric CO₂ sink in the North Atlantic and it is precisely in such high latitude regions as this that gas exchange rates are least well known. Clearly, accurate estimates of air-sea CO₂ exchange made on at least regional or preferably local scales are an urgent scientific requirement and, by helping to constrain the model results, may prove a powerful tool for resolving important controversies such as this.

In this review our aim is to provide an overview of the current status of research into air-sea gas exchange which is of value to biogeochemists working in the field, while remaining accessible to the non-specialist. It is not our intention, nor is it appropriate, to attempt to provide exhaustive coverage of so diverse a subject in a review of this length; rather, we aim to focus on those issues which we perceive to be the most pertinent. For those aspects of the subject addressed in rather less detail here, we direct the interested reader towards important key references. By re-examining some important basic concepts, we review progress towards parameterization of the air-sea gas exchange process using models and data from wind-tunnels. Subsequently, we summarize and compare the major micrometeorological and tracer techniques developed for estimating air-sea gas exchange rates in the field and in so doing, highlight a number of unresolved issues arising out of current deficiencies in our understanding. Lastly, we identify some potentially fruitful avenues for future research in this important area of global science.

Basic concepts

In the most basic conceptual model of air-water gas exchange, which derives from the work of Whitman (1923), the air/water interface is visualized as a simple layered system with gas transport effected both by molecular diffusion and turbulent mixing (Fig. 1). In this model, beyond several 10s of μm from the interface on either side of it, gas transport is dominated by rapid eddy motions because the rate of turbulent transport is several orders of magnitude greater than the rate of diffusion (Jähne et al. 1987b). However, with increasing proximity to the interface turbulent transport becomes progressively attenuated owing to the viscous

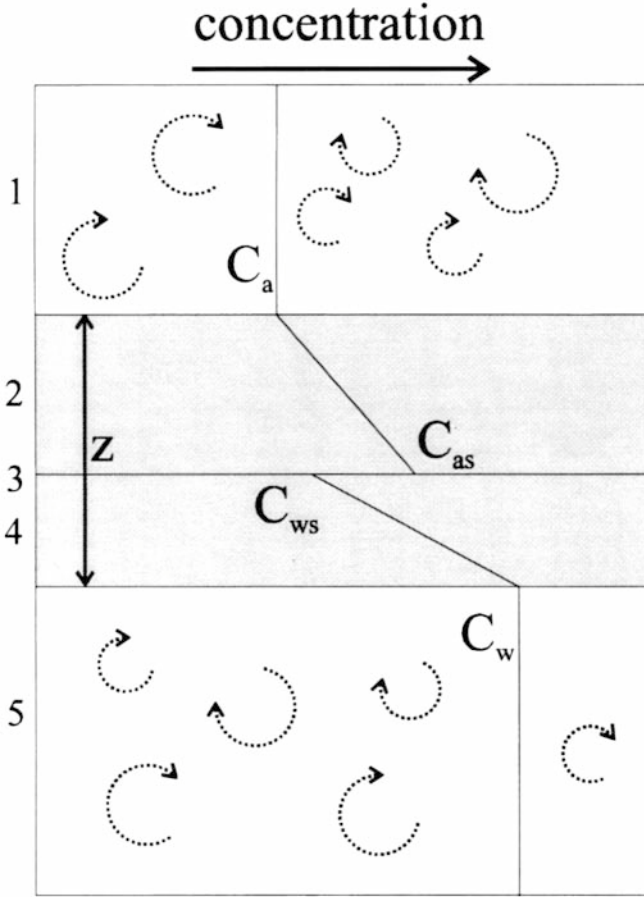


Figure 1 Schematic section of an idealized 1-dimensional steady-state air/water interface (Whitman 1923). Regions 1 and 5 are turbulent boundary layers in air and water, with gas concentrations C_a and C_w , respectively, and regions 2 and 4 are associated stagnant boundary layers, with respective depths $\approx 100 \mu\text{m}$ (air) and $\sim 20\text{--}100 \mu\text{m}$ (water). Region 3 is the interface. C_{as} and C_{ws} are gas concentrations at the air-side and water-side, respectively, of the air/water interface. The concentration discontinuity across the interface reflects solubility considerations.

properties of this boundary, so that molecular diffusion takes over as the dominant transport mechanism, giving rise to a stagnant boundary layer (sometimes referred to as the “stagnant film”) on each side of the interface. Consequently, for moderately reactive trace gases with measurable aquatic sources or sinks, a gas concentration gradient develops across each of the two stagnant boundaries (Fig. 1).

Fick’s law of diffusion in one-dimension (i.e. excluding advection) may be used to describe gas transport across the stagnant boundary layer:

$$F = -D \frac{\partial c}{\partial z} \quad (\text{Equ. 1}),$$

where F is the gas flux ($\text{ML}^{-2}\text{T}^{-1}$) through the layer, D is the molecular diffusion coefficient (diffusivity) (L^2T^{-1}) and ∂_c/∂_z is the concentration gradient (ML^{-4}) across a boundary layer of depth, Z (L). In practice this equation cannot be applied directly to the determination of gas fluxes; although D can be routinely quantified experimentally for a range of gases at stated temperatures (Hayduk & Laudie 1974, Jähne et al. 1987a, Saltzman et al. 1993, King & Saltzman 1995), direct measurements of gas concentration gradients across the stagnant boundary are precluded because Z is only several 10s of μm . Equation 1 is therefore restated in another way by specifying a variable known as the “total gas transfer velocity”, k_T (sometimes termed the “piston velocity” or “gas exchange coefficient”), which incorporates the effects of both D and Z , such that:

$$k_T = \frac{D}{Z} \quad (\text{Equ. 2}),$$

k_T has units of a velocity (LT^{-1} , typically cm h^{-1}) and describes the rate of approach to equilibrium of the system with respect to gas concentrations. Hence, the gas flux, F , can be described by:

$$F = k_T \Delta C \quad (\text{Equ. 3}).$$

In this case $-\Delta C$ is the gas concentration difference between the air- and water-phases either side of the stagnant boundaries. k_T can be conveniently separated into two component transfer velocities operative in the gas phase (k_a) and in water (k_w), such that:

$$k_a = \frac{F}{(C_a - C_{as})} \quad (\text{Equ. 4}),$$

and

$$k_w = \frac{F}{(C_w - C_{ws})} \quad (\text{Equ. 5}),$$

(refer to Fig. 1).

In order to evaluate the relative magnitudes of the two component transfer velocities k_a and k_w , it is conceptually most straightforward to envisage the two boundary layers as each offering a resistance to diffusive transport, analogous to an arrangement of serial resistors in an electrical circuit (Liss 1983, Liss & Merlivat, 1986). Hence the total resistance to gas exchange, R (L^{-1}T), is equivalent to $1/k_T$ and

$$R = r_w + r_a \quad (\text{Equ. 6}),$$

where the water-phase resistance, $r_w = 1/\varepsilon k_w$ and the air-phase resistance, $r_a = 1/H k_a$ (Liss & Slater 1974); H is the Henry Law Constant (i.e. $H = \text{equilibrium gas concentration in the air-phase}/\text{equilibrium concentration of unionized dissolved gas in the liquid phase}$) and ε is a factor accounting for the chemical enhancement of gas exchange due to gas/aqueous-phase reactions. For trace gases which are chemically “unreactive” in the aqueous-phase, such as DMS, CH_4 and N_2O , $\varepsilon \sim 1.0$, whereas for highly aqueous-phase reactive trace gases such as SO_2 , NH_3 and HCl , ε may typically be $>10^3$ (Liss 1971, 1988).

Experiments on the air- and water-phase resistances to gas transfer have been reviewed by Liss & Slater (1974) and Liss (1983). These show that for H_2O -vapour and the aqueous-phase reactive trace gases, $k_a \gg k_w$; the bulk of the resistance to gas transfer is in the air-

phase. This conclusion is intuitive for H₂O and similarly so for the reactive gases, where rapid aqueous-phase reactions preclude any possibility of measurable concentration gradients developing in the water-phase boundary layer. Conversely for the “chemically unreactive” gases, $r_w \gg r_a$; all of the resistance to gas transfer is in the water-phase and hence $k_w \gg k_a$. Because almost all environmentally important trace biogases fall into this category, k_a can be ignored and for all practical purposes $k_T = k_w$. Difficulties persist over the determination of $C_w - C_{ws}$ in equation 5 owing to the small spatial scale involved (Fig. 1), but these may be eliminated by inferring the value of C_{ws} from C_a and an appropriate solubility parameter β (the Bunsen solubility coefficient, $v/v \text{ atm}^{-1}$), so that

$$F = k_w (C_w - \beta C_a) \quad (\text{Equ. 7}).$$

Schmidt number

It may be logically concluded from equation 2 that if k_w is known for any given gas, its value may be inferred for any other gas, provided that both gas diffusivities are known. In reality this relationship is of practical value only when Z is fixed; interconversion over a range of film depths is elusive owing to the inherent measurement problems. A more useful approach may be derived by analogy with theories of heat and mass transfer, such as in the treatment given in Deacon (1977). In this approach k_w is treated as a function of the transfer coefficients of momentum (i.e. kinematic viscosity of water, ν) and mass (i.e. gas diffusivity, D), by defining the “Schmidt number”, Sc , where

$$Sc = \frac{\nu}{D} \quad (\text{Equ. 8}).$$

Hence Sc is analogous to the Prandtl number used in heat transport studies (Ledwell 1982) and it incorporates the effects of temperature and salinity (Wanninkhof 1992). The relationship between the k_w values for any two gases may then be stated in terms of their Schmidt numbers:

$$\frac{k_{w1}}{k_{w2}} = \frac{(Sc_2)^n}{(Sc_1)^n} \quad (\text{Equ. 9}),$$

where n , the so-called “Schmidt number exponent”, is a function of the film thickness.

Equation 9 remains valid only for as long as k_w remains independent of the gas solubility and so the influence of solubility dependent, bubble-mediated transport must be negligible. Hence, the value of the Sc conversion will come into question during periods of high wind speed with breaking waves, a point to which we shall return later. In addition, the value of Sc necessarily depends heavily upon the measurement accuracy for ν and D . A diffusivity-temperature dependence study by Jähne et al. (1987a) cites a maximum rms deviation of the data from the best fit as 5% or less for a range of inert and bioreactive gases. Adopting these relationships for D and an empirical equation (Wilke & Chang 1955) for additional gases not considered by Jähne et al. (1987a), Wanninkhof (1992) derived polynomial fits relating values of Sc for a range of gases (He, Ne, Ar, O₂, CH₄, CO₂, N₂, Kr, N₂O, Rn, SF₆, CCl₂F₂, CCl₃F) to temperature for salinities of 0 psu and 35 psu. Wanninkhof (1992) estimated the total error range for Sc at 3–10%, a significant improvement over previous estimates. The validity of this empirical approach has recently been verified for SF₆ by laboratory estimates of its diffusivity (King & Saltzman 1995), the difference between these estimates and the empirical determination of Wanninkhof (1992) being <4% at 20°C.

Friction velocity and drag coefficient

In most natural systems the degree of near-surface turbulence is fundamentally related to the surface wind speed, although under certain circumstances factors such as rainfall intensity (Bliven et al. 1993a, Ho et al. 1997) and in the case of shallow water bodies, interactions with bottom topography (Roberts 1984), may become important. Although gas exchange has most commonly been modelled by treating k_w as a simple function of wind speed, in reality the process is more complex than this, involving a range of geophysical forcings, and empirical gas exchange models based solely on wind speed tend to yield conflicting results (e.g. Liss & Merlivat 1986, Wanninkhof 1992). At least part of the discrepancy arises because the transfer of momentum to the water surface is a non-unique function of wind speed. Various attempts have been made to overcome this problem by reference to the “friction velocity”, u^* , a quantity which incorporates the vertical momentum flux or shear stress, t , such that:

$$u^* = \tau / \rho \quad (\text{Equ. 10}),$$

where ρ is the mean air density (Merlivat & Memery 1983). The wind speed may then be related to u^* as follows:

$$u^* = \sqrt{C_d U_{10}^2} \quad (\text{Equ. 11})$$

(Clark et al. 1994), where U_{10} is the measured wind speed converted to an equivalent value at a standard reference height of 10 m above the water surface and C_d is the dimensionless drag coefficient. In practice equation 11 is complicated because C_d is itself only a poorly constrained function of wind speed (Stauffer 1980). The value of C_d varies in relation to the surface roughness length, therefore, in addition to wind speed, other factors that contribute to wave formation—including over water wind fetch, local topography and surface contamination—need to be evaluated individually for each situation. Other roughness causing variables, such as rain, may also have to be included when estimating C_d (Bliven et al. 1993a). In view of these difficulties C_d has commonly been approximated as a constant (Wanninkhof et al. 1987, Clark et al. 1994). Additional modifications to surface turbulence arise from thermal instabilities driven by surface cooling (Erickson 1993), requiring further corrections to C_d . Because of these uncertainties, it is difficult in practice to derive u^* for a given system based on its value determined elsewhere. However, there have been advancements utilizing radar backscatter from a laboratory tank to estimate u^* (Bliven et al. 1993b).

Mechanistic models of gas exchange*Film models*

The classical film model of Whitman (1923), Figure 1, defines Z as a spatially and temporally invariant quantity. It follows from this that k_w is independent of Z and may be shown to be directly proportional to D^1 . Although this simple treatment has some merit in evaluating the role of chemical enhancement and in determining whether r_a or r_w dominates

gas exchange, the criterion of constant Z is only approximately fulfilled during conditions of extremely low surface turbulence (i.e. at very low wind speeds) and most wind-wave tunnel experiments do not support the D^1 dependence (e.g. Wanninkhof & Bliven 1991).

Because the base of the stagnant film is defined as the point at which turbulent mixing begins to dominate over diffusive transport, the value of Z is intimately linked to D (Ledwell 1982). This is problematic, as gases with contrasting diffusivities will necessarily have different values of Z for identical conditions of turbulence. In this simple form the film model clearly has limited practical value; however, Deacon (1977) developed a more refined version, the so-called “Boundary-layer model”. In this, gas transfer across a flat sea surface is considered by analogy with established theories of heat and momentum transfer across a rigid smooth surface. Deacon (1977) predicted k_w from the turbulent velocity profile over a smooth rigid surface developed by Reichardt (1951), which describes a smooth transition from turbulent to molecular transport towards the interface as turbulence becomes progressively attenuated by the viscous properties of the surface film. Because it does not involve a discrete layer characterized by purely molecular transport, i.e. turbulent fluctuations are detectable as close to the interface as can be practically resolved, the Deacon (1977) model is probably more realistic than that of Whitman (1923), and it describes k_w for a non-reactive gas as

$$k_w = 0.082 \left(\frac{P_a}{P_w} \right)^{0.5} Sc^{-0.67} u^* \quad (\text{Equ. 12}),$$

where P_a and P_w are the densities of air and water, respectively. Implicit in the model is a Schmidt number exponent, $n, = -0.67$, which is consistent with gas exchange measurements derived with wave tanks at low wind speeds (Jähne et al. 1979, Wanninkhof & Bliven 1991). In addition to specifying a smooth surface, the Deacon (1977) model assumes continuity of stress across the interface in order to convert the velocity profile in air to an equivalent profile in water. In view of the complexity of incorporating roughness parameters to describe the interface at high levels of turbulence (Kitaigorodskii 1984), it is not surprising that Deacon (1977) limited the model to the description of k_w at low wind speeds.

Surface renewal models

The surface renewal model was first proposed by Higbie (1935) in response to the inadequacies in the Whitman (1923) treatment. In the Higbie (1935) model, water making up the stagnant boundary layer is periodically replaced from below. The renewal rate, which describes the effects of turbulence upon the interface, is the rate-limiting step to gas exchange. However, the renewal rate is a complex function related to divergence and convergence of the water, which are influenced by the dynamics of the system, including wind stress (Ledwell 1982) and organic surface films. Asher & Pankow (1991) showed the model to describe k_w well for CO_2 only when such films were absent. Subsequent refinements to the basic Higbie (1935) model include those of Münnich & Flothman (1977), which incorporates a statistical description of the renewal of the entire stagnant boundary layer, and the model of Ledwell (1982), which draws upon theories of turbulent flow across smooth solid walls to describe surface renewal. Earlier derivatives of the surface renewal model

are reviewed by Danckwerts (1970). In whichever of these forms the surface renewal model is used, k_w is proportional to $D^{0.5}$, i.e. $n=-0.5$.

The rubber cloth model

This model (Witting 1971), originally conceived to describe heat transfer, is equally applicable to a description of gas exchange with substitution of the appropriate parameters (Wanninkhof 1986). The model allows for a periodic thickening and thinning of the waterside boundary layer, with the generation of short wavelength, high amplitude waves (capillary waves) leading to enhanced gas transfer. Although this phenomenon is well known from observations in wind-tunnels (e.g. Jähne et al. 1979), the model under-predicts an observed enhancement of gas exchange coincidental with the onset of gravity waves (Jähne et al. 1979, Wanninkhof & Bliven 1991).

Direct estimates of n

Direct estimates of the Sc exponent, n , have been made in wind and wave laboratory exchange tanks (e.g. Jähne et al. 1984b, Wanninkhof & Bliven 1991) and in enclosed water bodies in the field (e.g. Watson et al. 1991, Clark et al. 1995). These data are summarized in Table 1, along with some model-derived estimates of n . Although somewhat limited in number, these data provide a useful preliminary test of the validity of the various gas exchange models described above.

In laboratory studies, n has been evaluated with a range of gaseous tracers, including H_2 , He, Xe, N_2O and CH_4 , either singly or in various combinations (Ledwell 1982, Holmen & Liss 1984). For laboratory windspeeds $<10 \text{ m s}^{-1}$, corresponding to a rough but unbroken surface, $n \sim -0.5$ (Jähne et al. 1987b, Ledwell 1984). Beyond windspeeds of 10 m s^{-1} , where significant wave breaking is observed in wind and wave tanks, Wanninkhof & Bliven (1991) found n to increase to -0.26 ± 0.14 .

Direct field estimates of n are few. Two field studies carried out at low wind speeds in small lakes (Watson et al. 1991, Clark et al. 1995) involved measurements of the gaseous tracers sulphur hexafluoride, SF_6 , and 3He , using the relationship:

$$n = \frac{\ln\left(\frac{k_{^3He}}{k_{SF_6}}\right)}{\ln\left(\frac{Sc_{SF_6}}{Sc_{^3He}}\right)} \quad (\text{Equ. 13}).$$

Based on small datasets, Watson et al. (1991) found $n=-0.51$ for the SF_6 - 3He tracer pair for U_{10} between 3.8 m s^{-1} and 5.8 m s^{-1} . Similarly, Clark et al. (1995) report $n=-0.57 \pm 0.07$ for U_{10} between 1.9 m s^{-1} and 2.2 m s^{-1} . Earlier lake experiments by Torgersen et al. (1982) using Rn and He gave $n=-1.22$ ($\pm 0.12-0.35$). Holmen & Liss (1984) subsequently reevaluated these data with revised diffusivity values, giving $n=0.76$ ($\pm 0.2-0.4$). In the only direct measurements of n in a seagoing situation to date, Nightingale et al. (in prep.) report $n \sim -0.5$ for SF_6 - 3He , for $U_{10} < 14 \text{ m s}^{-1}$.

Table 1 Direct and model-derived estimates of the Schmidt number exponent, n .

n	Experimental/Model details	Reference
-1	Stagnant film model	Whitman 1923
-0.45	Laboratory experiment: n estimated from dependence of k_{O_2} on temperature. Calculated by Holmen & Liss (1984)	Downing & Truesdale 1955
-0	Laboratory experiment: n estimated from H_2 , N_2 and O_2 , at a very high level of turbulence	Kishinevsky & Serebryansky 1956
-0.62	Laboratory experiment: n estimated from He/N_2 and He/O_2 by Holmen & Liss (1984)	Metzger & Dobbins 1967
-0.1-0.6	Laboratory experiment: n estimated from dependence of k_{He} and k_{N_2} on temperature. Calculated by Holmen & Liss (1984)	Metzger & Dobbins 1967
-0.5	Surface renewal model	Münnich & Flothman 1977
-0.67	Boundary layer model: velocity profile in turbulent flow over a smooth planar surface	Deacon 1977
-0.41	Circular wind/wave tunnel: n estimated from dependence of k_{CO_2} on temperature	Jähne et al. 1979
-0.3-0.4	Laboratory tank: n estimated from dependence of k_{O_2} and k_{CO_2} on temperature	Martinelli 1979
-0.6±0.2	Wind/wave tank: n estimated using CO_2 and O_2	Siems 1980
-0.61±0.07	Laboratory study involving 12 tracer gases	Smith et al. 1980
-1.22	Small lake: n estimated from He and ^{222}Rn	Torgersen et al. 1982
-0.76 (+0.43->0.21)	Recalculation of Torgersen et al. (1982)	Holmen & Liss 1984
-0.73±0.15	Recalculation of Torgersen et al. (1982) using diffusivity data of Jähne et al. (1987a)	Jähne et al. 1987b
-0.47±0.14	18 m wind-tunnel: n estimated from He, N_2O and CH_4	Ledwell 1982, 1984
-0.5	Modelling of turbulent patches caused by breaking waves	Kitaigorodskii 1984
-0.67	Model of rough water surface	Kerman 1984
-0.57±0.15	Laboratory tank, stirrer providing turbulence, n estimated using H_2 , He and Xe	Holmen & Liss 1984
-0.67	Heidelberg circular wind tunnel: rough water surface	Jähne et al. 1984b, 1987b
-0.55±0.05	Heidelberg circular wind tunnel: smooth water surface	Jähne et al. 1984b, 1987b
-0.5	Capillary wave modelling	Coantic 1986
-0.5±0.2	Delft Wind/wave tank ($U_{10}<10 \text{ m s}^{-1}$)	Wanninkhof & Bliven 1991
-0.26±0.14	Delft Wind/wave tank ($U_{10}>10 \text{ m s}^{-1}$)	Wanninkhof & Bliven 1991
-0.51±0.01	Small lake: n estimated from $\text{SF}_6/{}^3\text{He}$; $U_{10} 3.8-5.8 \text{ m s}^{-1}$	Watson et al. 1991
-0.57±0.07	Small pond: n estimated from $\text{SF}_6/{}^3\text{He}$; $U_{10} 1.9-2.2 \text{ m s}^{-1}$	Clark et al. 1995
-0.5	North Sea: n estimated from $\text{SF}_6/{}^3\text{He}$; $U_{10}<14 \text{ m s}^{-1}$	Nightingale et al. (in prep.)

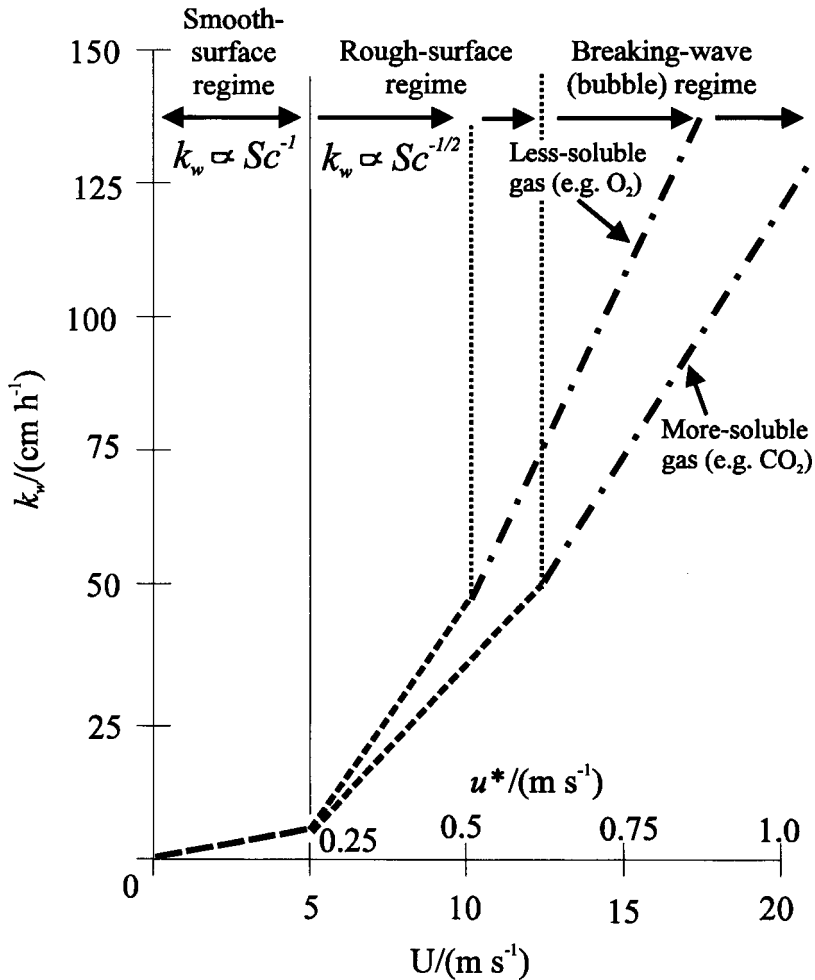


Figure 2 An idealized plot of the water-side gas transfer velocity (k_w) versus wind speed (U) and friction velocity (u^*), derived using data from laboratory wind-tunnel and wave-tank experiments. Reproduced from Liss & Merlivat (1986); Figure 1, p. 117, reproduced with kind permission from Kluwer Academic Publishers.

A summary of wind-tunnel and wave-tank data

Early results for gas exchange measured in wind tunnels and wave tanks are summarized in Liss (1983). One of the most useful summaries of the consensus wind-tunnel results is provided in an idealized gas exchange-wind speed relationship derived by Liss & Merlivat (1986), which identifies three regimes of gas exchange (Fig. 2).

In the “smooth surface regime”, for windspeeds up to $5 \pm 3 \text{ m s}^{-1}$, surface waves are absent and wind-tunnel studies (Jähne et al. 1979, 1984b) confirm that the boundary layer model (Deacon 1977) applies with k_w proportional to $D^{0.67}$ (i.e. $n = -0.67$). The “rough surface regime”, with windspeeds from 5 – $11 \pm 1 \text{ m s}^{-1}$, is characterized by a wave-covered but unbroken surface. Here the surface renewal model is apparently the most relevant and k_w

has been shown to be proportional to $D^{0.5} \cdot D^{0.6}$ (Ledwell 1984, Jähne et al. 1984b, Wanninkhof & Bliven 1991).

The transition point between the smooth and rough surface regimes occurs at the onset of capillary waves and it is therefore tempting to conclude that capillary waves initiate surface renewal in some way, thereby shifting the Sc exponent from $n=-0.67$ to $n=-0.5$ (Fig. 2). However, Hasse (1990) identifies two inconsistencies in this interpretation. First, capillary wave energy is not sufficient to overcome surface tension effects and secondly, the timescale of surface renewal is incompatible with the capillary wave period. In laboratory exchange tanks secondary flows initiated by tank geometry may constrain natural flows, thereby forcing surface renewal to occur. Hence, the possibility that the success of the surface renewal model in predicting gas exchange in the laboratory (e.g. Ledwell 1984, Jähne et al. 1984b, Wanninkhof & Bliven 1991) is, at least in some part, due to experimental artefact, cannot be discounted. The field estimates of n provided by Watson et al. (1991) and Clark et al. (1995) are consistent with a -0.5 dependence for this regime. However, whether or not this reflects an accurate description of natural conditions by the surface renewal model remains unclear.

At windspeeds beyond 11 m s^{-1} the “breaking wave (bubble) regime” applies. Here, bubbles resulting from wave breaking enhance gas transfer and so values of β for specific gases become important, the least soluble gases showing the most pronounced bubble-mediated transfer (Merlivat & Memery 1983). Because of a progressive increase in the contribution from bubble-mediated transfer with increasing windspeed, a unique value for n seems inappropriate with significant wave breaking (see later).

Techniques to measure gas exchange in the field

Dissolved gas balance

Because of biological and physical processes, gas partial pressures in surface waters are commonly out of equilibrium with their atmospheric values. By making time series measurements in the water column, appropriate gas budgets can be analyzed in terms of air-sea exchange. For example, for O_2 the method can be used to separate the effects of biological cycling and air—sea exchange:

$$\delta\text{O}_2^t = \delta\text{O}_2^e + \delta\text{O}_2^b \quad (\text{Equ. 14})$$

(Liss 1988), where δO_2^t is the total change in O_2 concentration in a given time period, δO_2^e is the change in O_2 due to air-sea exchange and δO_2^b is the O_2 contribution from biological processes. δO_2^b may be estimated from measurements of O_2 and phosphate using an assumed Redfield stoichiometry, the residual change in O_2 concentration is then ascribed to air-sea exchange. However, a number of uncertainties surround the choice of an appropriate Redfield ratio, particularly in situations where high productivity leads to active nutrient cycling, where advective effects are large or in enclosed coastal seas with significant benthic fluxes of nutrients. Problems of data interpretation associated with advective effects can be minimized by deploying measurement buoys equipped with vertical arrays of sensors.

The gas balance approach has been successfully employed for qualitative evaluations of O_2 exchange in the Atlantic Ocean (Wallace & Wirick 1992) and to quantify O_2 exchange in sub-oxic waters of the Georgia Strait (Farmer et al. 1993). Because these studies were

specifically designed to examine the roles of storm events and bubbles during air-sea gas exchange, the measurement buoys also housed scanning sonar for bubble cloud imaging, anemometers and thermistors. The method, therefore, has substantial potential in the evaluation of bubble-mediated gas exchange (see later), and because the time series data are available with high temporal resolution, it can provide excellent coverage during storm events.

Controlled flux method

In contrast to the dissolved gas balance method, which derives gas fluxes from temporal changes in dissolved gas content in response to some forcing environmental condition, the controlled flux method forces a flux event by the controlled invasion of heat across the air/water interface, the return heat flux back out of the water providing a proxy for the gas flux. By measuring the concentration difference across the interface and relating it to a change in the heat flux density, k_w can then be determined (GESAMP 1995). The technique is established in laboratory wind tunnels and typically uses an IR-radiator to force a heat flux across the interface, with an m-radiometer to measure variations in surface skin temperature (e.g. Jähne et al. 1989). Preliminary field measurements made during the “Marine Boundary Layer Project” (Haussecker & Jähne 1995) used a CO₂ laser heat source with an IR camera to track the heated areas. The method provides essentially instantaneous “snapshots” of k_w , i.e. on timescales of the order of a few minutes. Therefore, the method has the potential to provide highly localized, high-resolution data, which may enable its application to specific problems, such as in gas exchange through organic surface slicks for example. However, a major disadvantage of the technique lies in its inability to measure the bubble-mediated component of k_w , which would tend to compromise its use under the “breaking wave” regime.

Floating box method

In this relatively simple technique an inverted “floating box” on the sea surface is used to isolate a parcel of ambient air (gas concentration C_a) from the atmosphere, while permitting gas exchange with the underlying water. In this way, gas fluxes across the air/sea interface may be evaluated by monitoring changes in C_a with time. The method has been most widely used to estimate air-sea O₂ fluxes in the evaluation of metabolic O₂ budgets (e.g. Marino & Howarth 1993).

The principal criticisms of the floating box method are that, because it eliminates the effects of wind-induced turbulence and is difficult to deploy in anything beyond calm conditions, it has limited application at sea (Liss & Merlivat 1986). However, in systems where other forms of turbulence are more important, such as in shallow flowing waters where turbulence largely arises from the interaction of currents with bottom topography (Roberts 1984, Marino & Howarth 1993), the method has proved more successful. Perhaps the most important aspect of the method, however, is that it allows for initial gas mixing ratios in the headspace to be selected and modified, for example by flushing either with an inert pure gas or a bioreactive gas of interest, to enhance interfacial gas gradients or to force gas exchange in a particular direction. The latter allows investigation of the relationship between invasive and evasive gas exchange under identical field conditions (Conrad & Seiler 1988). Therefore it can in principle be used to investigate detailed aspects of gas exchange not possible with other techniques (see later).

Natural and bomb-produced $^{14}\text{CO}_2$

In these “global” techniques (e.g. Broecker & Peng 1974, 1984, Broecker et al. 1985) ^{14}C produced in the upper atmosphere from cosmic ray bombardment of gaseous N, or in the lower atmosphere from nuclear bomb testing, enters the global carbon cycle as $^{14}\text{CO}_2$ ($t^{1/2}=5680$ yr). The underlying assumptions of the methods are time-invariant ^{14}C production (for natural ^{14}C) and a steady-state ocean-atmosphere system in which the *in situ* ^{14}C decay rate in the oceans is balanced by the natural or “excess bomb” $^{14}\text{CO}_2$ invasion flux. Hence k_w (i.e. D/Z) is estimated from:

$$\frac{D}{Z} = \frac{[\Sigma\text{CO}_2]_{\text{ocean}}}{[\text{CO}_2]_{\text{mix}}} \frac{V}{A} \frac{\left[\frac{C^{14}}{C} \right]_{\text{ocean}} / \left[\frac{C^{14}}{C} \right]_{\text{atm}} \frac{\alpha C^{14}\text{O}_2}{\alpha \text{CO}_2}}{1 - \left[\frac{C^{14}}{C} \right]_{\text{mix}} / \left[\frac{C^{14}}{C} \right]_{\text{atm}} \frac{\alpha C^{14}\text{O}_2}{\alpha \text{CO}_2}} \lambda \quad (\text{Equ. 15}),$$

where $[\Sigma\text{CO}_2]_{\text{ocean}}$ is the mean total dissolved inorganic carbon content of sea water, $[\text{CO}_2]_{\text{mix}}$ is mixed layer dissolved CO_2 , V/A is the mean ocean depth and λ is the radioactive decay constant. Therefore k_w for CO_2 is estimated from the measured ^{14}C activities and an appropriate steady-state equation.

Because these methods are large-scale averaging techniques the value of k_w so obtained, ~ 20 cm h^{-1} , is a global long-term average, corresponding to a mean oceanic wind speed ~ 7.8 m s^{-1} (likely uncertainty $\pm 25\%$). Therefore, it does not reveal any information regarding spatial or temporal variation of k_w and consequently is of little value to studies requiring local or regional gas budgeting measurements. Nevertheless, these techniques provide a valuable “benchmark” figure for the mean CO_2 exchange rate over the ocean; the underlying models are essentially robust, having been calibrated using distributions of transient tracers such as ^3H (Broecker & Peng 1974). Any alternative method that yields greatly differing values for k_w should therefore be treated cautiously.

The method has also been applied on a smaller scale in lakes (Peng & Broecker 1980) and, notably, on a regional scale in the Red Sea (Cember 1989). In the latter, $-\Delta^{14}\text{C}$ measurements in corals used in conjunction with a box model of Red Sea circulation gave $k_w \sim 9 \pm 2$ cm h^{-1} (mean windspeed 4.7 m s^{-1}), consistent with the global value in conjunction with the CO_2 invasion-windspeed relation proposed by Broecker et al. (1985).

Radon-deficit method

Gaseous ^{222}Rn ($t^{1/2}=3.85$ days) is produced naturally in sea water by radioactive decay of ^{226}Ra , a long-lived ($t^{1/2}=1600$ yr) radiogenic daughter of ^{230}Th . In deep ocean waters below the thermocline, the activities of ^{222}Rn and ^{226}Ra are in secular equilibrium, whereas in the surface mixed layer a variable non-equilibrium occurs by virtue of ^{222}Rn loss to the atmosphere by sea-air gas exchange. By applying a simple steady-state equation to surface waters, in which the loss rate of ^{222}Rn to the atmosphere is balanced by the depth integrated “ ^{222}Rn deficit”, the ^{222}Rn transfer velocity may be determined as follows:

$$k_{Rn}(A_S - A_A) = \lambda \int_0^{\infty} (A_E - A_I) D I \quad (\text{Equ. 16})$$

where k_{Rn} is the transfer velocity of ^{222}Rn , A_s is the measured ^{222}Rn activity in the surface mixed layer, A_a is the corresponding activity in equilibrium with air, A_e is the expected ^{222}Rn activity in equilibrium with ^{226}Ra , A_l is the measured ^{222}Rn activity at depth l and λ is the ^{222}Rn decay constant (Liss 1988). In practice, because of low ^{222}Rn activities in air, $A_a \sim 0$. This technique is long established and has found widespread use, both at sea using natural ^{222}Rn levels (e.g. Broecker & Peng 1974, Peng et al. 1979, Kromer & Roether 1983, Hartman & Hammond 1984, Glover & Reeburgh 1987) and in lakes, often with ^{222}Rn addition to overcome large background signals (Emerson et al. 1973, Emerson 1975, Broecker et al. 1980).

Although the method works well in wind tunnels (e.g. Broecker & Siems 1984), in the ocean mixed layer ^{222}Rn profiles have response times to changes in surface wind speed (sometimes called the “wind lag”) of at least several days. Because of this, plots of k_w for ^{222}Rn against “instantaneous winds” yield only very weak correlations, especially where the measurements are made over long cruise tracks involving several wind regimes (Peng et al. 1979, Roether & Kromer 1984). Much stronger correlations are derived using wind data averaged over several days or even weeks prior to each estimate of k_w (Liss 1983, Liss & Merlivat 1986), or by using climatological wind averages (Smethie et al. 1985). Further sources of method uncertainty arise from violation of the premise that mixed layer ^{222}Rn profiles are homogeneous and therefore unaffected by advection or cross thermocline entrainment (Liss 1983). Notwithstanding these shortcomings, the k_w estimates so derived agree with those from the $^{14}\text{CO}_2$ techniques to within a factor somewhat better than two (e.g. Peng et al. 1979, Smethie et al. 1985). The principal advantage of using ^{222}Rn -deficit in preference to the ^{14}C methods lies in its far superior spatial and temporal resolution, typically 100s of km^2 over several weeks (e.g. Roether & Kromer 1984, Smethie et al. 1985).

Micrometeorological techniques

Although turbulent mixing in the atmospheric boundary layer directly above the Earth’s surface is very rapid, it is nevertheless possible in theory to measure small gas concentration gradients in air during active gas transfer. Such measurements form the basis of various micrometeorological techniques, of which the most commonly used for gases are briefly reviewed here. For a detailed treatment of flux measurements related to heat and momentum transfer, the reader is referred to Smith et al. (1996).

The so-called “Profile (or ‘Gradient’) method” is the theoretically most straightforward approach to measuring air-sea gas exchange in the air-side boundary. In this, gas concentration gradients directly above the sea surface are determined by making concentration measurements with a number of optimally placed sensors (Blanc 1983). However, Liss & Merlivat (1986) highlight inherent measurement problems for gases with $r_w \gg r_a$. Their reasoning uses an analogy with resistances in a serial electrical circuit; because differences in concentration are proportional to the size of the resistance, for gases with $r_w \gg r_a$ there is very little gradient to measure. As an example, the maximum observable change in CO_2 partial pressure between 1 m and 10 m height is $\sim 0.05 \mu\text{atm}$ (Deacon 1977), $< 0.2\%$ of the atmospheric mean value of $350 \mu\text{atm}$. Notwithstanding significant advances in appropriate gas sensor technology in recent years, for such measurements most sensors operate close to their design limits (Kohsiek 1997), resulting in substantial analytical uncertainty. The method is also extremely sensitive to flow distortions, requiring the use of specially designed towers (Miyake et al. 1970). Because of this, meaningful measurements from ships remain elusive (Smith et al. 1996).

Because of technological advances leading to the development of fast-response-time gas sensors, alternative micrometeorological techniques based on time-series measurements made at a single location, the so-called “local covariance methods” have developed rapidly in recent years (Smith et al. 1996). The most important example is the Eddy Correlation (EC) method, initially developed to study the fluxes of heat, water vapour and momentum across solid boundaries. The basis of the EC method is that if turbulence at a fixed point in the air-side boundary remains uniform, time-series eddy flux measurements averaged over time periods ~ 1 h are representative of surface fluxes. In theory, the instantaneous vertical transport of a species x (such as CO_2) is the product of its concentration, c_x and a vertical velocity, w . The average of the product wc_x over a given time interval gives the average flux, F_x , during that interval. The total flux can then be determined from:

$$F_x = \overline{wc_x} + \overline{w'c'_x} \quad (\text{Equ. 17}),$$

where the overbars denote time averages (Jacobs et al. 1997). Simultaneous measurement of the air-sea gas concentration difference, $-\Delta C$, gives an estimate of k_w . Because the method measures gas (CO_2) fluxes directly, inherent uncertainties associated with the Sc dependence and physico-chemical properties such as bubble-mediated transfer (see later) are avoided. The EC method requires the simultaneous measurement of w and c_x over a frequency range that enables the fluctuations contributing to the flux to be determined, i.e. 10^{-3} - 10^1 Hz (e.g. McBean 1972, Matson & Harris 1995).

Because of the requirement for a stable measurement platform (Fujitani 1985), most EC measurements to date have been made from rigid platforms in coastal regions, where inhomogeneity of the atmospheric and oceanic boundary layers may complicate the results, prompting a need for sophisticated data analysis (Businger & Oncley 1990, Smith et al. 1996). True oceanic measurements are rather rare (e.g. Wong & Chan 1991). Few studies have included sufficiently accurate measurements of $-\Delta C$, therefore the ability to measure small fluxes against a large ambient background has been rather limited (Jacobs et al. 1997). Numerous additional problems include large variations in gas fluxes on timescales ~ 1 h, requiring averaging over significantly longer times (Smith et al. 1991), inherently high signal: noise ratios requiring large interference corrections (e.g. Webb et al. 1980, Kohsiek 1997), platform instability and flow distortion (Fujitani 1985, Broecker et al. 1986, Oost et al. 1991), the misalignment of sensors (Wyngaard 1990) and sensor contamination by sea salt (Schmitt et al. 1978). Because of these complications, detailed data assessment in terms of such factors as small-scale spatial and temporal patchiness in CO_2 fluxes, boundary layer inhomogeneity or sensor performance has proved somewhat difficult.

Early EC measurements of CO_2 fluxes were up to 2 orders of magnitude higher than those based on ^{14}C or ^{222}Rn (e.g. Broecker et al. 1986, Smith & Jones 1986, Wesely 1986), but recent developments in measurement technology have reduced the mean discrepancy to a factor of between 2 and 5, although substantial data scatter remains inherent (Jacobs et al. 1997). The remaining discrepancy between EC and tracer-based flux measurements may be due largely to lateral variations in atmospheric CO_2 , such that CO_2 gradients unrepresentative of the true situation persist across the detector (Broecker et al. 1986). An alternative interpretation, that EC measurements of k_w in coastal seas are not amenable to comparison with globally averaged ^{14}C data owing to as yet unknown physico-chemical phenomena affecting CO_2 (Wesely 1986), seems somewhat less plausible.

In a variation of the EC method, the Relaxed Eddy Accumulation (REA) technique, air contained in a reservoir is pumped into a second reservoir when the vertical velocity is

positive and back again when it is negative (Pattey et al. 1993). This method, originally developed as a result of a lack of suitable fast-response-time sensors, is of most value when differences in mean concentrations between updrafts and downdrafts can be accurately resolved (Smith et al. 1996).

Purposefully-released tracers

Purposeful tracer releases for evaluating air-sea gas exchange on small spatial and temporal scales have developed rapidly during the past 15 yr or so (Wanninkhof et al. 1985, 1987, 1991, 1993, 1997, Upstill-Goddard et al. 1990, 1991, Watson et al. 1991, Clark et al. 1995, Nightingale & Upstill-Goddard 1995, Upstill-Goddard et al. 1997).

Gases such as SF₆, and ³He possess properties that make them excellent environmental tracers and ideal for applications such as this. ³He occurs naturally by ³H decay (Jenkins & Clarke 1976, Jähne et al. 1984a) via mantle degassing (Lupton et al. 1980, Jean-Baptiste et al. 1990, Hernandez et al. 1998) but surface water concentrations are usually within a few per cent of atmospheric equilibrium, $\sim 2.1 \times 10^{-15}$ mol kg⁻¹ at 25°C. Concentrations can be determined with high precision by mass spectrometry (Fuchs et al. 1987). SF₆ is sparingly soluble, non-toxic and chemically and biologically inert at ambient temperatures. It is manufactured for use in industry and industrial emissions dominate the current atmospheric mixing ratio, $\sim 3.6 \times 10^{-12}$ v/v, which is based on extrapolation of the temporal trend reported in Law et al. (1994). Although previously thought to have no natural sources, recent work has identified a relatively small crustal contribution, <3%, to the atmospheric inventory (Harnisch & Eisenhauer 1998). SF₆ can be routinely detected by electron-capture gas chromatography in ultra-trace amounts and its concentration in surface sea water is currently $\sim 3 \times 10^{-16}$ mol kg⁻¹, about ten times the current detection limit (Wanninkhof et al. 1991).

In constrained water bodies such as small lakes, k_w can be routinely determined by monitoring the rate of evasion to air of added SF₆, the behaviour of which is controlled solely by physical processes of mixing and gas exchange (Wanninkhof et al. 1985, 1987, Upstill-Goddard et al. 1990). Where it can be demonstrated that mixing is rapid relative to the timescale of gas exchange, k_w can be determined from the expression:

$$k_w = \frac{H}{\Delta t} \ln \left(\frac{C_i}{C_f} \right) \quad (\text{Equ. 18}),$$

where C_i and C_f are the initial and final gas concentrations in the water, respectively, during time period $-\Delta t$, and H is the mean water depth (Upstill-Goddard et al. 1990). k_w can also be estimated from the flux of ³He from enclosed water bodies using a steady state equation balancing ³He production from ³He decay and loss due to air-lake exchange, however this technique relies upon sufficient concentrations and homogenous dispersion of ³He throughout the water body (Jähne et al. 1984a). However, for unconstrained water masses, such as in the open ocean, measurements are somewhat more complicated, requiring the simultaneous release of a conservative tracer. Time-series concentration measurements of the volatile tracer used to assess k_w are then corrected for dispersive and advective dilution and downward entrainment, evaluated from temporal changes in the conservative tracer distribution.

Unfortunately, by the early 1990s an appropriate conservative tracer (i.e. one that is detectable in sufficiently low trace quantities, is non-toxic and non-radioactive) had not been identified (Watson & Ledwell 1988). Although rhodamine-B had been previously

used as a conservative tracer of tidal dispersion (Talbot & Talbot 1974), it was subsequently designated a class 1 carcinogen and its quoted detection limit (Talbot & Talbot 1974) is impractical for large-scale experiments typically requiring “tagging” of the dispersion of $\sim 10^9$ tonnes of water in tidally active waters for up to two weeks (Upstill-Goddard et al. 1991). This shortcoming lead Watson et al. (1991) to develop an alternative “dual-tracer technique” for use in coastal waters. In this, two inert volatile tracers with a large diffusivity contrast, i.e. SF_6 and ^3He , are released to sea water and their concentrations monitored with time as they decrease, by advection-dispersion and air-sea gas exchange. If dispersion effects are negligible, the total advection and dispersion of the two tracers will be equal. Subsequent to their release, the concentration ratio, R , of the two tracers changes with time in proportion to their gas transfer rates, according to:

$$\left(\frac{1}{R}\right) \frac{dR}{dt} = -\frac{k_{^3\text{He}} - k_{\text{SF}_6}}{H} \quad (\text{Equ. 19}),$$

where $k_{^3\text{He}}$ and k_{SF_6} are the transfer velocities of the two gases and R is adjusted for any background tracer concentrations existing prior to the release (Watson et al. 1991). The quantity actually measured with this approach is the difference between the k_w values for the two gases; calculation of the absolute values of k_w relies on use of an assumed Sc relationship, as in equation 9.

The principal advantage of the volatile tracer methods is that they facilitate high precision measurements of k_w on small spatial scales over short time periods, typically over areas $\sim 20\text{--}50$ km² every 24–48 h (Watson et al. 1991, Wanninkhof et al. 1993, 1997). Because wind conditions are very well defined on such scales, the relationship between k_w and wind speed can be much more tightly constrained than is possible with either the ^{14}C or ^{222}Rn -deficit methods. Furthermore, estimation of k_w is also possible for discrete storm events (Watson et al. 1991), previously regarded as a formidable task (Ledwell 1982). Although numerical modelling (Phillips 1995) indicates that the dual-tracer method describes the transfer of sparingly soluble gases well during periods when the surface renewal model is appropriate and moderately well during periods when the boundary layer model applies, the reliance on an assumed Sc relation is nevertheless a major potential disadvantage in the case of bubble-mediated transfer (Asher & Wanninkhof 1996, 1998a,b), a subject to which we shall return in greater detail later.

Relatively recently, conservative tracers more suited for the measurement of advection-dispersion during gas exchange studies have become available. These include spores of the microbe *Bacillus globigii* and two rhodamines, WT and Sulpho-G. Microbial tracer technology is not new, being well established for evaluating sewage dispersion in coastal waters (Pike et al. 1969) and monitoring the migration of contaminating microbes in groundwater (Keswick & Wang 1982). Bacterial spores are ideally suited to gas exchange studies because they persist in the environment in a metabolically inactive state and have better detection limits than many commonly used chemical tracers. They are innocuous in use, unlikely to interfere with natural microbial populations (Gameson 1986) and apparently conservative with respect to light exposure and microzooplankton grazing (Upstill-Goddard et al. 1997). Their use in gas exchange studies in open sea water has facilitated direct calculation of k_w independently for SF_6 and ^3He , making possible direct estimates of the Sc dependencies for these volatile tracers at sea, a significant advance over previous capabilities

(Nightingale et al. 1997). Rhodamines WT and Sulpho-G represent a new generation of safe “conservative” tracers which can be analyzed at high dilution by HPLC (Suijlen & Buyse 1994). Although both tracers are subject to small photolytic losses, and as such are non-conservative in the strictest sense, the difference in their photolytic loss rates is large enough that measurements of their concentration ratio with time can be used to correct for the non-conservative behaviour (den Das et al. 1997). In a recent gas exchange experiment in the southern North Sea these compounds were deployed simultaneously with SF₆, ³He and *Bacillus globigii* spores, generating independent estimates of k_w from five different combinations of tracers (i.e. ³He-SF₆, ³He-*Bacillus*, ³He-rhodamines, SF₆-*Bacillus*, and SF₆-rhodamines) (Nightingale et al. 1997, Upstill-Goddard et al. 1997). These estimates are internally consistent, thereby lending support to the central assumption of the ³He-SF₆ dual-tracer technique.

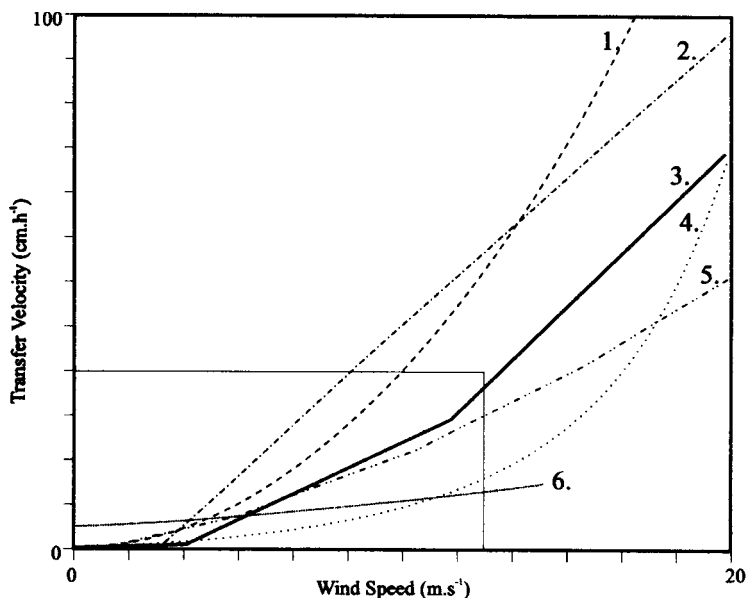
Multiple tracer releases of the type described here may find increasing use in biogeochemical cycling studies in general. For example, appropriate combinations of conservative and volatile tracers used in lagrangian studies in the open ocean will allow accurate measurements of productivity within well defined areas and facilitate estimates of carbon partitioning between air-sea exchange and biological cycling.

Comparisons of field and laboratory data

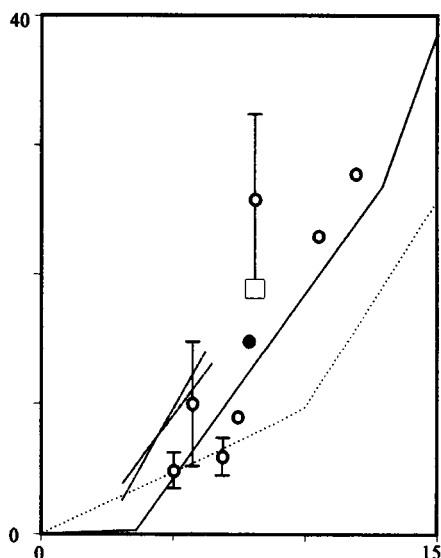
Various empirical relationships based on field measurements have been proposed to quantify the windspeed dependence of k_w (e.g. Deacon 1980, Hartman & Hammond 1984, Smethie et al. 1985, Smith 1985, Liss & Merlivat 1986, Wanninkhof et al. 1987, Upstill-Goddard et al. 1990, Wanninkhof 1992). Although these all show positive curvature, a comparison of several of them for the oceans by Wanninkhof (1992) revealed large discrepancies (Fig. 3). Of particular note, the four relationships based on ²²²Rn data (Fig. 3) show rather poor agreement, highlighting the frequently large uncertainties associated with measurements of this type.

Some other proposed k_w versus windspeed relationships are also summarized in Figure 3. The Liss & Merlivat (1986) curve is based on model and wind-tunnel results, as summarized in Figure 2 (p. 10), “calibrated” using the SF₆ evasion-rate data of Wanninkhof et al. (1985) obtained from a small lake for wind speeds up to 8 m s⁻¹. Its tri-linear response of k_w to wind speed contrasts strongly with earlier proposals for a distinct bi-linear relationship based on wind-tunnel data (Münnich et al. 1978, Jähne et al. 1979), the relationship of Smethie et al. (1985), which assumed $k_w=0$ for wind speeds up to 3 m s⁻¹ with a linear dependence beyond this threshold (Fig. 3), or its subsequent modification by Takahashi (1989) and Tans et al. (1990) who forced the Smethie plot through the global average k_w obtained with the bomb-¹⁴C inventory.

Although the field data used to construct the Liss & Merlivat curve are for a limited wind speed range, subsequent measurements using volatile and conservative tracers at higher wind speeds have generally supported its use, at least for coastal waters (Watson et al. 1991, Upstill-Goddard et al. 1997) and it has been extensively used to determine k_w based on measured wind speeds over the oceans (e.g. Liss et al. 1993, Bange et al. 1994, Rees et al. 1997). Nevertheless, Wanninkhof et al. (1987) found that the SF₆-derived k_w versus wind speed relationship in two Californian lakes was greater than that predicted from the Liss & Merlivat (1986) curve and Upstill-Goddard et al. (1990) derived a further relationship for two small lakes in southwest England (Fig. 3).



a.



b.

Figure 3 Empirical gas transfer—wind speed relationships (corrected to U_{10} and CO_2 at $20^\circ C$) **a.** reproduced from Wanninkhof (1992), where the dashed line (line 1) is the steady wind speed relationship derived by Wanninkhof (1992) using the ^{14}C data of Cember (1989), the single dot-dashed line (line 2) is the relationship suggested by Smethie et al. (1985) based on ^{222}Rn data and the solid line (line 3) is the Liss & Merlivat (1986) relationship. The dotted line (line 4), double dotted-dashed line (line 5) and the dotted line (line 6) are, respectively, the relationships proposed by Smith (1985), Hartman & Hammond (1984) and Deacon (1980), based on ^{222}Rn data.

The box in **a.** shows the area covered by the exploded view in **b.** where open circles show ^{222}Rn -derived values and the closed circle shows the GEOSECS ^{222}Rn -derived mean (Broecker & Peng 1974, Peng et al. 1979, Kromer & Roether 1983); open square, the global bomb- ^{14}C mean (Broecker et al. 1985). The solid line is the model equation of Liss & Merlivat (1986), the dotted line is the relationship found by Upstill-Goddard et al. (1990) from lake SF_6 work and the two short lines are lake SF_6 data from two Californian lakes (Wanninkhof et al. 1987).

Wind speed and the non-linear dependence of gas exchange

Routine comparison of the diverse datasets summarized in Figure 3 is necessarily complicated by inherent problems related to the reliable measurement of wind speed. Movement of the ship relative to the wind causes errors in wind speed measurements that require corrections. In the case of dual-tracer experiments that involve relatively rapid manoeuvring during surveys of the tracer “patch” (Watson et al. 1991, Nightingale et al. in prep.), these corrections are substantial but they can be applied automatically based on the ship’s navigational data (Upstill-Goddard et al. 1991). However, in some other gas exchange studies the application of such corrections remains unclear (e.g. Broecker & Peng 1974, Peng et al. 1979, Kromer & Roether 1983, Hartman & Hammond 1984, Glover & Reece 1987). Additional problems include anemometer “pumping” due to lateral rolling of the ship and flow distortion effects due to the vessel’s bulk, which can cause typical errors of 1–5% and up to 10%, respectively, in measured wind speeds (Taylor et al. 1995). Compensation for the errors as a result of air flow distortion is complex, involving three dimensional computation fluid dynamics (Yelland et al. in prep.). Wanninkhof et al. (1993) found that wind speeds obtained from shipboard anemometers, on a free floating drifter and on a fixed mooring showed significant differences and there is evidence to show that previous wind speed measurements obtained with anemometers mounted on the main masts of ships may overestimate true wind speeds by as much as 20% (Kahma & Lepparanta 1981, Taylor et al. 1995). Indeed, an apparent increase in mean wind speeds reported in recent years has been ascribed to the introduction of shipboard anemometers (Peterson & Hasse 1987, Ramage 1987). Clearly, the problem of obtaining meaningful wind speed data from ships is one requiring urgent attention.

Although remote wind speed estimates derived from the modelling of radiation backscatter from the ocean surface show great potential (Lee et al. 1995, Bourassa et al. 1997), they are currently less accurate than ship borne anemometer measurements, and the influence of additional controlling variables such as foam and whitecapping upon radiation backscatter remains unclear (Watts et al. 1996).

Notwithstanding the inherent problems involved in the accurate measurement of wind speed, a strong non-linearity of the k_w versus wind speed relationship is clear from most plots in Figure 3. Because of this, k_w determined for a particular average wind speed will depend on the ambient wind speed distribution during the measurement interval. Because of the disproportionate influence of higher wind speed on gas exchange, k_w estimated over long time periods with variable winds will necessarily be somewhat higher than corresponding estimates made over short timescales with steady winds (Wanninkhof 1992). Following this reasoning, the Liss & Merlivat curve (Fig. 2, p. 10), because it is based on steady wind speeds from wind tunnels and high time-resolution field data, essentially relates to k_w estimates at steady wind speed. Therefore, it should underestimate k_w for long-term averaged wind speeds, thereby explaining its departure from the long-term global and regional ^{14}C -derived k_w averages (Fig. 3). Wanninkhof (1992) developed this reasoning further and applied a quadratic dependence between k_w and wind speed (Fig. 3) in an attempt to compare the difference in proportionality between short-term (steady) and long-term (variable) wind speed averages. The rationale for using a quadratic was that it adequately described wind-tunnel measurements (e.g. Wanninkhof & Bliven 1991), reasonably approximated field data (e.g. Hartman & Hammond 1984, Broecker et al. 1985) and approximated the Liss & Merlivat curve over the wind speed range 0–15 m s⁻¹ (in the form $k_w=0.177(U_{10})^2$, Wanninkhof 1992). Using ^{14}C data from Broecker et al. (1985, 1986) and

Cember (1989) combined with CO₂ partial pressures and solubilities, Wanninkhof (1992) derived the following relationship for long-term winds:

$$k_w = 0.39 (U_{10av.})^2 (Sc/660)^{-0.5} \quad (\text{Equ. 20}),$$

where $U_{10av.}$ is the long-term average 10-metre wind speed. For short-term steady winds, Wanninkhof (1992) applied an assumed frequency distribution to global wind speeds modelled with the ¹⁴C data, deriving an equation for use with instantaneous wind speeds from anemometers or remotely from scatterometers or radiometers:

$$k_w = 0.31 (U_{10})^2 (Sc/660)^{-0.5} \quad (\text{Equ. 21}).$$

This synthesis goes some way in explaining the discrepancy between the global mean ¹⁴C-based estimates of k_w (Broecker et al. 1985) and values determined using ²²²Rn with short-term winds during GEOSECS (Peng et al. 1979) (Fig. 3). Nevertheless, the relationships proposed by Wanninkhof (1992) have large inherent uncertainties $\sim \pm 25\%$ related to the ¹⁴C data and there are additional uncertainties over the wind speed averages that remain unqualified. Similarly, allowing for the wind speed variance, Nightingale et al. (in prep.) applied a quadratic fit to dual-tracer data from the southern North Sea, with U_{10} corrected for atmospheric stability affects (Large & Pond 1982) and using the U_{10} - neutral drag coefficient relationship proposed for the region by Oost (1998). Their equation, of the form

$$k_w = a (U_{10})^2 + b (U_{10}) \quad (\text{Equ. 22}),$$

with constants a and b determined by a least-squares method, accounted for >80% of the total variance in k_w .

Clearly, none of the various gas exchange relationships discussed here is able to account for all of the data scatter observed within the individual datasets, or the discrepancies between the different datasets (Fig. 3). Particularly problematical is that the ¹⁴C-invasion k_w estimates are higher than equivalent mean values derived using ²²²Rn or dual-tracers, even after accounting for the inherent wind speed variability. Even though Boutin & Etcheto (1996, 1997) and Boutin et al. (1996) have recalculated the mean global k_w for CO₂ with a revised mean global wind speed, and Hesshaimer et al. (1994) have suggested downward revision of the rate of ¹⁴C uptake, a significant discrepancy persists, the scaling factor required to reconcile these data being ~ 1.4 . It therefore seems clear that additional geophysical forcings other than wind speed and its inherent variability may be important in defining relationships both within and between the various datasets plotted in Figure 3.

Fetch dependence of k_w

Because waves increase in power and size over large oceanic distances (Ebuchi et al. 1992) and whitecapping is more common at lower wind speeds when associated with large fetch waves (Monahan & O'Muircheartaigh 1986), some fetch dependence of surface turbulence is certain. In linear wind-wave tank experiments, Jähne et al. (1989) observed wave growth over a fetch of ~ 100 m which resulted in differences in k_w measured at different parts of the tunnel; however, some workers have questioned whether the development of wave spectra in a confined laboratory tank meaningfully represents the natural situation (Broecker et al. 1978, Ledwell 1982). The transfer of momentum from the wind to the air/water interface on lakes has been shown to be partly fetch-dependent (MacIntyre 1984) and in lake gas exchange

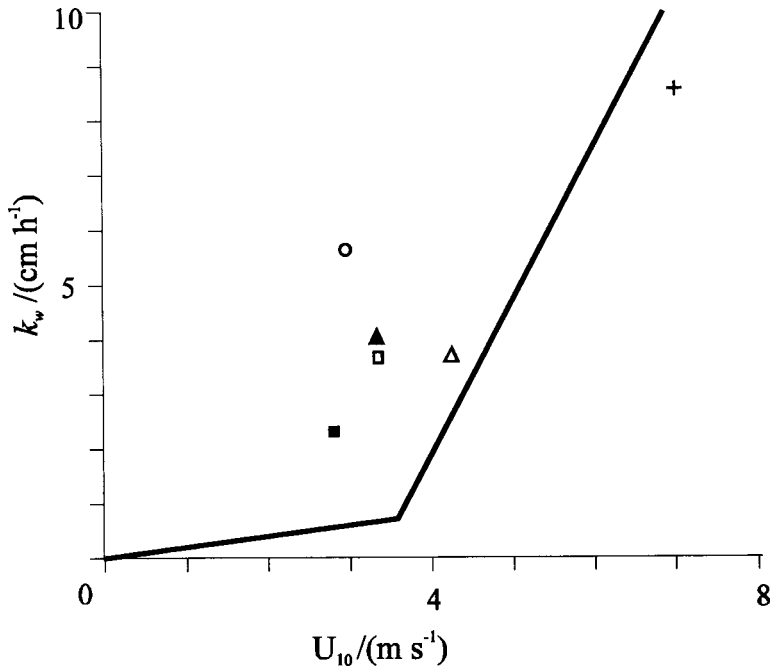


Figure 4 Averaged SF_6 gas transfer velocities, corrected to CO_2 at 20°C , from lake tracer experiments: plus symbol, Siblyback lake, area 0.5 km^2 (Upstill-Goddard et al. 1990); solid square, ELA lake 302N, area 0.13 km^2 (Crucius & Wanninkhof 1990); open triangle, Rockland lake, area 1 km^2 (Wanninkhof et al. 1985); open square, Mono lake, area 200 km^2 (Wanninkhof et al. 1987); solid triangle, Crowley lake, area 20 km^2 (Wanninkhof et al. 1987); open circle, Pyramid lake, area 500 km^2 (Wanninkhof et al. 1991). The line is the Liss & Merlivat (1986) relationship. The larger lakes show higher average k_w values at a particular wind speed. Reproduced from Wanninkhof (1992).

experiments, those with the largest surface area and therefore greatest fetch tend to yield the highest k_w values for a given wind speed (Fig. 4). Nevertheless, in a detailed treatment of their 5-min wind averages measured during dual-tracer experiments in the southern North Sea, Nightingale et al. (in prep.) were unable to identify any significant relationship between k_w and wind direction (i.e. fetch).

Breaking waves and bubbles

At the onset of the breaking wave regime, at wind speeds $\sim 10\text{--}12 \text{ m s}^{-1}$ defined from wind-tunnel studies (Fig. 2, p. 10), the nature of the air/water interface changes radically; turbulence increases significantly, spray and bubbles begin to be generated and gas transfer increases rapidly. Enhanced gas transfer owing to breaking waves and bubble formation (so-called “whitcapping events”) is a well documented phenomenon (e.g. Liss & Merlivat 1986, Wanninkhof & Bliven, 1991) and strong positive relationships between k_w and the fractional area coverage of bubble plumes have been demonstrated experimentally for

various gases (e.g. Asher et al. 1992, Asher & Parley 1995). Early theories proposed that observed increases in gas exchange rates resulted from spray and bubbles contributing to an enhanced surface area for exchange, consistent with no fundamental change in the prevailing exchange mechanism (e.g. Deacon 1977). However, such notions were subsequently discarded; Merlivat & Memery (1983) observed a 30–40% increase in gas exchange rate with the onset of bubbles, but only an ~5% increase could be directly ascribed to increased surface area.

Monahan & Spillane (1984) proposed a mechanism whereby surfacing bubbles produce a low-resistance pathway through the diffusive microlayer, creating regions of enhanced gas exchange where bubbles escape to the atmosphere. However, a more likely alternative involves a fundamental change within the bubbles themselves, i.e. variation in their internal gas partial pressures during vertical displacement under breaking waves. Bubbles have been observed to penetrate to depths >16 m during wave breaking (Farmer et al. 1993), sufficient to decrease bubble volume by >50%. A resultant change in a bubbles' internal gas pressure would drive gas transfer across the bubble/water interface. Such a mechanism can force gas supersaturations even when the gas partial pressure in surface-water is at or near atmospheric equilibrium (Memery & Merlivat 1985, Woolf & Thorpe 1991, Keeling 1993, Woolf 1993). Gas supersaturations generated in this way are typically small but significant and the effect is greatest for low-solubility gases such as CH₄, for which supersaturations due to bubbles are typically ~1–2% (Woolf & Thorpe 1991). In contrast, for CO₂, which is about an order of magnitude more soluble than CH₄, the global mean supersaturation because of bubbles is ~0.08% (Keeling 1993). Similarly, the effect is larger for those gases which are most undersaturated in the water column (Farmer et al. 1993).

There is some evidence for asymmetry in the rate of gas exchange across bubble surfaces, dependent upon whether the initial gas partial pressure inside the bubble is higher or lower than that of the surrounding water; rates of gas invasion into bubbles subject to pressurization have been observed to be more rapid than rates of gas evasion (Anderson & Johnson 1992, Wallace & Wirick 1992). The presence of bubbles can therefore cause an apparent asymmetry between k_w for invasion and k_w for evasion (Asher & Wanninkhof 1998b). This asymmetry is most significant when the air-sea concentration difference is near equilibrium, which for many trace gases in open ocean waters is typically the case (e.g. CH₄; Lamontagne et al. 1973, N₂O; Bange et al. 1996a, b).

Perhaps the most fundamentally important consequence of the involvement of bubbles in gas exchange is that the assumption of a constant value for n for all gases becomes invalid because of the additional solubility dependence, and the dependence of k_w on both Sc and β is now well established (Merlivat & Memery 1983, Keeling 1993, Woolf 1993, Asher et al. 1996). The models of Woolf & Thorpe (1991) and Woolf (1993) identify an additional gas transfer velocity term due to bubbles, k_b , and a bubble-generated supersaturation term, O , in the classical gas exchange equation:

$$F=(k_r+k_b)[C_w-\beta C_a(1+O)] \quad (\text{Equ. 23}),$$

and Keeling (1993) has attempted to model k_b in terms of $Sc(D)$ and β :

$$k_b=\beta^{-0.3}D^{0.35} \quad (\text{Equ. 24}).$$

Unfortunately, the direct calculation of k_b for a given gas at a particular wind speed remains elusive and the dependence of k_b on wind speed varies considerably between datasets.

Formal descriptions of gas exchange due to bubbles have previously proved problematic because of inherent uncertainties over the quantification of ambient bubble size spectra.

This is important because the functional dependence of β only becomes significant for bubble radii $<500 \mu\text{m}$ when gases completely dissolve or come to equilibrium with the surrounding water (Merlivat & Memery 1983, Keeling 1993). Larger bubbles, which do not reach equilibrium most likely contribute to gas exchange via increased surface area only (Keeling 1993). However, recent advances in laboratory and field measurements mean that bubble sizes, volume concentrations and depth distributions can now be estimated to a reasonable accuracy and the measurements show good agreement (e.g. Walsh & Mulhearn 1987, Vagle & Farmer 1992, Asher & Parley 1995). Furthermore, these advances have shown that simulated whitecapping events such as are generated by a whitecap simulation tank agree with measurements of oceanic bubbles (Asher & Parley 1995).

A non-unique value for n under wave breaking conditions has important implications for k_w estimates derived with the dual-tracer technique because the use of equation 9, which assumes constant n , will cause these estimates to be in error. In an attempt to overcome this problem, Wanninkhof et al. (1993) applied an iterative solubility correction to dual-tracer data by estimating bubble-mediated changes in n for given values of k_w for ^3He , using appropriate laboratory data from Asher et al. (1992). However, these corrections over-predicted the effect of bubbles on ^3He exchange because the importance of bubble-mediated transfer estimated by Asher et al. (1992) was an overestimate (Asher et al. 1996). In the wave breaking regime the value of n is unique to a given pair of gases (Asher et al. 1996), therefore use of the dual-tracer technique to calculate k_w for another gas such as CO_2 may also be in error. In order to overcome this difficulty, Asher & Wanninkhof (1995) proposed substitution of n by an apparent Sc exponent which is unique to a given pair of gases and defined as a function of bubble concentration, water temperature and turbulence. Because calculation of the apparent Sc exponent required prior knowledge of k_w for ^3He and SF_6 , these quantities had to be estimated empirically using contemporary parameterizations of bubble-mediated gas transfer (Merlivat & Memery 1983, Asher et al. 1996). In a subsequent re-analysis of earlier dual-tracer data, Asher & Wanninkhof (1998b) re-estimated k_w for ^3He with and without bubble-mediated transfer. For $U_{10} < 10.6 \text{ m s}^{-1}$, the increase in k_w (^3He) due to the inclusion of bubble-mediated effects was $\approx 5\%$, in part due to the similarity of β for ^3He and SF_6 , in agreement with the modelling study of Woolf (1997) and field results obtained by Nightingale et al. (in prep.), both of which indicate that, for these gases, n does not deviate significantly from a value of -0.5 in the bubble-breaking wave regime. However, for CO_2 calculated from the ^3He data and with the inclusion of bubble effects, k_w decreased by $\sim 18\%$ (Asher & Wanninkhof 1998b). When applied to the dual-tracer data of Watson et al. (1991) for $U_{10} = 17.5 \text{ m s}^{-1}$, the decrease in k_w (CO_2) due to bubbles was 23% (Asher & Wanninkhof 1998b). These corrections reconcile some of the discrepancy between the original dual-tracer results of Watson et al. (1991) and Wanninkhof et al. (1993) but considerable differences still remain to be resolved (Asher & Wanninkhof, 1998b).

In the natural situation, breaking waves and bubbles can occur at much lower wind speeds than is observed in wind and wave tanks or tunnels. In the latter, breaking waves tend to be initiated at a sharply defined point dictated by the specific geometry of the facility. For example, wave breaking began at a wind speed $\sim 9 \text{ m s}^{-1}$ in the linear wind tunnel used by Merlivat & Memery (1983) and at $\sim 12 \text{ m s}^{-1}$ in a circular tunnel (Jähne et al. 1985). However in the oceans, long fetch waves can begin to break at wind speeds as low as $2\text{--}3 \text{ m s}^{-1}$ (Monahan & O'Muircheartaigh 1986). In addition, when bubbles begin to form in salt water they are smaller, more numerous and have longer residence times in the water column than their freshwater counterparts formed under equivalent conditions (Thorpe 1982, Haines & Johnson 1995). These differences are reflected in a larger contribution from

bubble-mediated gas exchange for sea water than for fresh water under the same conditions, irrespective of differences in D and β , which tend to operate in the opposite direction (Gat & Shatkey 1991, Shatkey & Ronen 1992). Caution should therefore be exercised over the extrapolation of wind- and wave-tank data to the oceanic situation.

An early model incorporating the effects of bubble-mediated gas transfer in an oceanic situation was developed by Monahan & Spillane (1984), who were prompted by the similarity between contour charts of North Atlantic k_w values and mean whitecap coverage. Their model defines gas exchange by

$$k_e = k_w (1-W) + k_c W \quad (\text{Equ. 25}),$$

where k_e is the local gas transfer velocity, k_c is the gas transfer velocity associated with a turbulent whitecap event and W is the fractional sea surface coverage by whitecaps.

The enhanced gas exchange associated with a whitecap event is believed to cover an area seven times that of the visible whitecap (Kerman 1980) and may be up to 50 times the exchange rate without whitecapping (Erickson 1993). The difficulty in calculating fractional whitecap coverage has led to the development of novel solutions, including characterization of the degree of thermal skin layer disruption using infrared imagery (Jessup et al. 1997) and microwave brightness (Asher et al. 1992, 1996). The use of ship-mounted video photography coupled with a pixel analysis technique devised by Monahan (1993) has also been successfully used to estimate fractional whitecap coverage (Asher & Wanninkhof 1998b). However, data must be corrected for ship wake and cannot be collected at night, during periods of sun glint or during periods of heavy rain. Whitecap coverage can be estimated during periods when direct data collection is not possible if a suitable empirical relationship between U_{10} and whitecap coverage can be found (Asher & Wanninkhof 1998b). In addition to wind speed, other forms of turbulence such as air-sea temperature stability differences (Erickson 1993) may make significant contributions to whitecapping events.

Surfactant films

Surface active substances (surfactants) are defined by their fundamental ability to reduce surface tension. It initially seems intuitive that a reduction in surface tension would lead to increased gas exchange due to increased deformation of the water surface for a given degree of turbulence. In reality, however, the opposite occurs; surfactants form continuous films, reducing k_w (Broecker et al. 1978, Jähne et al. 1984b). The suppression of gas exchange by surfactants is effected through two separate mechanisms, directly, via the barrier effect of the film molecules, and indirectly through hydrodynamical damping, in which the transport of gas in eddies approaching the surface film from below is impeded (Davies 1966). Surfactant films also act to inhibit both the formation and breaking of small waves and they tend to increase the rate of capillary ripple decay (Broecker et al. 1978), thereby decreasing turbulence at the interface. Studies on surfactant film effects have commonly found gas exchange reductions of around 50% (Frew et al. 1990) and occasionally as high as 80–85% (Broecker et al. 1978, Jähne et al. 1984b, 1987b). Based on these results, it seems conceivable that the first break of slope on the Liss & Merlivat (1986) curve (windspeed=3.6 m s⁻¹) might correspond to the disruption of surfactant films. Following disruption, surfactant films undergo renewal from the bulk water on timescales of a few hours under stagnant conditions. In contrast, because rising bubbles have been observed to scavenge surfactants from the bulk water after only a few centimetres and deposit it at the

Table 2 Chemical and biological enrichments in the microlayer relative to underlying bulk water.

Chemical or Biological factor	Sample Area	Range of EF*	Reference
Bacteria	Swedish west coast	10–76	Norkrans 1980
Bacteria	Off Pacific coast of Mexico	1.25–2.5	Carlucci et al. 1985
Bacteria	Off Pacific coast of USA	2.32	Carlucci et al. 1985
Chlorophyll <i>a</i>	Off Pacific coast of USA	1.67	Carlucci et al. 1985
Chlorophyll <i>a</i>	Off Pacific coast of Mexico	0.93–2	Carlucci et al. 1985
Dinoflagellates	Off Californian coast	28.43	Harvey 1966
Ciliates	Off Californian coast	3.3	Harvey 1966
Diatoms	Off Californian coast	0.058	Harvey 1966
Electron Transport Activity	Bay of Marseilles, France	1.4–26.4	Garabétian 1990
Bacteria	Pacific and Atlantic Ocean	~95	Sieburth 1971
Phytoplankton cells	Estuaries, USA	3.7–147.1	Manziet et al. 1977
Total cell concentration	Temperate marine lagoon	1.42–7.98	Hardy 1973
Taxonomic diversity	Temperate marine lagoon	0.79–1.06	Hardy 1973
Chlorophyll <i>a</i>	Temperate marine lagoon	1.55–5.57	Hardy 1973
Photosynthetic production	Temperate marine lagoon	2.84	Hardy 1973
Photosynthetic assimilation rate	Temperate marine lagoon	0.63	Hardy 1973
Bacteria	Various	10 ² –10 ⁴	Hardy 1982
Phytoneuston	Various	1–10 ²	Hardy 1982
Zooneuston	Various	1–10	Hardy 1982
Bacteria	Sequim Bay, Washington	2444 (mean)	Hardy & Apts 1984
Microalgae	Sequim Bay, Washington	380 (mean)	Hardy & Apts 1984
Chlorophyll pigments	Sequim Bay, Washington	12	Hardy & Apts 1984
Photosynthesis (estimated gross)	Sequim Bay, Washington	40	Hardy & Apts 1984
Carbon	California Bight and Gulf of Maine	3.9–16	Frew & Nelson 1992
Particulate organic carbon	Mediterranean Sea	11–40	Garabétian et al. 1993
O ₂	Mediterranean Sea	0.94–0.97	Garabétian et al. 1993
Phytoneuston	Sequim Bay, Washington	37–154	Hardy & Apts 1989
Particulate carbon fixation	Sequim Bay, Washington	2–52	Hardy & Apts 1989
Dissolved carbon excretion	Sequim Bay, Washington	17–63	Hardy & Apts 1989
Total chlorophylls	Sequim Bay, Washington	1.3–18	Hardy & Apts 1989
Dissolved organic carbon	North Atlantic	1.6	Sieburth et al. 1976
Carbohydrates	North Atlantic	2.0	Sieburth et al. 1976
ATP (size fraction 0.2–3 μm)	North Atlantic	2.5	Sieburth et al. 1976
ATP (size fraction 3–1000 μm)	North Atlantic	3.1	Sieburth et al. 1976
Adenosine triphosphate (ATP), chlorophyll <i>a</i> , microplankton and bacteria	Southern Gulf of California and off west coast of Baja California	1.3–2	Williams et al. 1986
Particulate carbon and nitrogen, dissolved and particulate protein	Southern Gulf of California and off west coast of Baja California	1.1–3.7	Williams et al. 1986
Soluble inorganic nutrients (NH ₄ ⁺ , NO ₂ ⁻ , NO ₃ ⁻ , PO ₄ ³⁻ , SiO ₃ ²⁻) dissolved organic carbon and nitrogen, urea, carbohydrate and lipid.	Southern Gulf of California and off west coast of Baja California	1.1–2.4	Williams et al. 1986

*EF or “enrichment factor”, given by $EF = [X]_m / [X]_b$, where $[X]_m$ is the microlayer concentration of species X and $[X]_b$ is the concentration of X in the underlying bulk water.

sea/air interface (Scott 1975), surface films are rapidly re-established following wave breaking events (GESAMP 1995).

Ambient surfactant concentrations can directly influence rates of bubble-mediated air-sea gas exchange, depending upon whether or not a bubble is “dirty”, i.e. with a film of surfactants, or “clean”, i.e. surfactant-free. Woolf (1993) estimated a contribution to the mean global k_w for CO₂ of 8.5 cm h⁻¹ for “clean” bubbles, but only 2.6 cm h⁻¹ for “dirty” bubbles. However, Blanchard (1983) showed bubbles became covered with material after only travelling a few centimetres through the water column.

Previously, surfactant films were assumed to be a rather rare phenomenon in the open ocean, however recent observations in the Indian Ocean by Romano (1996) suggest that they may be commonplace, at least in some areas. Romano (1996) reported extensive surfactant films in 30% of coastal and 11% of open sea observations, but only for wind speeds below 6 m s⁻¹, and noted an inherent rhythm of film formation in coastal waters due to the diurnal variation of wind speed and direction, which was absent from the open ocean. Space-borne observations of filamentous and eddy-like structures have been interpreted as surface films of sufficient thickness to suppress large gravity waves, generated by local convergence (Scully-Power 1986). Indeed, satellite data are a potentially very valuable tool for mapping surface films, especially because routine retrieval of the required high resolution data, using techniques such as Synthetic Aperture Radar (SAR) (Espedal et al. 1996), is now within reach.

Frew et al. (1990) hypothesize that the major constituent of surfactant films may be a sugar bound to an amino acid or lipopolysaccharide produced from the carbohydrate pool. Because phytoplankton excrete up to 30% of their assimilated carbon, mainly in the form of polysaccharides, they are a potentially major contributor to this pool (Sharp 1977, Mykkestad 1995, Malinsky-Rushansky & Legrand 1996). Alternatively, surfactant films may be a more complex organic mixture derived from the high concentrations of organic matter found at the air/sea interface, including carbohydrates, proteins and lipids. Surfactant films observed in association with phytoplankton blooms under laboratory conditions were found to have compositions consistent with species composition (Vojvodic & Cosovic (1996). Within cultures of flagellates, these workers observed the majority of surface-active compounds to be hydrophobic (slick forming), whereas compounds generated by diatoms were dominantly hydrophilic, perhaps explaining the higher enrichment of flagellates at the interface compared with diatoms (Table 2).

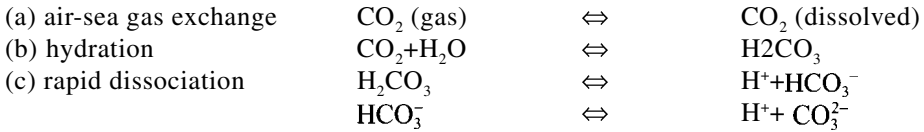
Chemical enhancements of gas exchange

Gases that participate in chemical reactions in the aqueous phase, such as CO₂, are subject to enhanced gas exchange. This can be conveniently conceptualized as a partial short circuit of the liquid phase resistance to transfer in the boundary layer and for such gases an enhancement factor, ϵ , should therefore be included in the total resistance to gas exchange (R), giving

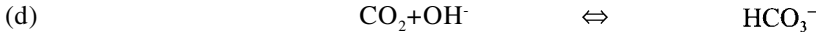
$$R=(\epsilon.r_w)+r_a \quad (\text{Equ. 26}),$$

where $\epsilon=1.0$ in the case of zero enhancement (Wanninkhof 1986).

The high aqueous-phase reactivity of CO₂ strongly influences the chemistry of sea water via direct control of the pH. The important reactions, termed the “carbonate equilibria” (e.g. Hoover & Berkshire 1969) can be summarized as follows:



The relative proportions of the various ionic species are set by the pH of the system. As pH increases, reaction of CO_2 and hydroxyl ions becomes quantitatively more important:



For pH values <4 , the concentration of ionic species is negligible and CO_2 essentially behaves as an inert gas, however at pH ~ 6.5 , reactions (b)–(d) above become significant (Hoover & Berkshire 1969) and reaction (d) predominates at pH >10 (Goldman & Dennett 1983). At typical sea water pHs (i.e. ~ 7.5 – 8.4), reactions (b) and (c) predominate and $>99\%$ of CO_2 is present as CO_3^{2-} and HCO_3^- . Because the carbonate system consumes five molecules of CO_2 for every six absorbed (Ledwell 1982), the oceans have a slow response time, ~ 6 months, to changes in atmospheric CO_2 , which complicates the direct measurement of CO_2 exchange.

The stagnant-film model forms the basis for most formal descriptions of the contribution of chemical enhancement to CO_2 exchange (Bolin 1960, Hoover & Berkshire 1969, Quinn & Otto 1971, Kirk & Singh 1992). With increasing film thickness the time available for CO_2 reaction also increases and the contribution of CO_2 reactivity to total CO_2 exchange is enhanced. Therefore, wind-induced surface turbulence, in addition to pH and temperature (Johnson 1982), is important for defining the contribution of chemical enhancement to total CO_2 exchange. Chemical enhancement of CO_2 exchange has been demonstrated experimentally. Hoover & Berkshire (1969) found that CO_2 exchange was enhanced when pH was increased to a value commensurate with the hydration reaction and Liss (1973) found enhancements for CO_2 relative to O_2 . Broecker & Peng (1974) demonstrated higher CO_2 exchange rates in sea water relative to acidified sea water; Wanninkhof et al. (1987) demonstrated an enhancement of CO_2 transfer relative to SF_6 using lake water at pH 9.8, and the experimental results of Wanninkhof & Knox (1996) were found to agree with theoretical calculations within experimental error. However, a detailed treatment of the available experimental and theoretical evidence (Wanninkhof 1992) shows that in sea waters with typical pHs, chemical enhancement of CO_2 exchange for steady wind speeds >5 – 7 m s^{-1} is negligible. Even at pHs higher than are found in sea water, chemical enhancement of CO_2 exchange is more than a factor of four below that needed to explain the discrepancy between the ^{14}C -invasion rate and ^{222}Rn or dual-tracer measurements of k_w (Wanninkhof et al. 1987). These results imply that when globally averaged (global mean wind speed $\sim 7.8 \text{ m s}^{-1}$), chemical enhancement can play only a minor role in the air-sea exchange of CO_2 . Even so, it may still be significant locally in certain situations. For example, using the Wanninkhof (1992) relationship for variable winds (equation 19), k_w values derived for the equatorial regions characterized by light winds $\sim 4.7 \text{ m s}^{-1}$ increased by $\sim 20\%$ when a chemical enhancement parameter was included (Wanninkhof 1992). Subsequently, using constant wind speeds Wanninkhof & Knox (1996) derived enhancements ~ 4 – 8% for these regions.

It has been suggested that large scale enhancement of CO_2 exchange could occur in the oceans if suitable catalytic compounds are available at the sea surface to speed the reactions (Berger & Libby 1969, Quinn & Otto 1971, Liss 1973). The most likely candidate is the enzyme carbonic anhydrase, however experimental work by Goldman & Dennett (1983) has largely disproved both the possibility of large enhancements and the existence of sufficient quantities of catalytic compounds at the air/sea interface.

In addition to CO₂, some other gases are subject to chemically enhanced air-sea exchange. For example, SO₂, which has a higher reactivity rate constant than CO₂, takes part in rapid aqueous-phase hydration and oxidation. Because these reactions are so rapid, the concentration of SO₂ in the surface ocean is assumed to be zero and therefore the oceans act as a perfect sink for atmospheric SO₂ (Liss & Slater 1974). Air-water exchange of NH₃ is also at least partially dependent upon aqueous-phase chemistry in some situations. Using a derivation of the stagnant-film model, Kirk & Singh (1992) studied the interactive chemical buffering of NH₃ and CO₂ exchange in a rice paddy. They showed that a decrease in pH due to elevated CO₂ concentration initially caused the suppression of NH₃ evasion. However, as the pH rose due to the slowed loss of NH₃, the NH₃ flux again increased causing pH to fall again. Increased evasion of CO₂, by causing a rise in pH, lead to an enhancement of the NH₃ flux. Because high concentrations of carbonic anhydrase may exist in rice paddies through cell decomposition and active cell secretion (Price & Morel 1990). Kirk & Singh (1992) also modelled the effect of carbonic anhydrase on CO₂-NH₃ interaction. Their results showed significantly increased evasion of NH₃ resulting from the elevated pH due to enhanced loss of CO₂ to air.

Cool skin of the oceans

The existence of a “cool skin” on the ocean surface has long been known (e.g. Ewing & McAlister 1960, Grassl 1976) and is typically defined by a sharp temperature gradient ~0.1–0.3°C over ~1 mm (e.g. McAlister & McLeish 1969, Grassl 1976, Robinson et al. 1984). Mean bulk-skin temperature differences ($-\Delta T$) of 0.1–0.2°C have been reported by Schluessel et al. (1990) in the North Atlantic and 0.3°C by Wong et al. (1995) in the Pacific. The largest temperature differences, ~0.75°C, are for the boreal winter in the Kuroshio and the Gulf Stream Currents (Van Scoy et al. 1995).

The cool skin is the direct consequence of a net ocean to atmosphere heat flux (Schluessel et al. 1990). Although several types of heat are implicated in its generation, because of the high emissivity of water in the infrared (Friedmann 1969), longwave irradiance causes the most rapid response in the thickness and temperature of the skin layer, consequently day length and cloud cover are important defining variables (Schluessel et al. 1990). Occasionally the absorption of longwave radiation generates a warm skin (Schluessel et al. 1990). The cool skin is ubiquitous for wind speeds below ~10 m s⁻¹ (Clauss et al. 1970) but beyond this it is destroyed by breaking waves.

The cool skin increases β at the sea surface, thereby increasing gas concentration gradients across the air/sea interface. The effects on global gas exchange rates were quantified for CO₂ by Robertson & Watson (1992), whose skin temperature correction based on limited pCO₂ data revised upward the oceanic sink for CO₂ by ~0.7 Gt C yr⁻¹, accounting for a significant fraction of the imbalance in the global carbon cycle (Houghton et al. 1990). Subsequently, Van Scoy et al. (1995) re-determined the cool skin effect using global wind patterns. Their estimates, ~0.17 Gt C yr⁻¹ based on the Liss & Merlivat (1986) curve and ~0.35 Gt C yr⁻¹ using the k_w -windspeed relationship of Tans et al. (1990), highlight the large uncertainties that exist in calculations of this nature and the need for a definitive wind speed-gas transfer relationship to be developed. For the latitude band 15–25°S, Wong et al. (1995) report increases in net CO₂ fluxes due to the cool skin of 5% during the austral winter and 56% during the austral summer.

The cool skin is a useful indicator of sea state, therefore it is potentially important for parameterizing gas transfer (Jessup et al. 1997). When the surface is disrupted by a breaking wave the temperature structure of the cool skin breaks down but is usually re-established on a timescale of several seconds (Ewing & McAlister 1960, Clauss et al. 1970, Katsaros 1977). This recovery time is a function of the ambient heat flux and, importantly for the quantification of wave breaking, the speed of the breaking wave crest; rapidly moving waves dissipate their energy quickly and result in long recovery times (Jessup et al. 1997). The area disrupted by a breaking wave can be remotely sensed using infrared radiometry, which detects the temperature of the uppermost 10 μm of the sea surface (within the skin layer) (e.g. McKeown et al. 1995). Such technology is now reaching the stage where it may be possible to study remotely the thermal structure of the interface (McKeown et al. 1995). Remote measurements may facilitate more accurate estimates of the frequency and magnitude of wave breaking events across the oceans, allowing the development of gas exchange models which incorporate a more well defined contribution from whitecapping events than hitherto has been possible.

Irreversible thermodynamics

It has been suggested that diffusion based on a gas concentration gradient alone gives an insufficient representation of the gas transfer process and that a role for irreversible thermodynamics should also be considered (Phillips 1991a,b, 1994a,b,c). The underlying theory states that when a gas dissolves in water, heat is generated or consumed by the change in free energy resulting from the phase transition. Therefore, additional to the effect of sea surface temperature on $-\Delta C$ by virtue of changes in β , a coupled system of heat and mass transfer implies a correction due to the surface temperature flux effect on k_w . Phillips (1991a,b, 1994a,b,c, 1995) attempted to demonstrate the potential importance of this correction through the reworking of existing data. The calculations, however, were subsequently criticized on the grounds both of inconsistency in the treatment of the molecular boundary layer, and because the assumed influence of heat and mass coupling may have been greatly overestimated (Doney 1995a,b). Such conclusions are consistent with earlier experimental evidence presented by Liss et al. (1981), which could demonstrate no measurable effect of condensation (and hence heat flux) upon k_w .

Thermal stability

A related temperature effect on air-water gas exchange is when cold air overlies relatively warm water. In this situation the air/water interface is said to be unstable and this condition can theoretically give rise to enhanced gas exchange relative to thermally neutral conditions (i.e. when the air and water temperatures are equal). The instability arises because cooling of the water surface leads to the generation of enhanced turbulence as the surface layers become more dense, initiating buoyancy effects (Erickson 1993). In the converse case, in which warm air overlies cooler water, the interface is said to be stable. In this situation gas transfer is theoretically reduced relative to thermally neutral conditions because the water surface warms, becoming less dense than the underlying bulk water. The effect of thermal stability on CO_2 exchange at constant wind speed has been modelled by Erickson (1993). Figure 5 shows typical contributions of 20–50% for modest air-sea temperature differences,

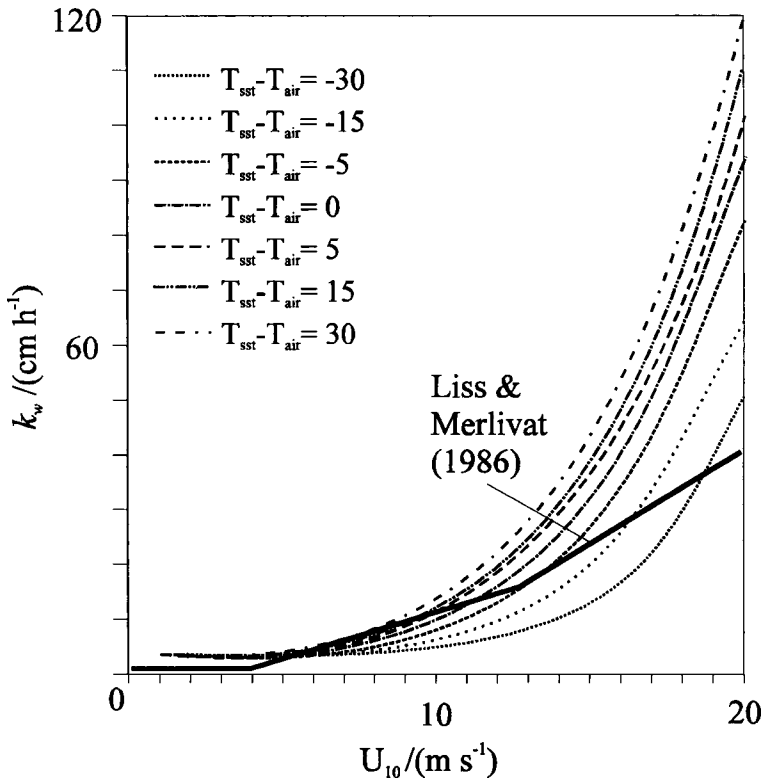


Figure 5 Family of curves showing the stability dependence of k_w for CO_2 at 20°C as a function of wind speed, the stability conditions are shown in the key, given as the difference between sea surface temperature (T_{sst}) and air temperature (T_{air}). Negative values causing more stable conditions are reflected in the model by a lower response of k_w to wind speed. Also shown for comparison is the model of Liss & Merlivat (1986). Reproduced from Erickson (1993).

and as much as 100% during periods of intense stability or instability. Clearly, the role of thermal stability in gas exchange is a potentially important one demanding more intense scrutiny in future studies.

Humidity

The effect of relative humidity on air-water gas exchange was first demonstrated in wind-tunnel experiments by Hoover & Berkshire (1969) who found that if the water temperature fell below the local dew point gas transfer was inhibited. Subsequently, Quinn & Otto (1971) suggested that the effect was due to condensation on the water surface, leading to the suppression of evaporation-driven convective motions. In later work, Münnich et al. (1978) showed that during net evaporation from the water surface gas transfer increased at low wind speeds, which was attributed to disruption of the surface film. In contrast, Liss et al. (1981) could find no measurable enhancement of gas transfer under evaporating conditions,

but a 30% reduction in gas exchange was observed during condensing conditions. Liss et al. (1981) described the retardation of gas exchange in terms of a stratification parameter at the interface and pointed out that although evaporation predominates at natural air/water interfaces, condensing conditions occur with sufficient frequency to render such corrections important. Beyond these studies, humidity effects have been intensively studied with regard to spray and droplet formation (e.g. Smith et al. 1996), but the role of humidity in gas exchange in natural systems has yet to be examined in detail.

Rain

Because raindrops striking a water surface create turbulence, rainfall has the potential to enhance gas exchange. Bopp et al. (1981) first suggested such a possibility in order to explain gas transfer results for a model estuarine system. Banks et al. (1984) measured experimentally O_2 invasion rates into deoxygenated water with and without artificial rainfall and derived a relationship in which O_2 exchange was proportional to the power of the rainfall. However, because the raindrops did not reach terminal velocity prior to impacting the water surface, these results may not be directly applicable in a field situation. Results from a subsequent field study also using O_2 (Belanger & Korzun 1991) were consistent with a linear relationship. In the most detailed study to date, Ho et al. (1997) observed the effect of rainfall at terminal velocity and a range of known drop sizes, upon SF_6 evasion from a laboratory tank, and found significant and systematic enhancements. By deducing the kinetic energy flux to the water surface from measured rain rates and drop sizes, Ho et al. (1997) found the enhancement of SF_6 evasion to be independent of drop size and were able to quantify the gas exchange rate solely in terms of the kinetic energy flux between the raindrops and the water surface. The dominant exchange mechanism accounting for the rainfall enhancement effect remains uncertain. However, rain-induced turbulence noted by Bliven et al. (1993a) as small structures such as craters, stalks and ring-waves must make a contribution (Bopp et al. 1981). In addition, Ho et al. (1997) suggested that raindrops may entrain air bubbles leading to effects similar to those described earlier, and further speculated on how rain temperatures and the dispersal of surface films by rain may also be important. In the oceanic situation rainfall may have other implications associated with the initiation of small-scale density stratification for example. Ho et al. (1997) also identify possible amplification of wind stress upon a water surface in the presence of rain, first noted by Caldwell & Elliott (1972).

A biogeochemical role for the sea-surface microlayer?

The air/sea interface is highly chemically and microbiologically enriched (Table 2, p. 26). However, because measurements of k_w are of necessity either physically or chemically based, they are unable to identify explicitly any potential biogeochemical modifications to air-sea gas exchange.

From a microbiological perspective, the “sea-surface microlayer”, sometimes called the neuston and hereinafter referred to simply as “the microlayer”, is operationally defined as the interface between the uppermost 1000 μm of the sea surface and the lower 50–500 μm of the atmosphere (GESAMP 1995) and it is important here to draw a distinction between

this definition and that of the “stagnant boundary layer”, which is defined by purely physical constraints. Although the two coincide at the air/sea interface, they are not necessarily of the same depth. Largely because of its small physical extent, $\sim 10^{-4}$ % of total euphotic zone volume, the microlayer has previously received very little attention as a potentially important site for the modification of energy and material transfer between water surfaces and the atmosphere.

The biogeochemical properties of the microlayer are unique. It has been described as a highly efficient and selective “microreactor” because of its chemical and biological reactivity, which results in an accumulation of reactive trace species with the potential to form a “reaction barrier” to trace gas transport (GESAMP 1995). Microlayer bacterial cells typically have enrichment factors (EF) of up to 10^4 relative to the underlying bulk water (Table 2), possibly as a consequence of hydrophobic interactions leading to bacterial adsorption at the air/sea interface (Powelson & Mills 1996). Furthermore, bacterial transport in this region may be furnished via advancing surfactant slicks which act to redistribute existing bacterial communities and introduce new ones into the microlayer (Hale & Mitchell 1997).

Potential roles for microlayer biogeochemistry in air-sea gas exchange have been identified in a number of studies. In an experiment to determine the photochemical enrichment of low-molecular-weight carbonyl compounds (LMWCCS) in the microlayer relative to bulk water, Zhou & Mopper (1997) found EF values ~ 1.2 – 21 for LMWCCS in the microlayer. Modelled LMWCC residence times for the microlayer were $\sim 10^1$ – 10^2 seconds, however residence times consistent with the observed microlayer enrichments were $\sim >10^3$ seconds. These longer residence times most likely result from LMWCC-organic interactions within the microlayer leading to modification of molecular transport rates and relevant partition coefficients (Zhou & Mopper 1997). Consequently, the control of air-sea LMWCC exchange due to photochemical enrichment is likely influenced by subsequent biogeochemical transformations in the microlayer. Micro-organisms in the surface microlayer have been invoked to directly consume atmospheric CO (Conrad & Seiler 1982, Conrad et al. 1982), although the possibility that these conclusions arise from an artefact due to enzymatic regulation cannot be completely excluded (GESAMP 1995). Experimental studies of CO₂ behaviour in the microlayer inform conflicting opinions regarding the role of the microlayer in CO₂ exchange. Some studies indicate enhanced CO₂ production (Hardy 1973, Garabétian 1990), whereas in others, rates of respiratory breakdown of particulates are considered too slow to measurably affect the rate of air-sea CO₂ exchange (GESAMP 1995). However, the microlayer may play a disproportionately large role in organic matter respiration because of the affinity of surface-active material for the interface. Assuming that $\sim 1\%$ of the particulate carbon produced in the water column reaches the surface and undergoes breakdown in the microlayer, the increase in CO₂ concentrations may be sufficient to significantly reduce the rate of CO₂ influx from the atmosphere, a process known as “flux capping” (GESAMP 1995). An alternative possibility for apparent biogeochemical modification of CO₂ exchange by the microlayer arises during CO₂ production from the photochemical decomposition of dissolved organic carbon (DOC) (Miller & Zepp 1992).

Limited circumstantial evidence for an active role for the microlayer in air-sea gas exchange comes from k_w estimates for some bioreactive gases (CH₄, N₂O, CO and H₂) obtained from direct measurements of air-sea exchange made with a free-floating flux box at sea, in which gas partial pressures in a headspace were selected and modified in order to force invasive or evasive gas transfer (Conrad & Seiler 1988). It is important that these results showed rates of invasive gas transfer to exceed those for evasion under the same

conditions of turbulence and the discrepancy between the two sets of measurements was similar to that for invasive ^{14}C as compared with ^{222}Rn or dual-tracer evasion. Subsequent experiments of this type for N_2O in a laboratory exchange tank gave similar results (Upstill-Goddard & Brown 1996). Because the possibility of experimental artefact due to system leakage was precluded by the experimental design (Upstill-Goddard & Brown 1996), these results imply active microbial gas consumption in the surface microlayer, the only plausible gas sink in the experiments. If such findings are substantiated by further study, existing gas transfer models applied to gases with significant bioreactivity may require major revision. Of wider reaching significance are the global biogeochemical implications of net exchange flux calculations for reactive gases based on k_w “scaled up” from inert tracers. Clearly, further laboratory and field studies on the possible biogeochemical role of the microlayer in gas transfer processes are urgently required.

Concluding remarks

Air-sea gas exchange is a fundamentally important component of global biogeochemical cycling. Because of this, intense research efforts during the past decade or so have focused on improvements to our understanding of the important environmental controls on gas transfer, as well as on the direct measurement of gas transfer velocities and fluxes. Although substantial improvements have been made in both of these areas, large uncertainties still remain, such that the true functional dependence of k_w can even now only be approximated. Much of this uncertainty has arisen from the largely limited interdisciplinary scope of most investigations. Discrepancies between techniques and problems of scaling wave and bubble characteristics measured in the laboratory to the field situation have arisen because many such studies tend to have been carried out in isolation. Because there is now a substantial body of data on which to build, strategies for the optimization of results through the integration of field and laboratory measurements with associated modelling seem timely. Such approaches are increasingly desirable in view of the high economic costs of mounting individual studies, particularly those with a significant seagoing requirement. Central to such an approach, there is an urgent need to resolve the current conflict between k_w values determined with the micrometeorological and gaseous tracer techniques. Because the former avoid the complications which arise with the dual-tracer technique under wave breaking conditions, the simultaneous use of these techniques to measure k_w values for a range of gases within integrated programmes should provide the data required to elucidate further the important mechanisms of gas transfer, especially in the wave breaking regime, enabling detailed refinements to existing gas exchange models.

An ultimate aim for gas exchange studies into the millennium must be to develop a predictive capability based on global remote sensing of turbulence-related variables from satellites. Because approaches such as the direct determination of sea surface roughness and wind speeds from scatterometer measurements of sea surface radar backscatter and the use of infrared imagery of the thermal skin to determine areas affected by breaking waves are fast becoming a routine capability (e.g. Bourassa et al. 1997), the acquisition of relevant high-resolution, global gas exchange parameters is now within reach. However, the value of such data in predicting air-sea gas exchange rates requires the development of extremely fine-resolution models of the air-sea gas exchange process, applicable over a range of environmental situations. This is the key challenge for the start of the next century.

Acknowledgements

This review began life as part of an interim PhD progress report prepared by T.F. We would like to thank Professor N.J.P.Owens for initially encouraging us to write it, and the University of Newcastle upon Tyne Research Committee for providing the requisite financial support.

References

- Anderson, M.L. & Johnson, B.D. 1992. Gas transfer—a gas tension method for studying equilibration across a gas/water interface. *Journal of Geophysical Research, Oceans* **97**(11), 17899–904.
- Andreae, M.O. & Ferek, R.J. 1992. Photochemical production of carbonyl sulfide in sea water and its emission to the atmosphere. *Global Biogeochemical Cycles* **6**(2), 175–83.
- Asher, W.E. & Farley, P.J. 1995. Phase-Doppler anemometer measurement of bubble concentrations in laboratory-simulated breaking waves. *Journal of Geophysical Research* **100**(C4), 7045–56.
- Asher, W.E., Farley, P.J., Wanninkhof, R., Monahan, E.C. & Bates, T.S. 1992. Laboratory and field measurements concerning the correlation of fractional area foam coverage with air-sea gas transport. In *Precipitation scavenging and atmosphere-surface exchange. Vol. 2, The Semonin volume: atmosphere-surface exchange processes*, S.E.Schwartz & W.G.N.Slinn (eds). Washington, DC: Hemisphere, 815–28.
- Asher, W.E., Higgins, B.J., Karle, L.M., Farley, P.J., Sherwood, C.R., Gardiner, W.W., Wanninkhof, R.H., Chen, H., Lantry, T.P., Steckley, M., Monahan, E.C., Wang, Q. & Smith, P.M. 1996. Measurements of gas transfer, whitecap coverage, and brightness temperature in a surf pool: an overview of WABEX-93. *Proceedings, Third International Symposium on Air-Water-Gas Transfer*. Heidelberg, Germany: Aeon Verlag & Studio, 205–16.
- Asher, W.E. & Pankow, J.F. 1991. Prediction of gas/water mass transport coefficients by a surface renewal model. *Environmental Science and Technology* **25**(7), 1294–300.
- Asher, W.E. & Wanninkhof, R. 1995. The effect of breaking waves on dual-tracer gas exchange experiments. In *Air-water gas transfer*, B.Jähne & E.C.Monahan (eds). Hanau, Germany: Aeon Verlag, 517–28.
- Asher, W.E. & Wanninkhof, R. 1998a. Transient tracers and air-sea gas transfer. *Journal of Geophysical Research* **103**(C8), 15939–58.
- Asher, W.E. & Wanninkhof, R. 1998b. The effect of bubble-mediated gas transfer on purposeful dual tracer experiments. *Journal of Geophysical Research* **103**(C5), 10555–60.
- Asher, W.E. & Wanninkhof, R.H. 1996. The effect of breaking waves on the analysis of dual-tracer gas exchange measurements. *Proceedings, Third International Symposium on Air-Water-Gas Transfer*. Heidelberg, Germany: Aeon Verlag & Studio, 517–28.
- Bange, H.W., Bartell, U.H., Rapsomanikis, S. & Andreae, M.O. 1994. Methane in the Baltic and North Seas and a reassessment of the marine emissions of methane. *Global Biogeochemical Cycles* **8**(4), 465–80.
- Bange, H.W., Rapsomanikis, S. & Andreae, M.O. 1996a. Nitrous oxide in coastal waters. *Global Biogeochemical Cycles* **10**(1), 197–207.
- Bange, H.W., Rapsomanikis, S. & Andreae, M.O. 1996b. Nitrous oxide emissions from the Arabian Sea. *Geophysical Research Letters* **23**(22), 3175–8.
- Banks, R.B., Wickramanayake, B. & Lohani, B.N. 1984. Effect of rain on surface reaeration. *Journal of Environmental Engineering* **110**(1), 1–14.
- Belanger, T.V. & Korzun, E.A. 1991. Rainfall re-aeration effects. In *Air-water mass transfer, proceedings of the second international symposium on gas transfer at water surfaces*. S.C.Wilhelms & J.S.Gulliver (eds). New York: American Society of Chemical Engineering, 388–99.
- Berger, R. & Libby, W.F. 1969. Equilibration of atmospheric carbon dioxide with sea water: possible enzymatic control of the rate. *Science* **164**, 1395–7.
- Blanc, T.V. 1983. A practical approach to flux measurements of long duration in the marine atmospheric surface layer. *Journal of Climate and Applied Meteorology* **33**, 1093–110.
- Blanchard, D.C. 1983. The production, distribution and bacterial enrichment of the sea-salt aerosol. In *Air-sea exchange of gases and particles*, P.S.Liss & W.G.N.Slinn (eds). Dordrecht, Holland: Kluwer Academic Press, 407–54.

- Bliven, L.F., Branger, H., Sobieski, P. & Giovanangeli, J.P. 1993a. An analysis of scatterometer returns from a water-surface agitated by artificial rain—evidence that ring-waves are the main feature. *International Journal of Remote Sensing* **14**(12), 2315–29.
- Bliven, L.F., Giovanangeli, J.P., Wanninkhof, R.H. & Chapron, B. 1993b. A laboratory study of friction-velocity estimates from scatterometry—low and high regimes. *International Journal of Remote Sensing* **14**(9), 1775–85.
- Bolin, B. 1960. On the exchange of carbon dioxide between the atmosphere and the sea. *Tellus* **12**, 274–81.
- Bopp, R.F., Santschi, P.H., Li, Y.-H. & Deck, B.L. 1981. Biodegradation and gas-exchange of gaseous alkanes in model estuarine ecosystems. *Organic Geochemistry* **3**, 9–14.
- Bourassa, M.A., Freilich, M.H., Legler, D.M., Liu, W.T. & O'Brien, J. 1997. Wind observations from new satellite and research vessels agree. *Eos, Transactions of the American Geophysical Union* **78**(51), 597–602.
- Boutin, J. & Etcheto, J. 1996. Consistency of GEOSAT, SSM/I, and ERS-1 global surface wind speeds—comparison with *in situ* data. *Journal of Atmospheric and Oceanic Technology* **13**(1), 183–97.
- Boutin, J. & Etcheto, J. 1997. Long-term variability of the air-sea CO₂ exchange coefficient: consequences for the CO₂ fluxes in the equatorial Pacific Ocean. *Global Biogeochemical Cycles* **11**(3), 453–70.
- Boutin, J., Siefridt, L., Etcheto, J. & Barnier, B. 1996. Comparison of ECMWF and satellite ocean wind speeds from 1985 to 1992. *International Journal of Remote Sensing* **17**(15), 2897–913.
- Braziunas, T.F., Fung, I.Y. & Stuiver, M. 1995. The preindustrial atmospheric (CO₂)-C-14 latitudinal gradient as related to exchanges among atmospheric, oceanic, and terrestrial reservoirs. *Global Biogeochemical Cycles* **9**(4), 565–84.
- Broecker, H.-C., Petermann, J. & Siems, W. 1978. The influence of wind on CO₂-exchange in a wind-wave tunnel, including the effects of monolayers. *Journal of Marine Research* **36**, 595–610.
- Broecker, H.-C. & Siems, W. 1984. The role of bubbles for gas transfer from water to air at higher windspeeds; experiments in the wind-wave facility in Hamburg. In *Gas transfer at water surfaces*, W.Brutsaert & G.H.D.Jirka (eds). Dordrecht, The Netherlands: D.Reidel Publishing, 229–37.
- Broecker, W.S., Ledwell, J.R., Takahashi, T., Weiss, R., Merlivat, L., Memery, L., Peng, T.-H., Jähne, B. & Münnich, K.O. 1986. Isotopic versus micrometeorological ocean CO₂ fluxes: a serious conflict. *Journal of Geophysical Research* **91**(C9), 10517–27.
- Broecker, W.S. & Peng, T.-H. 1974. Gas exchange rates between air and sea. *Tellus* **26**, 21–35.
- Broecker, W.S. & Peng, T.-H. 1984. Gas exchange measurements in natural systems. In *Gas transfer at water surfaces*. W.Brutsaert & G.H.D.Jirka (eds). Dordrecht, The Netherlands: D.Reidel Publishing, 479–93.
- Broecker, W.S., Peng, T.-H., Mathieu, G., Hesslein, R. & Torgersen, T. 1980. Gas exchange rate measurements in natural systems. *Radiocarbon* **22**(3), 676–83.
- Broecker, W.S., Peng, T.-H., Ostlund, G. & Stuiver, M. 1985. The distribution of bomb radiocarbon in the ocean. *Journal of Geophysical Research* **90**(C4), 6953–70.
- Businger, J.A. & Oncley, S.P. 1990. Flux measurements with conditional sampling. *Journal of Atmospheric and Oceanic Technology* **7**, 349–52.
- Butler, J.H. 1994. The potential role of the ocean in regulating atmospheric CH₃Br. *Geophysical Research Letters* **21**(3), 185–8.
- Caldwell, D.R. & Elliott, W.P. 1972. The effect of rainfall on the wind in the surface layer. *Boundary-Layer Meteorology* **3**, 146–51.
- Cao, M. & Woodward, I. 1998. Dynamic responses of terrestrial ecosystem carbon cycling to global climate change. *Nature* **393**, 249–52.
- Carlucci, A.F., Craven, D.B. & Henrichs, S.M. 1985. Surface-film microheterotrophs—amino-acid metabolism and solar-radiation effects on their activities. *Marine Biology* **85**(1), 13–22.
- Cember, R. 1989. Bomb radiocarbon in the Red Sea: a medium-scale gas exchange experiment. *Journal of Geophysical Research* **94**(C2), 2111–23.
- Charlson, R.J., Lovelock, J.E., Andreae, M.O. & Warren, S.G. 1987. Oceanic phytoplankton, atmospheric sulphur, cloud albedo and climate. *Nature* **326**, 655–61.
- Clark, J.F., Schlosser, P., Wanninkhof, R., Simpson, H.J., Schuster, W.S. F. & Ho, D.T. 1995. Gas transfer velocities for SF₆ and ³He in a small pond at low wind speeds. *Geophysical Research Letters* **22**(2), 93–6.

- Clark, J.F., Wanninkhof, R., Schlosser, P. & James, H. 1994. Gas exchange rates in the Hudson River using a dual tracer technique. *Tellus* **46B**, 274–85.
- Clauss, E., Hinzpeter, H. & Mueller-Glewe, J. 1970. Messungen der Temperaturstruktur im Wasser an der Grenzfläche Ozean-Atmosphäre. *Meteor Forschungsergebnisse, Reihe B* **5**, 90–94.
- Coantic, M. 1986. A model of gas transfer across air/water interfaces with capillary waves. *Journal of Geophysical Research* **91**(C3), 3925–43.
- Conrad, R. & Seiler, W. 1982. Utilization of traces of carbon monoxide by aerobic oligotrophic microorganisms in ocean, lake and soil. *Archives of Microbiology* **132**, 41–6.
- Conrad, R. & Seiler, W. 1988. Influence of the surface microlayer on the flux of nonconservative trace gases (CO, H₂, CH₄, N₂O) across the ocean-atmosphere interface. *Journal of Atmospheric Chemistry* **6**, 83–94.
- Conrad, R., Seiler, W., Bunse, G. & Giehl, H. 1982. Carbon monoxide in sea water (Atlantic Ocean). *Journal of Geophysical Research* **87**, 8852–93.
- Crucius, J. & Wanninkhof, R. 1990. A gas transfer exchange wind speed relationship measured on lake 302N with SF₆. *Eos, Transactions of the American Geophysical Union* **71**, 1234 only.
- Crutzen, P.J. 1991. Methanes sinks and sources. *Nature* **350**, 380–81.
- Danckwerts, P.V. 1970. *Gas-liquid reactions*. London: McGraw-Hill.
- Davies, J.T. 1966. The effects of surface films in damping eddies at a free surface of a turbulent liquid. *Proceedings of the Royal Society of London, Series A* **290**, 515–26.
- Deacon, E.L. 1977. Gas transfer to and across an air/water interface. *Tellus* **29**, 363–74.
- Deacon, E.L. 1980. Sea-air gas transfer: the wind speed dependence. *Boundary-Layer Meteorology* **21**, 31–7.
- den Daas, J.H., Suijlen, J.M. & Helder, W. 1997. *Measurements of sulpho rhodamine G and rhodamine WT concentrations in seawater samples taken during the multiple tracer experiment ASGAMAGE (1996)*. Nederlands Instituut voor Onderzoek der Zee Technical Report No. 21, 20 pp.
- Doney, S.C. 1995a. Irreversible thermodynamics and air-sea exchange. *Journal of Geophysical Research* **100**(C5), 8541–53.
- Doney, S.C. 1995b. Comment on “Experimental demonstration of coupling of heat and matter fluxes at a gas/water interface” by Leon F. Phillips. *Journal of Geophysical Research* **100**(D7), 14347–50.
- Downing, A.L. & Truesdale, G.A. 1955. Some factors affecting the rate of solution of oxygen in water. *Journal of Applied Chemistry* **5**, 570–81.
- Ebuchi, N., Kawamura, H. & Toba, Y. 1992. Growth of wind waves with fetch observed by the geosat altimeter in the Japan Sea under winter monsoon. *Journal of Geophysical Research* **97**(C1), 809–19.
- Emerson, S. 1975. Gas exchange rates in small Canadian shield lakes. *Limnology and Oceanography* **20**(5), 754–61.
- Emerson, S., Broecker, W.S. & Schindler, D.W. 1973. Gas exchange rates in a small lake as determined by the radon method. *Journal of Fisheries Research Board of Canada* **30**, 1475–84.
- Erickson III, D.J. 1993. A stability dependent theory for air-sea gas exchange. *Journal of Geophysical Research* **98**(C5), 8471–88.
- Espedal, H.A., Johannessen, O.M. & Knulst, J. 1996. Satellite detection of natural films on the ocean surface. *Geophysical Research Letters* **23**(22), 3151–4.
- Ewing, G. & McAlister, E.D. 1960. On the thermal boundary layer of the ocean. *Science* **131**, 1374–6.
- Farmer, D.M., McNeil, C.L. & Johnson, B.D. 1993. Evidence for the importance of bubbles in increasing air-sea flux. *Nature* **361**, 620–23.
- Frew, N.M., Goldman, J.C., Dennett, M.R. & Johnson, A.S. 1990. Impact of phytoplankton-generated surfactants on air-sea gas exchange. *Journal of Geophysical Research* **95**(C3), 3337–51.
- Frew, N.M. & Nelson, R.K. 1992. Isolation of marine microlayer film surfactants for ex situ study of their surface physical and chemical properties. *Journal of Geophysical Research* **97**(C4), 5281–90.
- Friedmann, D. 1969. Infrared characteristics of ocean water (1.5–15 μm). *Applied Optics* **8**, 2073–8.
- Fuchs, G., Roether, W. & Schlosser, P. 1987. Excess He-3 in the ocean surface-layer. *Journal of Geophysical Research, Oceans* **92**(C6), 6559–68.
- Fujitani, T. 1985. Method of turbulent flux measurements on a ship by using a stable platform system. *Journal of the Meteorology Society, Japan* **36**, 157–70.

- Gameson, A.H.L. 1986. Tracers for the water industry. Water Research Centre, Marlow, England.
- Garabétian, F. 1990. CO₂ production at the sea-air interface. An approach by the study of respiratory processes in surface microlayer. *International Revue of Geophysical Hydrobiology* **75**, 219–29.
- Garabétian, F., Romano, J.C., Paul, R. & Sigoillot, J.C. 1993. Organic matter composition and pollutant enrichment of sea surface microlayer inside and outside slicks. *Marine Environmental Research* **35**, 323–39.
- Gat, J.R. & Shatkey, M. 1991. Gas exchange with saline waters. *Limnology and Oceanography* **36**, 988–97.
- GESAMP (IMC/FAO/Unesco-ICC/WMO/WHO/IAEA/UN/UNEP Joint Group of Experts on the Scientific Aspects of Marine Environmental Protection) 1995. The sea surface microlayer and its role in global climate change. *GESAMP Reports and Studies* **59**, 76 pp.
- Glover, D.M. & Reeburgh, W.S. 1987. Rn-222 and Ra-226 in south-eastern Bering Sea shelf waters and sediment. *Continental Shelf Research* **7**(5), 433–56.
- Goldman, J.C. & Dennett, M.R. 1983. Carbon dioxide exchange between air and sea water: no evidence for rate catalysis. *Science* **220**, 199–201.
- Grassl, H. 1976. The dependence of the measured cool skin of the ocean on windstress and total heat flux. *Boundary-Layer Meteorology* **1**, 190–98.
- Haines, M.A. & Johnson, B.D. 1995. Injected bubble populations in sea water and fresh-water measured by a photographic method. *Journal of Geophysical Research, Oceans* **100**(C4), 7057–68.
- Hale, M.S. & Mitchell, J.G. 1997. Sea surface microlayer and bacterioneuston spreading dynamics. *Marine Ecology Progress Series* **147**(1–3), 269–76.
- Hardy, J.T. 1973. Phytoneuston ecology of a temperate lagoon. *Limnology and Oceanography* **18**(4), 525–33.
- Hardy, J.T. 1982. The sea-surface microlayer—biology, chemistry and anthropogenic enrichment. *Progress in Oceanography* **11**(4), 307–28.
- Hardy, J.T. & Apts, C.W. 1984. The sea-surface microlayer: phytoneuston productivity and effects of atmospheric particulate matter. *Marine Biology* **82**, 293–300.
- Hardy, J.T. & Apts, C.W. 1989. Photosynthetic carbon reduction: high rates in the sea-surface microlayer. *Marine Biology* **101**, 411–17.
- Harnisch, J. & Eisenhauer, A. 1998. Natural CF₄ and SF₆ on Earth. *Geophysical Research Letters* **25**, 2401–4.
- Hartman, B. & Hammond, D.E. 1984. Gas exchange rates across the sediment-water and air-water interfaces in south San Francisco Bay. *Journal of Geophysical Research* **89**(C3), 3593–603.
- Harvey, G.W. 1966. Microlayer collection from the sea surface: a new method and initial results. *Limnology and Oceanography* **11**, 608–14.
- Hasse, L. 1990. On the mechanism of gas exchange at the air-sea interface. *Tellus* **42B**, 250–53.
- Haussecker, H. & Jähne, B. 1995. In situ measurements of the air-sea gas transfer rate during the MBL/COOP west coast experiment. In *Air-water gas transfer*, B.Jähne & E.C.Monahan (eds). Hanau, Germany: Aeon Verlag, 775–84.
- Hayduk, W. & Laudie, H. 1974. Prediction of diffusion coefficients for nonelectrolytes in dilute aqueous solutions. *American Institute for Chemical Engineering Journal* **20**, 611–15.
- Hernandez, P.A., Perez, N.M., Salazar, J.M., Nakai, S., Notsu, K. & Wakita, H. 1998. Diffuse emission of carbon dioxide, methane, and helium-3 from Teide volcano, Tenerife, Canary Islands. *Geophysical Research Letters* **25**(17), 3311–14.
- Hesshaimer, V., Heimann, M. & Levin, I. 1994. Radiocarbon evidence for a smaller oceanic carbon dioxide sink than previously believed. *Nature* **370**, 201–3.
- Higbie, R. 1935. The rate of absorption of pure gas into a still liquid during short periods of exposure. *Transactions American Institute of Chemical Engineers* **35**, 365–69.
- Ho, D.T., Bliven, L.F. & Wanninkhof, R. 1997. The effect of rain on air-water gas exchange. *Tellus* **49B**, 149–58.
- Holmen, K. & Liss, P. 1984. Models for air water gas transfer—an experimental investigation. *Tellus Series B-Chemical and Physical Meteorology* **36**(2), 92–100.
- Hoover, T.E. & Berkshire, D.C. 1969. Effects of hydration on carbon dioxide exchange across an air-water interface. *Journal of Geophysical Research* **74**(2), 456–64.
- Houghton, J.T., Filho, L.G.M., Callander, B.A., Harris, N., Kattenberg, A. & Maskell, K. 1996. *Climate change 1995. The science of climate change. Contribution of working group I to the second assessment report of the Intergovernmental Panel on Climate Change*. Cambridge, NY: Cambridge University Press.

- Houghton, J.T., Jenkin, G.J. & Ephraim, J.J. (eds) (1990). *Climate Change. The IPCC Scientific Assessment*. Cambridge, NY: Cambridge University Press.
- Jacobs, C.M.J., Kohsiek, W. & Oost, W.A. 1997. *Direct determination of the air-sea transfer velocity of CO₂ during ASGAMAGE*. Scientific Report. 97-06, Koninklijk Nederlands Meteorologisch Instituut, De Bilt, The Netherlands, 30 pp.
- Jähne, B., Fischer, K.H., Ilmberger, J., Libner, P., Weiss, W., Imboden, D., Lemmin, U. & Jaquet, J. M. 1984a. Parametrization of air/lake gas exchange. In *Gas transfer at water surfaces*, W.Brutsaert & G.H.Jirka (eds). Dordrecht, The Netherlands: D.Reidel Publishing, 459–66.
- Jähne, B., Heinz, G. & Dietrich, W. 1987a. Measurements of the diffusion coefficients of sparingly soluble gases in water. *Journal of Geophysical Research* **92**(C10), 10767–76.
- Jähne, B., Huber, W., Dutzi, A., Wais, T. & Ilmberger, J. 1984b. Wind/wave-tunnel experiment on the Schmidt Number—and wave field dependence of air/water gas exchange. In *Gas transfer at water surfaces*, W.Brutsaert & G.H.Jirka (eds). Dordrecht, The Netherlands: D.Reidel Publishing, 303–9.
- Jähne, B., Libner, P., Fischer, R., Billenand, T. & Plate, E.J. 1989. Investigating the transfer processes across the free aqueous viscous boundary layer by the controlled flux method. *Tellus* **41B**, 177–95.
- Jähne, B., Münnich, K.O., Bosinger, R., Dutzi, A., Huber, W. & Libner, P. 1987b. On the parameters influencing air-water gas exchange. *Journal of Geophysical Research* **92**(C2), 1937–49.
- Jähne, B., Münnich, K. & Siegenthaler, U. 1979. Measurements of gas exchange and momentum transfer in a circular wind-water tunnel. *Tellus* **31**, 321–9.
- Jähne, B., Wais, T., Memery, L., Caulliez, G., Merlivat, L., Münnich, K.O. & Coantic, M. 1985. He and Rn gas exchange experiments in the large wind-wave facility of IMST. *Journal of Geophysical Research* **90**(C6), 11989–97.
- Jean-Baptiste, P., Belviso, S., Alaux, G., Nguyen, B.C. & Mihalopoulos, N. 1990. He-3 and methane in the Gulf of Aden. *Geochimica et Cosmochimica Acta* **54**(1), 111–16.
- Jenkins, W.J. & Clarke, W.B. 1976. The distribution of ³He in the western Atlantic Ocean. *Deep-Sea Research* **23**, 481–94.
- Jessup, A.T., Zappa, C.J., Loewen, M.R. & Hesany, V. 1997. Infrared remote sensing of breaking waves. *Nature* **385**, 52–5.
- Johnson, J.E. & Bates, T.S. 1996. Sources and sinks of carbon monoxide in the mixed layer of the tropical South Pacific Ocean. *Global Biogeochemical Cycles* **10**(2), 347–59.
- Johnson, K.S. 1982. Carbon dioxide hydration and dehydration kinetics in sea water. *Limnology and Oceanography* **27**, 849–55.
- Kahma, K.K. & Lepparanta, M. 1981. On errors in wind speed observations on the R/V Aranda. *Geophysica* **17**, 155–65.
- Katsaros, K.B. 1977. The sea surface temperature deviation at very low wind speeds; is there a limit? *Tellus* **29**, 229–39.
- Keeling, C.D. 1968. Carbon dioxide in surface ocean waters (4. Global distribution). *Journal of Geophysical Research* **73**(14), 4543–53.
- Keeling, R.F. 1993. On the role of large bubbles in air-sea gas exchange and supersaturation in the ocean. *Journal of Marine Research* **51**, 237–71.
- Kerman, B.R. 1980. *Gas transfer at the air/sea interface by breaking waves*. Report AQRB-81-018-L, Atmospheric Environment Service, Canada.
- Kerman, B.R. 1984. A model of interfacial gas transfer for a well-roughed sea. In *Gas transfer at water surfaces*, W.Brutsaert & G.H.Jirka (eds). Dordrecht, The Netherlands: D.Reidel Publishing, 211–320.
- Keswick, B.H. & Wang, D.S. 1982. The use of microorganisms as ground water tracers. *Ground Water* **20**, 142–9.
- Kim, K.H. & Andreae, M.O. 1992. Carbon disulfide in the estuarine, coastal, and oceanic environments. *Marine Chemistry* **40**(3–4), 179–97.
- King, D.B. & Saltzman, E.S. 1995. Measurement of the diffusion coefficient of sulfur hexafluoride in water. *Journal of Geophysical Research* **100**(C4), 7083–8.
- Kirk, G.J.D. & Singh, R.-D. 1992. Simultaneous transfer across an air-water interface of gases that interact through acid-base reactions. *Atmospheric Environment* **26A**(9), 1651–60.
- Kishinevsky, M.Kh. & Serebryansky, V.T. 1956. The mechanism of mass transfer at the gas-liquid interface with vigorous stirring. *Journal of Applied Chemistry USSR* **29**, 29–33.

- Kitaigorodskii, S.A. 1984. On the fluid dynamical theory of turbulent gas transfer across an air-sea interface in the presence of breaking wind-waves. *Journal of Physical Oceanography* **14**, 960–72.
- Kohsiek, W. 1997. Measurement of CO₂ fluxes with the IFM during ASGAMAGE. In The ASGAMAGE workshop, W.Oost (ed.). Scientific Report 98–02, Koninklijk Nederlands Meteorologisch Instituut, De Bilt, The Netherlands, 126 pp.
- Kromer, B. & Roether, W. 1983. Field measurements of air-sea gas exchange by the radon deficit method during JASIN (1978) and FGGE (1979). *Meteor Forschungsergebnisse* **24A/B**, 55–75.
- Lamontagne, R.A., Swinnerton, J.W., Linnenbom, V.J. & Smith, W.D. 1973. Methane concentrations in various marine environments. *Journal of Geophysical Research* **78**(24), 5317–24.
- Large, W.G. & Pond, S. 1982. Sensible and latent heat flux measurements over the ocean. *Journal of Physical Oceanography* **12**, 464–82.
- Law, C.S. & Owens, N.J.P. 1990. Significant flux of atmospheric N₂O from the north-west Indian ocean. *Nature* **346**, 826–8.
- Law, C.S., Watson, A.J. & Liddicoat, M.I. 1994. Automated vacuum analysis of sulfur-hexafluoride in sea water—derivation of the atmospheric trend (1970–1993) and potential as a transient tracer. *Marine Chemistry* **48**(1), 57–69.
- Ledwell, J.R. 1982. *Gas exchange across the air-water interface*. PhD thesis, Harvard University, Boston, Massachusetts.
- Ledwell, J.R. 1984. The variation of the gas transfer coefficient with molecular diffusivity. In *Gas transfer at water surfaces*, W.Brutsaert & G.H.Jirka (eds), Dordrecht, The Netherlands: D.Reidel Publishing, 293–302.
- Lee, P.H.Y., Barter, J.D., Beach, K.L., Hindman, C.L., Lake, B.M., Rungaldier, H., Shelton, J.C., Williams, A.B., Yee, R. & Yuen, H.C. 1995. X band microwave backscattering from ocean waves. *Journal of Geophysical Research* **100**(C2), 2591–611.
- Liss, P.S. 1971. Exchange of SO₂ between the atmosphere and natural waters. *Nature* **233**, 327–9.
- Liss, P.S. 1973. Processes of gas exchange across an air-water interface. *Deep-Sea Research* **20**, 221–38.
- Liss, P.S. 1983. *Air-sea exchange of gases and particles*. P.S.Liss & W.G.N.Slinn (eds), Dordrecht, The Netherlands: D.Reidel Publishing, 241–98.
- Liss, P.S. 1988. Tracers of air-sea exchange. *Philosophical Transactions of the Royal Society of London* **325**, 93–103.
- Liss, P.S., Balls, P.W., Martinelli, F.N. & Coantic, M. 1981. The effect of evaporation and condensation on gas transfer across an air-water interface. *Oceanologica Acta* **4**(2), 129–38.
- Liss, P.S. & Merlivat, L. 1986. Air-sea gas exchange rates: introduction and synthesis. In *The role of air-sea exchange in geochemical cycling*, P.Buat-Menard (ed.). Dordrecht, The Netherlands: D. Reidel Publishing, 113–29.
- Liss, P.S. & Slater, P.G. 1974. Flux of gases across the air-water interface. *Nature* **274**, 181–4.
- Liss, P.S., Watson, A.J., Liddicoat, M.I., Malin, G., Nightingale, P.D., Turner, S.M. & Upstill-Goddard, R.C. 1993. Trace gases and air-sea exchanges. *Philosophical Transactions of the Royal Society of London, Series A-Mathematical Physical and Engineering Sciences* **343**, 531–41.
- Lobert, J.M., Butler, J.H., Montzka, S.A., Geller, L.S., Myers, R.C. & Elkins, J.W. 1995. A net sink for atmospheric CH₃Br in the east Pacific Ocean. *Science* **267**, 1002–5.
- Lupton, J.E., Klinkhammer, G.P., Normark, W.R., Haymon, R., Macdonald, K.C., Weiss, R.F. & Craig, H. 1980. Helium-3 and manganese at the 21°N East Pacific Rise hydrothermal site. *Earth and Planetary Science Letters* **50**, 115–27.
- MacIntyre, S. 1984. Current fluctuations in the surface waters of small lakes. In *Gas transfer at water surfaces*, W.Brutsaert & G.H.Jirka (eds). Dordrecht, The Netherlands: D.Reidel Publishing, 125–31.
- Malinsky-Rushansky, N.Z. & Legrand, C. 1996. Excretion of dissolved organic carbon by phytoplankton of different sizes and subsequent bacterial uptake. *Marine Ecology Progress Series* **132**, 249–55.
- Manziet, J.J., Stofan, P.E. & Dupuy, J.L. 1977. Spatial heterogeneity of phytoplankton populations in estuarine surface microlayers. *Marine Biology* **41**, 29–38.
- Marino, R. & Howarth, R.W. 1993. Atmospheric oxygen exchange in the Hudson River: dome measurements and comparison with other natural waters. *Estuaries* **16**(3A), 433–45.
- Martinelli, F.N. 1979. *The effect of surface films on gas exchange across the air-sea interface*. PhD thesis, University of East Anglia, Norwich, England.

- Matson, P.A. & Harriss, R.C. 1995. *Methods in ecology-biogenic trace gases: measuring emissions from soil and water*. Oxford, UK: Blackwell Science, 126–63, 358–83.
- McAlister, E.D. & McLeish, W. 1969. Heat transfer in the top millimetre of the ocean. *Journal of Geophysical Research* **74**, 3408–14.
- McBean, G.A. 1972. Instrument requirements for eddy correlation measurements. *Journal of Applied Meteorology* **11**, 1078–84.
- McKeown, W., Bremerton, F., Huang, H.L., Smith, W.L. & Revercomb, H.L. 1995. Sounding the skin of water—sensing air-water-interface temperature-gradients with interferometry. *Journal of Atmospheric and Oceanic Technology* **12**(6), 1313–27.
- Memery, L. & Merlivat, L. 1985. Modelling of gas flux through bubbles at the air/water interface. *Tellus* **37B**, 272–85.
- Merlivat, L. & Memery, L. 1983. Gas exchange across an air-water interface: experimental results and modelling of bubble contribution to transfer. *Journal of Geophysical Research* **88**(C1), 707–24.
- Metzger, I. & Dobbins, W.E. 1967. Role of fluid properties in gas transfer. *Environmental Science and Technology* **1**, 57–65.
- Miller, W.L. & Zepp, R.G. 1992. Photochemical carbon cycling in aquatic environments: formation of atmospheric carbon dioxide and carbon monoxide. *Preprint extended abstracts, Division of Environmental Chemistry, ACS National Meeting, San Francisco* **32**, 158–60.
- Miyake, M., Donelan, M., McBean, G., Paulson, C., Badgley, F. & Leavitt, E. 1970. Comparison of turbulent fluxes over water determined by profile and eddy correlation techniques. *Quarterly Journal of the Royal Meteorology Society* **96**, 132–7.
- Monahan, E.C. 1993. Occurrence and evolution of acoustically relevant sub-surface bubble plumes and their associated, remotely monitorable, surface whitecaps. In *Natural Physical Sources of Underwater Sound*, B.Kerman (ed.). Norwell, Massachusetts, USA: Kluwer Academy, 503–17.
- Monahan, E.C. & O’Muircheartaigh, I. 1986. Optimal power-law description of oceanic whitecap coverage dependence on wind speed. *Journal of Physical Oceanography* **10**, 2094–9.
- Monahan, E.C. & Spillane, M.C. 1984. The role of whitecaps in air-sea gas exchange. In *Gas transfer at water surfaces*, W.Brutsaert & G.H.Jirka (eds). Dordrecht, The Netherlands: D.Reidel Publishing, 495–503.
- Münnich, A.S. & Flothman, A.M. 1977. *Gas exchange in relation to other air/sea interaction phenomena*. SCOR workshop on Air/Sea Interaction Phenomena, Miami, Fla., 8–12 December 1975. Background paper for the Ocean Sciences Board, Natural Research Council, Washington, DC.
- Münnich, K.O., Clarke, W.B., Fischer, K.H., Flothmann, D., Kromer, B., Roether, W., Siegenthaler, U., Top, Z. & Weiss, W. 1978. Gas exchange and evaporation studies in a circular wind tunnel, continuous radon-222 measurements at sea, and tritium/helium-3 measurements in a lake. *Turbulent fluxes through the sea surface, wave dynamics, and prediction*. NATO Conference Series, V, *Air-sea interactions*, A.Favre & K.Hasselmann (eds). New York: Plenum Press, **1**, 151–66.
- Myklestad, S.M. 1995. Release of extracellular products by phytoplankton with special emphasis on polysaccharides. *The Science of the Total Environment* **165**, 155–64.
- Nevison, C.N., Weiss, R.F. & Erickson III, D.J. 1995. Global oceanic emissions of nitrous oxide. *Journal of Geophysical Research* **100**(C8), 15809–20.
- Nightingale, P., Upstill-Goddard, R.C., Malin, G., Ho, D., Schlosser, P., Broadgate, W. & Sjöberg, T. 1997. *Measurements made during challenger 129—a contribution to ASGAMAGE*. The ASGAMAGE workshop, W.Oost (ed.). Scientific Report 98–02. Koninklijk Nederlands Meteorologisch Instituut, De Bilt, The Netherlands, 126 pp.
- Nightingale, P.D., Malin, G. & Liss, P.S. 1995. Production of chloroform and other low-molecular-weight halocarbons by some species of macroalgae. *Limnology and Oceanography* **40**, 680–89.
- Nightingale, P.D. & Upstill-Goddard, R.C. 1995. *Measurements of air-sea gas exchange using the dual tracer technique*. Report of the ASGASEX '94 workshop, W.Oost (ed.). Technical Report No. TR-174. Koninklijk Nederlands Meteorologisch Instituut, De Bilt, The Netherlands, 62 pp.
- Norkrans, B. 1980. Surface microlayers in aquatic environments. In *Advances in microbial ecology*, M.Alexander (ed.). New York: Plenum Press, 51–85.
- Nriagu, J.O., Holdway, D.A. & Coker, R.D. 1987. Biogenic sulfur and the acidity of rainfall in remote areas of Canada. *Science* **237**, 1189–92.
- Oost, W.A. 1998. The KNMI HEXMAX stress data—a reanalysis. *Boundary-Layer Meteorology* **86**, 447–68.

- Oost, W.A., Fairall, C.W., Edson, J.B., Smith, S.D., Anderson, R.J., Wills, J.A.B., Katsaros, K.B. & DeCosmo, J. 1991. Flow distortion calculations and their application in HEXMAX. *Journal of Atmospheric and Oceanic Technology* **11**, 366–86.
- Owens, N.J.P., Law, C.S., Mantoura, R.F.C., Burkill, P.H. & Llewellyn, C.A. 1991. Methane flux to the atmosphere from the Arabian Sea. *Nature* **354**, 293–6.
- Pattey, E., Desjardins, R.L. & Rochette, P. 1993. Accuracy of the Relaxed Eddy-Accumulation technique. Evaluated using CO flux measurements. *Boundary-Layer Meteorology* **66**, 341–55.
- Peng, T.-H. & Broecker, W. 1980. Gas exchange rates for three closed-basin lakes. *Limnology and Oceanography* **25**(5), 789–96.
- Peng, T.-H., Broecker, W.S., Mathieu, G.G., Li, Y.-H. & Bainbridge, A.E. 1979. Radon evasion rates in the Atlantic and Pacific Oceans. *Journal of Geophysical Research* **84**(C5), 2471–86.
- Peterson, E.W. & Hasse, L. 1987. Did the Beaufort scale or the wind change climate? *American Meteorological Society* **17**, 1071–4.
- Phillips, L.F. 1991a. Steady-state heat and matter exchange at a phase interface. *Journal of the Chemical Society Faraday Transactions* **87**(14), 2187–91.
- Phillips, L.F. 1991b. CO₂ Transport at the air-sea interface: effect of coupling of heat and matter fluxes. *Geophysical Research Letters* **18**(7), 1221–4.
- Phillips, L.F. 1994a. Experimental demonstration of coupling of heat and matter fluxes at a gas-water interface. *Journal of Geophysical Research* **99**(D9), 18577–84.
- Phillips, L.F. 1994b. Steady-state thermodynamics of transfer through a gas-liquid interface treated as a limiting case of thermo-osmosis. *Chemical Physics Letters* **228**(6), 533–8.
- Phillips, L.F. 1994c. The theory of air-sea gas exchange. *Accounts of Chemical Research* **27**(8), 217–23.
- Phillips, L.F. 1995. CO₂ transfer at the air-sea interface: numerical tests of the dual-tracer method. *Geophysical Research Letters* **22**(19), 2597–600.
- Pike, E.B., Bufton, A.W.J. & Gould, D.J. 1969. The use of *Serratia marcescens* and *Bacillus subtilis* var *niger* spores for tracing sewage dispersion in the sea. *Journal of Applied Bacteriology* **32**, 206–16.
- Plass-Dülmer, C., Khedim, A., Koppmann, R., Johnen, F.J., Rudolph, J. & Kuosa, H. 1993. Emissions of light nonmethane hydrocarbons from the Atlantic into the atmosphere. *Global Biogeochemical Cycles* **7**(1), 221–8.
- Powelson, D.K. & Mills, A.L. 1996. Bacterial enrichment at the gas-water interface of a laboratory apparatus. *Applied Environmental Microbiology* **62**(7), 2593–7.
- Price, N.M. & Morel, F.M.M. 1990. The role of extracellular enzymatic reactions in natural waters. In *Aquatic chemical kinetics*, W. Stumm (ed.). New York: Wiley-Interscience, pp. 235–57.
- Quinn, J.A. & Otto, N.C. 1971. Carbon dioxide exchange at the air-sea interface: flux augmentation by chemical reaction. *Journal of Geophysical Research* **76**(6), 1539–49.
- Ramage, C.S. 1987. Secular change in reported surface wind speeds over the ocean. *American Meteorological Society* **26**, 525–8.
- Rees, A.P., Owens, N.J.P. & Upstill-Goddard, R.C. 1997. Nitrous oxide in the Bellingshausen Sea and Drake Passage. *Journal of Geophysical Research, Oceans* **102**(C2), 3383–91.
- Reichardt, H. 1951. Vollständige Darstellung der turbulenten Geschwindigkeitsverteilung in glatten Leitungen. *Zeitschrift Angewandter Mathematik und Mechanik* **31**, 208–19.
- Roberts, P.V. 1984. Dependence of oxygen transfer rate on energy dissipation during surface aeration and in stream flow. In *Gas transfer at water surfaces*, W. Brutsaert & G.H. Jirka (eds). Dordrecht, The Netherlands: D. Reidel Publishing, 347–55.
- Robertson, J.E. & Watson, A.J. 1992. Thermal skin effect of the surface ocean and its implications for CO₂ uptake. *Nature* **358**, 738–40.
- Robinson, I.S., Wells, N.C. & Charnock, H. 1984. The sea-surface thermal-boundary layer and its relevance to the measurement of sea-surface temperature by airborne and spaceborne radiometers. *International Journal of Remote Sensing* **5**(1), 19–45.
- Roether, W. & Kromer, B. 1984. In *Gas transfer at water surfaces*, W. Brutsaert & G.H. Jirka (eds). Dordrecht, The Netherlands: D. Reidel Publishing, 447–57.
- Romano, J.C. 1996. Sea-surface slick occurrence in the open sea (Mediterranean, Red-Sea, Indian-Ocean) in relation to wind-speed. *Deep-Sea Research Part 1—Oceanographic Research Papers* **43**(4), 411–23.

- Saltzman, E.S., King, D.B., Holmen, K. & Leck, C. 1993. Experimental determination of the diffusion coefficient of dimethylsulfide in water. *Journal of Geophysical Research* **98**, 16481–4.
- Sarmiento, J.L., Hughes, T.M.C., Stouffer, R.J. & Manabe, S. 1998. Simulated response of the ocean carbon cycle to anthropogenic climate warming. *Nature* **393**, 245–9.
- Sarmiento, J.L., Le Quere, C. & Pacala, S.W. 1995. Limiting future atmospheric carbon dioxide. *Global Biogeochemical Cycles* **9**, 121–38.
- Sarmiento, J.L. & Sundquist, E.T. 1992. Revised budget for the oceanic uptake of anthropogenic carbon dioxide. *Nature* **356**, 589–93.
- Schimmel, D.S. 1998. The carbon equation. *Nature* **393**, 208–9.
- Schimmel, D.S., Alves, D., Enting, I., Heimann, M., Joos, F., Raynaud, D., Wigley, T., Prather, M., Derwent, R., Enhalt, D., Fraser, P., Sanhueza, E., Zhou, X., Jonas, P., Charlson, R., Rodhe, H., Sadasivan, S., Shine, K.P., Fouquart, Y., Ramaswamy, V., Solomon, S., Srinivasan, J., Albritton, D., Derwent, R., Isaksen, I., Lal, M. & Wuebbles, D. 1996. *Climate Change 1994*, J.T.Houghton et al. (eds). Cambridge: Cambridge University Press, 65–131.
- Schluessel, P., Emery, W.J., Grassl, H. & Mammen, T. 1990. On the bulk-skin temperature difference and its impact on satellite remote sensing of sea surface temperature. *Journal of Geophysical Research* **95**(C8), 13341–56.
- Schmitt, K.F., Friehe, C.A. & Gibson, C.H. 1978. Humidity sensitivity of atmospheric temperature sensors by salt contamination. *Journal of Physical Oceanography* **8**, 141–61.
- Schwartz, S.E. 1988. Are global cloud albedo and climate controlled by marine-phytoplankton. *Nature* **336**, 441–5.
- Schwartz, S.E. 1989. Sulfate aerosols and climate. *Nature* **340**, 515–16.
- Scott, J.C. 1975. The preparation of water for surface-clean fluid mechanics. *Journal of Fluid Mechanics* **69**, 339–51.
- Scully-Power, P. 1986. *Navy oceanographer shuttle observations, mission report*. Report STSS 41-G, NUSC Technical Document 7611. Newport, R.I. Naval Underwater Systems Center 2.2, 5.3.
- Sharp, J.H. 1977. Excretion of organic matter by phytoplankton: do healthy cells do it? *Limnology and Oceanography* **22**, 381–99.
- Shatky, M. & Ronen, D. 1992. Bubble populations and gas exchange in hypersaline solutions: a preliminary study. *Journal of Geophysical Research* **97**(C5), 7361–72.
- Sieburth, J.M. 1971. Distribution and activity of oceanic bacteria. *Deep-Sea Research* **18**, 1111–21.
- Sieburth, J.M., Willis, P.-J., Johnson, K.M., Burney, C.M., Lavoie, D.M., Hinga, K.R., Caron, D.A. & French III, F.W. 1976. Dissolved organic matter and heterotrophic microneuston in the surface microlayers of the North Atlantic. *Science* **194**, 1415–18.
- Siegenthaler, U. & Sarmiento, J.L. 1993. Atmospheric carbon dioxide and the ocean. *Nature* **365**, 119–25.
- Siems, W. 1980. *Modeluntersuchungen zur Verdunstung und zum Gasaustausch zwischen Wassae und Luft: der Einfluss von Wellen und Oberflächenverunreinigungen*. PhD thesis, University of Hamburg, Germany.
- Smethie, W.M., Takahashi, T. & Chipman, D.W. 1985. Gas exchange and CO₂ flux in the tropical Atlantic Ocean determined from ²²²Rn and pCO₂ measurements. *Journal of Geophysical Research* **90**(C4), 7005–22.
- Smith, J.H., Bomberger, D.C. & Haynes, D.L. 1980. Prediction of the volatilization rates of high-volatility chemicals from natural water bodies. *Environmental Science and Technology* **14**, 1332–7.
- Smith, S.D., Anderson, R.J., Jones, E.P., Desjardins, R.L., Moore, R.M., Hertzman, O. & Johnson, B.D. 1991. A new measurement of CO eddy flux in the nearshore atmospheric surface layer. *Journal of Geophysical Research* **96**, 8881–7.
- Smith, S.D., Fairall, C.W., Geernaert, G.L. & Hasse, L. 1996. Air-sea fluxes: 25 years of progress. *Boundary-Layer Meteorology* **78**, 247–90.
- Smith, S.D. & Jones, E.P. 1986. Isotopic and micrometeorological ocean CO₂ fluxes—different time and space scales. *Journal of Geophysical Research—Oceans* **91**(C9), 529–32.
- Smith, S.V. 1985. Physical, chemical and biological characteristics of CO₂ flux across the air-water interface. *Plant Cell Environment* **8**, 387–98.
- Stauffer, R.E. 1980. Windpower time series above a temperate lake. *Limnology and Oceanography* **25**, 513–28.

- Suijlen, J.M. & Buyse, J.J. 1994. Potentials of photolytic rhodamine Wt as a large-scale water tracer assessed in a long-term experiment in the Loosdrecht Lakes. *Limnology and Oceanography* **39**(6), 1411–23.
- Takahashi, T. 1989. The carbon dioxide puzzle. *Oceanus* **32**, 22–9.
- Talbot, J.W. & Talbot, G.A. 1974. Diffusion in shallow seas and in English coastal and estuarine waters. *Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer* **167**, 93–110.
- Tans, P.P., Fung, I.Y. & Takahashi, T. 1990. Observational constraints on the global atmospheric CO₂ budget. *Science* **247**, 1431–8.
- Taylor, P.K., Kent, E.C., Yelland, M.J. & Moat, B.I. 1995. The accuracy of wind observations from ships. In *The International comprehensive ocean-atmosphere data set winds workshop*, Kiel, Germany, 31 May to 2 June 1994, Boulder, Colorado: Environmental Research Laboratories, National Oceanic and Atmosphere Administration, 132–55.
- Thorpe, S.A. 1982. On the cloud of bubbles formed by breaking wind-waves in deep water, and their role in air-sea gas transfer. *Philosophical Transactions of the Royal Society of London* **304**, 155–210.
- Torgersen, T., Mathieu, G., Hesslein, R.H. & Broecker, W.S. 1982. Gas-exchange dependency on diffusion-coefficient—direct Rn-222 and He-3 comparisons in a small lake. *Journal of Geophysical Research-Oceans and Atmospheres* **87**(C1), 546–56.
- Turner, S.M., Malin, G., Liss, P.S., Harbour, D.S. & Holligan, P.M. 1988. The seasonal variation of dimethyl sulfide and dimethylsulfoniopropionate concentrations in nearshore waters. *Limnology and Oceanography* **33**(3), 364–75.
- Turner, S.M., Malin, G., Nightingale, P.D. & Liss, P.S. 1996. Seasonal variation of dimethyl sulfide in the North Sea and an assessment of fluxes to the atmosphere. *Marine Chemistry* **54**(3–4), 245–62.
- Uher, G. & Andreae, M.O. 1997. The diel cycle of carbonyl sulfide in marine surface waters: field study results and a simple model. *Aquatic Geochemistry* **2**, 313–44.
- Upstill-Goddard, R.C. & Brown R.H. 1996. Invasive and evasive transfer velocities of N₂O in a laboratory gas exchange tank: significant differences observed. Internal Report, Department of Marine Sciences and Coastal Management, University of Newcastle, Newcastle upon Tyne, 12 pp.
- Upstill-Goddard, R.C., Nightingale P.D. & Malin G. 1997. Sea-air transfer velocities in the southern North Sea measured with volatile and conservative tracers: first results from the ASGAMAGE experiment, October 1996. *Annales Geophysicae Part II, Supplement. II*, **15**. European Geophysical Society, The Hague, Netherlands.
- Upstill-Goddard, R.C., Watson, A.J., Liss, P.S. & Liddicoat, M.I. 1990. Gas transfer velocities in lakes measured with SF₆. *Tellus* **42B**, 364–77.
- Upstill-Goddard R.C., Watson, A.J., Wood, J. & Liddicoat, M.I. 1991. Sulphur hexafluoride and helium-3 as sea-water tracers: deployment techniques and continuous underway analysis for sulphur hexafluoride. *Analytica Chimica Acta* **249**, 555–62.
- Vagle, S. & Farmer, D.M. 1992. The measurement of bubble-size distributions by acoustic backscatter. *Journal of Atmospheric and Oceanic Technology* **9**, 630–44.
- Van Scoy, K.A., Morris, K.P., Robertson, J.E. & Watson, A.J. 1995. Thermal skin effect and the air-sea flux of carbon dioxide: a seasonal high-resolution estimate. *Global Biogeochemical Cycles* **9**(2), 253–62.
- Vojvodic, V. & Cosovic, B. 1996. Fractionation of surface active substances on the XAD-8 Resin—Adriatic Sea samples. *Marine Chemistry* **54**(1), 119–33.
- Wallace, D.W.R. & Wirick, C.D. 1992. Large air-sea gas fluxes associated with breaking waves. *Nature* **356**, 694–6.
- Walsh, A.L. & Mulhearn, P.J. 1987. Photographic measurements of bubble populations from breaking wind waves at sea. *Journal of Geophysical Research* **92**, 14553–65.
- Wanninkhof, R. 1992. Relationship between wind speed and gas exchange over the ocean. *Journal of Geophysical Research* **97**(C5), 7373–82.
- Wanninkhof, R., Asher, W., Weppernig, R., Chen, H., Schlosser, P., Langdon, C. & Sambrotto, R. 1993. Gas transfer experiment on Georges Bank using two volatile deliberate tracers. *Journal of Geophysical Research* **98**(C11), 20237–48.

- Wanninkhof, R., Hitchcock, G., Wiseman, W.J., Vargo, G., Ortner, P.B., Asher, W., Ho, D.T., Schlosser, P., Dickson, M.L., Masserini, R., Fanning, K. & Zhang, J.Z. 1997. Gas exchange, dispersion and biological productivity on the west Florida Shelf: results from a Lagrangian tracer study. *Geophysical Research Letters* **24**(14), 1767–70.
- Wanninkhof, R., Ledwell, J.R. & Broecker, W.S. 1985. Gas exchange-wind speed relation measured with sulphur hexafluoride on a lake. *Science* **227**, 1224–6.
- Wanninkhof, R., Ledwell, J.R. & Broecker, W.S. 1987. Gas exchange on Mono lake and Crowley lake, California. *Journal of Geophysical Research* **92**(C13), 14567–80.
- Wanninkhof, R., Ledwell, J.R. & Watson, A.J. 1991. Analysis of sulphur hexafluoride in seawater. *Journal of Geophysical Research* **96**(C5), 8733–40.
- Wanninkhof, R.H. 1986. *Gas exchange across the air-water interface determined with man made and natural tracers*. PhD thesis, Columbia University, New York.
- Wanninkhof, R.H. & Bliven, L.F. 1991. Relationship between gas exchange, wind speed, and radar backscatter in a large wind-wave tank. *Journal of Geophysical Research* **96**(C2), 2785–96.
- Wanninkhof, R.H. & Knox, M. 1996. Chemical enhancement of CO₂ exchange in natural waters. *Limnology and Oceanography* **41**(4), 689–97.
- Watson, A.J. & Ledwell, J.R. 1988. Purposefully released tracers. *Philosophical Transactions of the Royal Society of London, Series A—Mathematical Physical and Engineering Sciences* **325**(1583), 189–200.
- Watson, A.J., Upstill-Goddard, R.C. & Liss, P.S. 1991. Air-sea exchange in rough and stormy seas measured by a dual-tracer technique. *Nature* **349**, 145–7.
- Watts, P.D., Allen, M.R. & Nightingale, T.J. 1996. Wind speed effects on sea surface emission and reflection for the Along Track Scanning Radiometer. *Journal of Atmospheric and Oceanic Technology* **13**(1), 126–41.
- Webb, E.K., Pearman, G.I. & Leuning, R. 1980. Correction of flux measurements for density effects due to heat and water vapour transfer. *Quarterly Journal of the Royal Meteorology Society* **106**, 85–100.
- Wesely, M.L. 1986. Response to “Isotopic versus micrometeorological ocean CO₂ fluxes: a serious conflict” by W.Broecker et al. *Journal of Geophysical Research* **91**(C9), 10533–5.
- Whitman, W.G. 1923. A preliminary experimental confirmation of the two-film theory of gas absorption. It seems to explain satisfactorily the well-recognized differences of absorption rate for varying concentrations. *Chemical and Metallic Engineering* **29**, 146–8.
- Wigley, T.M.L. 1989. Possible climate change due to SO₂-derived cloud condensation nuclei. *Nature* **339**, 365–7.
- Wilke, C.R. & Chang, P. 1955. Correlation of diffusion coefficients in dilute solutions. *Journal of the American Institute of Chemical Engineers* **1**, 264–70.
- Williams, P.M., Carlucci, A.F., Henrichs, S.M., Vanleet, E.S., Horrigan, S.G., Reid, F.M.H. & Robertson, K.J. 1986. Chemical and microbiological studies of sea-surface films in the southern Gulf of California and off the west-coast of Baja-California. *Marine Chemistry* **19**(1), 17–98.
- Witting, J. 1971. Effects of plane progressive irrotational waves on thermal boundary layers. *Journal of Fluid Mechanics* **68**, 49–70.
- Wong, C.S. & Chan Y.-H. 1991. Temporal variations in the partial pressure and flux of CO at ocean station P in the subarctic northeast Pacific Ocean. *Tellus* **43B**, 206–23.
- Wong, C.S., Chan, Y.-H. & Page, J.S. 1995. Geographical, seasonal and interannual variations of air-sea CO₂ exchange in the subtropical Pacific surface waters during 1983–1988 (ii). Air-sea CO₂ fluxes with skin-temperature adjustments. *Tellus* **47B**, 431–46.
- Woolf, D. 1997. Bubbles and their role in air-sea gas exchange. In *The sea surface and global change*, P.S.Liss & R.A.Duce (eds). Cambridge: Cambridge University Press, 173–205.
- Woolf, D.K. 1993. Bubbles and the air-sea transfer velocity of gases. *Atmosphere-Ocean* **31**(4), 517–40.
- Woolf, D.K. & Thorpe, S.A. 1991. Bubbles and the air-sea exchange of gases in near-saturation conditions. *Journal of Marine Research* **49**, 435–66.
- Wyngaard, J.C. 1990. Scalar fluxes in the planetary boundary-layer—theory, modeling, and measurement. *Boundary-Layer Meteorology* **50**(1–4), 49–75.
- Zhou, X.L. & Mopper, K. 1997. Photochemical production of low-molecular-weight carbonyl compounds in seawater and surface microlayer and their air-sea exchange. *Marine Chemistry* **56**, 201–13.

THE ROLE OF BENTHIC MICROALGAE IN NERITIC ECOSYSTEMS

LAWRENCE B.CAHOON

*Department of Biological Sciences and
Center for Marine Science Research,
University of North Carolina at Wilmington,
Wilmington, NC, USA 28403*

Abstract Benthic microalgae include pennate and centric diatoms, cyanobacteria, chlorophytes, and other microscopic algae living at the sediment/water interface in neritic ecosystems. Increasingly, numerous studies have now documented microalgal production, biomass, and other aspects of their ecology in much of the world's neritic habitats, although substantial gaps in the geographical and depth distributions of these studies remain. Analysis of 85 studies of benthic microalgal production yields a global estimate of annual benthic microalgal productivity of about 500 million tons of carbon, somewhat higher than previous estimates. Information on the depth distribution and compensation light intensity for benthic microalgae suggests that in many areas productive benthic microalgae extend to depths well below those where they have been studied.

The high biomass concentrations attained by benthic microalgae at the sediment/water interface reflect a variety of adaptations and selective advantages likely to result from those adaptations. Stabilization of the sediment surface by microalgal growth and extrapolymeric substance production is an important feature of the ecology of benthic microalgae. Regulation of nutrient fluxes, gas exchange, and redox conditions may result from microalgal stabilization of the sediments and create conditions more favourable to microalgal growth. Grazing and physical perturbations can act to disrupt the stabilizing effects of microalgal growth on the sediment surface. These ideas are presented as a new paradigm that proposes a key role for benthic microalgae in neritic ecosystems along a spectrum of light limitation and physical disturbance.

Introduction

Benthic microalgae, also termed "microphytobenthos", have received increasing attention from marine scientists in recent decades as the potential importance of these somewhat cryptic primary producers has been recognized. Phytoplankton, marsh grasses, and macroalgae have been much more extensively studied worldwide, with the result that their basic ecology, global productivity, and trophic significance are much more thoroughly understood and quantified. However, recognition of the importance of sediment/water interactions coupled with development of techniques suitable for measurements of properties and processes at the interface have led to much greater knowledge of the roles of benthic microalgae in neritic ecosystems. This review will attempt to summarize major portions of that knowledge and to synthesize that knowledge into a new paradigm emphasizing the important functions mediated by benthic microalgae in neritic habitats, particularly continental shelf ecosystems.

Previous reviews

Early reviews of benthic microalgal ecology focused primarily on the taxonomy and distribution of benthic and littoral zone diatoms. Round (1971) distinguished supratidal, intertidal, subtidal, estuarine, and cryophilic biotopes for benthic diatoms. He also characterized the substratum affinities of diatoms as epilithic (on rock substrata), epipelagic (on mud), epipsammic (on sand), endopelagic (inside sediment), endolithic (inside rock), epiphytic (on macrophytes), epizooic (on animals), and psychrophilic (on ice). Although there was already an extensive literature on the taxonomy of benthic diatoms at that time, comparatively little was known about the depth distribution, productivity, or biomass of benthic diatoms. This paucity of information reflected methodological limitations as well as the limited appreciation at that time for the potential importance of benthic microalgae. A subsequent review of marine littoral diatoms by McIntire & Moore (1977) similarly focused on the taxonomy and distribution of various diatom assemblages. This review presented results of several studies of benthic microalgal production, but these were mostly limited to estuarine and intertidal habitats, e.g. Pomeroy (1959), Grøntved (1960), Pamatmat (1968), Steele & Baird (1968). Admiraal (1984) reviewed the ecology of estuarine benthic diatoms from the standpoint of both field studies, particularly in northeast Europe, and laboratory investigations. This review briefly considered some of the same issues as previous reviews, such as diatom life modes and interactions with sediment characteristics, but also examined the state of knowledge about the physiology and ecology of benthic diatoms. Potentially limiting factors in the estuarine environment include insufficient or excessive light flux, extremes of temperature and salinity, nutrient limitation, exposure to toxic compounds, grazing, competition for space, and interference competition among diatoms.

Admiraal (1984) also reviewed production methodologies, including *in situ* bell jar techniques employing measurements of changes in dissolved oxygen concentration or ^{14}C uptake, similar measurements made on sediment-water slurries, or microelectrode measurements of dissolved oxygen and/or carbon dioxide gradients across the sediment/water interface. Each technique offers certain advantages but each has limitations that make adoption of a single standard technique difficult and comparisons of production estimates from different studies problematic. One of the clear points from this review is the relative lack of data sufficient to provide a synthetic overview of the role of benthic microalgae in estuarine systems in comparison with the amount of data and level of understanding then available in the area of phytoplankton ecology.

MacIntyre et al. (1996) and Miller et al. (1996) provide the most comprehensive recent overviews of benthic microalgal ecology. A considerable body of work was published in the interval between the review by Admiraal (1984) and these reviews. MacIntyre et al. (1996) focused on microphytobenthic biomass, production, and response to light. Although the methods used to estimate microalgal biomass and production are not standardized and have given somewhat variable results, the body of evidence is now sufficient to support the view that benthic microalgal biomass and production frequently equal or exceed the biomass and production of phytoplankton in the overlying water-column, at least in shallow habitats. Benthic microalgae frequently form mats at the sediment/water interface, but vertical migration, physical disturbance, and bioturbation can distribute viable microalgae to depths well below the photic zone in the sediments. Microalgal biomass distributions are also very patchy on horizontal scales of centimetres to metres, complicating efforts to sample them representatively. Microalgal production (P) can be expressed as a function of biomass (chlorophyll *a*) and incident light flux (I), but variation in P versus I relationships

occurs on both spatial and temporal scales. Miller et al. (1996) examined the ability of benthic microalgae to enhance sediment cohesion via secretion of mucus, which reduces erodibility and alters activities by micro-, meio- and macrobenthos. A considerable body of work illustrates the trophic significance of benthic microalgae as major producers and food sources of generally high quality for benthic deposit feeders and, via resuspension, for suspension feeders. However, the principle focus of these reviews is on very shallow-water habitats, where benthic microalgae are undeniably important, and they do not attempt to make broader comparisons with other primary producers and habitats.

Microalgal taxonomic composition

Diatoms, particularly pennate diatoms, are clearly the most important benthic microalgal taxa in most circumstances. Diatoms also preserve well and the techniques used to prepare them for identification generally damage cells of other taxa beyond recognition. Consequently, diatoms are the most well-studied members of the benthic microalgae. The diatom species compositions of a number of neritic habitats have now been described, including the littoral zone near Beaufort, North Carolina, USA (Hustedt 1955), the littoral zone in Long Island Sound, New York, USA (Burkholder et al. 1965), an intertidal sand flat in Barnstable Harbor, Massachusetts, USA (Round 1979), Manukau Harbour estuary in New Zealand (Wilkinson 1981), the Brittany coast of France (Riaux 1983), the estuarine Pettaquamscutt River in Rhode Island, USA (Kennett & Hargraves 1984), San Francisco Bay, USA (Laws 1988), the Westerschelde estuary in the Netherlands (Sabbe & Vyverman 1991), the Brazilian coast (Garcia-Baptista & Baptista 1992), and the North Carolina continental shelf (Cahoon & Laws 1993). The dominant members of these assemblages have been pennate diatoms, frequently including members of the genera *Amphora*, *Cocconeis*, *Diploneis*, *Navicula*, and *Nitzschia*, and many others. A variety of centric diatoms are also frequently found in benthic assemblages, including some that are likely to have settled from the plankton and some that are more closely associated with the benthos but are frequently resuspended (so-called “tychopelagic” forms, Bold & Wynne 1985).

A number of other taxa can be important members of the benthic microalgae, however, and their presence may signal other interesting and important aspects of this community. These taxa have been identified by direct microscopy and, more recently, by high performance liquid chromatography (HPLC) pigment analyses. Microscopic analyses of sediments have shown the presence, in addition to that of various diatoms, of cyanobacteria (Burkholder et al. 1965, Meadows & Anderson 1968, Sournia 1976a, Asmus 1982, Zedler 1982, Hackney et al. 1989, Garcia-Baptista & Baptista 1992), chlorophytes (Zedler 1982, Hackney et al. 1989, Garcia-Baptista & Baptista 1992), dinoflagellates (Burkholder et al. 1965, Garcia-Baptista & Baptista 1992), and euglenoids (Burkholder et al. 1965, Garcia-Baptista & Baptista 1992). A special assemblage, so called “turf algae” associated with the flats around coral reefs, includes diatoms and cyanobacteria, as well as generally microscopic, filamentous chlorophytes, phaeophytes, and rhodophytes (Hackney et al. 1989). HPLC analyses of pigments extracted from intertidal and subtidal sediments have also shown the presence of pigment markers for diatoms, cyanobacteria, chlorophytes, and euglenoids (Klein & Riaux-Gobin 1991, Cariou-Le Gall & Blanchard 1995, Brotas & Plante-Cuny 1996). The presence of these other taxa suggests that in addition to the production, oxygen flux, and nutrient uptake associated with all microalgae, nitrogen fixation by cyanobacteria and heterotrophic uptake of organic material by many taxa might also be significant interface processes when these taxa are important members of the benthic microalgae.

A number of studies have now established that the importance of benthic microalgal production and biomass extends into continental shelf and other subtidal, neritic ecosystems, e.g. Plante-Cuny (1978), Cahoon & Cooke (1992). Consequently there is a need to evaluate the magnitude and distribution of benthic microalgal production and biomass in these ecosystems and to consider the broader implications of this evaluation.

Neritic ecosystems

Continental shelves and other neritic ecosystems represent a relatively small but ecologically important proportion of the total area of the oceans. Using a depth of 200 m as a lower limit for the extent of neritic ecosystems, Sverdrup et al. (1962) calculate that 7.6% of all the ocean area may be considered neritic habitat. A large portion of this habitat represents “adjoining seas”, generally shallow coastal seas, such as Hudson Bay and the South China Sea (Fig. 1, p. 61), but also includes shallow areas around islands and archipelagos. Menard & Smith (1966) also quantified the hypsometry of the oceans, calculating that approximately 7.5% of the ocean area (equal to 27.122×10^6 km²) lies at depths less than 200m, and quantifying the distribution of these shallow waters in the various basins (Table 1). Sharp (1988) derived a slightly higher total area, 28.003×10^6 km², for major neritic areas of the world ocean.

Continental shelves and other neritic ecosystems are disproportionately productive in comparison with their area. Estimates of phytoplankton production in shelf or “coastal” habitats have been generated by a number of approaches but are well within an order of magnitude (Table 2). Most of the earlier estimates, i.e. those of Wollast & Billen (1981), Walsh (1984), Cushing (1988), Sharp (1988) and Wollast (1991) rely on numerous ¹⁴C production estimates, most of them with values obtained before about 1980 and therefore likely to be underestimates, owing to the subsequent adoption of more accurate “clean”

Table 1 Areas (10^6 km²) of major oceans and adjoining seas with depth <200 m; data from Menard & Smith (1966).

Basin	Area
Atlantic	6.080
Gulf of Mexico/Caribbean	1.021
Mediterranean	0.513
Black Sea	0.177
Baltic Sea	0.381
Arctic	5.771
Indian	2.622
Red Sea	0.188
Persian Gulf	0.238
Pacific	2.712
Bering Sea	1.050
East Asia	1.583
Gulf of California	0.071
SE Asia-Australia	4.715

Table 2 Estimates of total neritic zone (depth 0–200 m) production by phytoplankton.

g C m ⁻² yr ⁻¹	Production		Method	References
	Gt C yr ⁻¹			
220	5.94 ^a		¹⁴ C	Wollast & Billen 1981
200	5.4 ^a		¹⁴ C	Walsh 1984
250	9.0		clean ¹⁴ C	Martin et al. 1987
129	3.494		¹⁴ C	Cushing 1988**
92–275	4.4		¹⁴ C	Sharp 1988
–	6.9		¹⁴ C	Wollast 1991
238–385	8.9–14.4		CZCS/Chla	Longhurst et al. 1995

^a cited in Wollast (1991).

* calculated by averaging reported productivity values for each of the neritic sub-basins identified by Menard & Smith (1966) and computing an area-weighted average.

techniques (Martin et al. 1987). Longhurst et al. (1995) used an entirely different approach (remote sensing of chlorophyll and use of pigment-light-productivity algorithms to calculate production) and obtained estimates very similar to those generated by the “clean” ¹⁴C method. The global productivity estimates of Martin et al. (1987) and Longhurst et al. (1995), of about 9 and a range of 8.9–14.4 Gt C m⁻² yr⁻¹ (Gt=10⁹), respectively, represent approximately 20% of estimated global ocean productivity (about 50 Gt C m⁻² yr⁻¹ in each case). However, none of these estimates takes into account the contribution to total neritic production of benthic microalgae.

Several reviews have attempted to estimate the contribution of benthic microalgal production to total oceanic production. Plante-Cuny (1984) reviewed results of 32 studies of benthic microalgal production. Nine of these studies were done in tropical areas. Of these, two were done in intertidal habitats, two extended to depths greater than 20 m, and the rest were done in relatively shallow subtidal waters. Essentially all of them were done in close proximity to coral reef habitats, and several were studies of the portion of total reef production attributable to benthic microalgal production. The other 23 studies reviewed by Plante-Cuny (1984) were from temperate and polar ecosystems. Sixteen of these were conducted in the intertidal zone or at depths less than 5 m, with 18 m the deepest depth studied. All of them were done in Europe or North America, with only one at a latitude higher than 60°N. In summary, the information presented in this review about production in tropical habitats, where high light flux and year-long production should drive high annual rates of production, is very limited and does not adequately represent production at deeper depths or in habitats other than coral reefs. The information presented about production in other ecosystems is also very limited in geographical and depth distribution. Consequently, although reasonable inferences about the potential global significance of benthic microalgal production may be drawn from this review, it is difficult to make quantitative comparisons.

Charpy-Roubaud & Sournia (1990) produced a more comprehensive assessment of oceanic productivity that included the contributions of benthic microalgae as well as phytoplankton and benthic macroalgae, although they did not provide a detailed review of the literature on benthic microalgal production. They recognized the limitations of geographical coverage and depth distribution of measurements of benthic microalgal

production described above. Furthermore, they discussed the differences in methodologies used to measure benthic microalgal production and the variability in results that may arise, at least in part, from those methodological differences. Given these constraints, they identified a pattern of generally higher benthic microalgal production in tropical ecosystems with somewhat lower values in temperate regions and much lower in polar regions, although they included production by ice algae in their assessment of polar production by benthic microalgae. They also included production in intertidal areas, which they considered generally higher than in subtidal habitats, and derived a very approximate estimate of annual benthic microalgal production at $50 \text{ g C m}^{-2} \text{ yr}^{-1}$ for a depth range of 0–50 m. Using Menard & Smith's (1966) estimate of $27.122 \times 10^6 \text{ km}^2$ for total shelf area at depths of 0–200 m and assuming that one-fourth of this area (50 m/200 m) supports benthic production, this estimate yields a global production figure of approximately $0.34 \text{ Gt C yr}^{-1}$. If accurate, this figure would represent about 0.7% of total global oceanic production and 2.4–3.7% of the continental shelf production estimated by Martin et al. (1987) and Longhurst et al. (1995). Two significant points derive from these estimates. First, these production estimates represent production not measured or calculated by any of the techniques or methods previously used to derive the estimates of global and shelf production discussed above or in Table 2. Thus, benthic microalgal production in shelf habitats is additional production not previously included in global estimates of carbon or nutrient fluxes. Secondly, the concentration of benthic microalgal production at the sediment/water interface potentially presents very different ecological consequences than production by phytoplankton or benthic macroalgae. These consequences include physical alteration of the sediment/water interface, effects on nutrient fluxes and other biogeochemical processes, and constraints for grazers.

The aim of this review is to evaluate benthic microalgal production in neritic, especially continental shelf, ecosystems in a more rigorous quantitative context. *A priori*, some of the same limitations of earlier attempts to review this subject must be conceded, such as temporal and spatial limitations of sampling efforts, variability in the methodologies used, and the comparability of many different studies. Two approaches are used here to circumvent these difficulties. First, I have sought to find as complete a set of relevant studies as possible to maximize spatial coverage and give the highest confidence in the resulting estimates. Secondly, I use three different approaches to attempt to define the likely extent and magnitude of benthic microalgal production in neritic habitats. I begin by examining the information available on measurements of benthic microalgal production in both intertidal and subtidal habitats. This is a useful comparison in that it defines some of the biases in the existing dataset and provides the most direct estimate of average production rates, although coverage is still terribly sparse in comparison with measures of phytoplankton production. I then consider studies measuring the quantity and depth distribution of benthic microalgal biomass in subtidal habitats in order to define the depth distribution, i.e. the likely zone of benthic microalgal production, in neritic ecosystems. Biomass can be a useful proxy for the distribution of production, although there are also methodological limitations to this approach. Next, I consider the relationships between benthic microalgal production and light flux derived in both field and laboratory studies in order to determine the approximate light-depth zone in which benthic microalgal production might occur.

The significance of benthic microalgal production must also be viewed in a context broader than the magnitude and distribution of productivity and biomass. Benthic microalgae can have significant effects on the sediment/water interface and processes across that interface. Therefore, I consider the effects benthic microalgae have on the physical properties

of the interface, on nutrient fluxes across the interface, on biogeochemical processes in the interface zone, and on grazing. This review concludes by offering a new paradigm that synthesizes the role of benthic microalgae in continental shelf ecosystems.

Benthic microalgal production

A variety of approaches have been used to measure benthic microalgal production. Some of the variability in approaches derives from logistical constraints, such as limitations on the use of radioisotopes in the field, but some of it derives from the physical constraints posed by working at the sediment/water interface. One consequence of these physical constraints has been the tendency for many of the studies of benthic microalgal production to be conducted in shallow subtidal or intertidal habitats. As a result, datasets on benthic microalgal production have always been biased towards under-representation of deeper habitats. Another effect of these constraints has been the frequent practice of measuring productivity in sediment samples collected in the field and returned to the laboratory. It is highly likely that this approach introduces artifacts of light quality, pore-water quality, nutrient flux, and microscale perturbations of the sediment/water interface (Varela 1985). However, differences among habitats studied, production measurement techniques, and the microalgal communities themselves confound attempts to resolve the significance of these artifacts.

There is no standard method for measuring benthic microalgal production, unlike the situation with measurement of phytoplankton production, in which there are generally recognized procedures and cautions to apply (Fitzwater et al. 1982, Marra & Heinemann 1984). Most studies quantifying benthic microalgal production have used some variant on the light-dark chamber method and measurements of either dissolved oxygen flux or uptake of ^{14}C -labelled substratum. There are several constraints that apply to any of these methods: the need for adequate replication to address the patchy distribution of benthic microalgae, the effects of perturbation during *in situ* chamber placement or core sample retrieval, artifacts introduced by stirring in chambers (Cahoon 1988, Huettel & Gust 1992), and incubation time artifacts. Some of the earlier production studies, e.g. Grøntved (1960, 1962), first slurried their sediment samples, then incubated them, probably inducing higher production values than under true *in situ* conditions.

Benthic microalgal biomass and production rates are frequently high enough that oxygen measurements are adequately sensitive to yield significant differences in light- and dark-chamber incubations under submerged but not subaerial conditions. Oxygen flux measurements permit calculation of gross and net production, although "net" production estimates are really measures of total sediment community activity. The development of oxygen electrodes and miniaturization of these has permitted increasingly fine-scale measurement and data retrieval, such that very capable remote benthic lander devices can now be employed (e.g. Jahnke & Christiansen 1989, Cahoon 1996). Oxygen microelectrodes have been employed to study very fine-scale photosynthetic and respiratory oxygen fluxes at the sediment/water interface, although derivation of areal production estimates by these techniques is difficult (Revsbech & Jørgensen 1983).

Radiolabelling techniques, primarily using ^{14}C -labelled compounds, offer several advantages over oxygen exchange methods, including greater sensitivity (although that is not always necessary), ability to conduct subaerial as well as submerged measurements

(Darley et al. 1976), and the ability to use the tracer to quantify excretion and consumption of labelled photosynthate. Drawbacks include the need to introduce uniformly labelled medium throughout the likely production zone across the interface and to establish specific activity of the labelled compound(s) in the sediment/water interface microhabitat, and the inability of radiolabelling techniques to distinguish accurately gross and net production.

A few studies have estimated benthic microalgal production by measuring light flux and microalgal biomass and using P versus I relationships to determine production, e.g. MacIntyre & Cullen (1996). While light flux and biomass measurements pose fewer difficulties than direct productivity measurements, variations in the P versus I relationship across habitat space, over time, and as light exposure histories and photoadaptation responses change, can be problematic.

Given the lack of a standard method for measuring benthic microalgal production, the limitations posed by the methods that have been used over time, and the inherent variability of the sediment/water interface habitat, one might expect estimates of benthic microalgal production to be wildly variable or for the differences to be uninterpretable. However, several direct comparisons of methods have revealed broadly similar results, e.g. Hunding & Hargrave (1973), Revsbech et al. (1981). Furthermore, for the purpose of deriving a reasonable working estimate of global production by benthic microalgae in neritic ecosystems, some degree of variability is tolerable.

Table 3 presents marine benthic microalgal production estimates from 85 studies done in all regions of the world. Wherever possible gross production estimates are reported and calculated, although use of methods other than oxygen flux may yield estimates in between true gross and net production. The studies reported here cover almost 40 years of attempts to measure benthic microalgal production and include measurements made in the waters of every continent and ocean.

Table 4 summarizes the major patterns in the annual production data presented in Table 3 by region and depth range. Shaffer & Onuf (1985) discussed proper methods for deriving daily, monthly and annual estimates of benthic microalgal production, but few of the published studies in Table 3 satisfy the criteria they use for their better estimation methods. Consequently, I use several conservative assumptions (10-h production days, production years of 365, 270, and 90 days in tropical, temperate and polar zones, respectively, and a conservative formula to calculate mean production values from range data) to calculate annual production. Several important conclusions can be derived from these patterns. First, there are some obvious gaps in the geographical and depth coverage, with no data or only a few from some geographical zones and depths. Consequently, large portions of the world's shallow seas, especially in polar areas, are badly under-represented in terms of actual measurements. There is quite clearly a bias towards studies in temperate zones, with 74 of 108 reported depth-location estimates of production from temperate zones, although they are widely distributed within those zones (Fig. 1). This bias probably results from the ease of local access by relatively well funded and numerous investigators from the major industrial countries. Relatively few tropical zone locations have been studied, despite the clearly higher values of benthic microalgal production more frequently found in this zone. Similarly, there are very few measurements of benthic microalgal production at depths greater than 20m. The deepest measurement was made at 60m (Plante-Cuny 1978). This bias probably results from depth-time limitations on SCUBA diving and the lack of remotely operated vehicles or landers for conducting these measurements. Although a general trend of benthic microalgal production declining with depth range is evident in Table 4, the lack of deeper measurements and evidence produced in the next sections of this review suggest

Table 3 Benthic microalgal production estimates reported from intertidal (I) and subtidal locations worldwide (refer to Fig. 1). Estimates are mean (single datum) or range values. Annual production values in parentheses are calculated from reported hourly or daily production values as follows. Reported mean hourly values are multiplied by 10 to yield a daily production estimate. Calculated or reported mean daily values are multiplied by 365 for tropical locations (Tr, 0°–30° N or S), by 270 for temperate locations (Te, 30°–60° N or S), and by 90 for polar locations (Po, 60°–90° N or S). Reported ranges are converted to representative hourly, daily, or yearly values by adding 0.3 times the difference between maximum and minimum values to the minimum value and then following the above calculation procedures as appropriate. “Tech.” refers to basic techniques used to measure production.

Location	Depth m	Production			Location	Tech.	Reference
		mg C m ⁻² h ⁻¹	mg C m ⁻² day ⁻¹	g C m ⁻² yr ⁻¹			
Wadden Sea, Netherlands	I		100–535	115	Te	O ₂ ^a	Asmus 1982
Long Is. Sound, CT, USA	I	3–44		(41)	Te	¹⁴ C ^b	Baillie 1986
Golfe de Fos, France	3.5–4	1.5–36		(32)	Te	O ₂	Barranguet et al. 1994
Golfe de Fos, France	<1			100	Te	O ₂	Barranguet et al. 1996
	9–13			26.5			
Newport Estuary, NC, USA	I		18–204	(20)	Te	¹⁴ C	Bigelow 1977
Golfe de Fos, France	0.5	20		(54)	Te	O ₂	Bodoy & Plante-Cuny 1984
Caribbean	3–64	11.2		(40.9)	Tr	O ₂	Bunt et al. 1972
Long Reef, FL, USA	16	3.7		(13.5)			
Wadden Sea, Netherlands	I			130	Te	¹⁴ C	Cadée 1980
Wadden Sea, Netherlands	I		15–1120	(94)	Te	¹⁴ C	Cadée & Hegeman 1974
Wadden Sea, Netherlands	I			85	Te	¹⁴ C	Cadée & Hegeman 1977
NC Shelf, USA 15–20	15–20	18.7		(50.5)	Te	O ₂	Cahoon & Cooke 1992
	20–30	34.8		(94)			
	30–41	20.6		(55.6)			
Massachusetts Bay, USA	21–28	10.2–21.3		(36)	Te	O ₂	Cahoon et al. 1993
St Croix, Virgin Islands	1.5–2		2000–3000	(840)	Tr	O ₂	Carpenter 1985

Table 3 continued

Location	Depth m	mg C m ⁻² h ⁻¹	Production			Tech.	Reference
			mg C m ⁻² day ⁻¹	g C m ⁻² yr ⁻¹	Location		
Tuamotu Archipelago	0-5		469	(171)	Tr	O ₂	Charpy-Roubaud 1988
	5-10		422	(154)			
	10-15		374	(137)			
	15-20		326	(119)			
	20-25		278	(101)			
	25-30		230	(84)			
	30-35		182	(66)			
35-40		135	(49)				
Ems-Dollard, Netherlands	1	37		(100)	Te	¹⁴ C	Colijn & de Jonge 1984
Sapelo Is., GA, USA	1	6.4-16.0		(25)	Te	¹⁴ C	Darley et al. 1981
Sapelo Is., GA, USA	1	8.6-245		(214)	Te	¹⁴ C	Darley et al. 1976
Netarts Bay, OR, USA	0.5-1.5			(106)	Te	O ₂	Davis & McIntire 1983
Laguna de Terminos, Mexico	0-3.5		200	(73)	Tr	O ₂	Day et al. 1982
McMurdo Sound, Antarctica	18	51.3-95.2		(58)	Po	¹⁴ C	Dayton et al. 1986
Ems Dollard, Netherlands	1			132	Te	O ₂	Van Es 1982
Langebaan Estuary, South Africa	1	17.4-69.5		(7)	Te	¹⁴ C	Fielding et al. 1988
Hokkaido, Japan	1		51	19	Te	I×Chla ^c	Fuji et al. 1991
Salt marsh, DE, USA	1	10-68		(74)	Te	O ₂	Gallagher & Daiber 1974
Øresund, Denmark	1-2		30-1100	(95)	Te	¹⁴ C	Gargas 1970
Smålandshavet, Denmark	1-8		0-1100	(89)	Te	¹⁴ C	Gargas 1972
Danish fjord	0.5		15	15	Te	¹⁴ C	Gargas 1980
	6			5			
Signy Is., S. Orkney Is.	8	13.1-29.2		(16)	Po	¹⁴ C	Gilbert 1991a
Savin Hill Cove MA, USA	1	41-136		(188)	Te	¹⁴ C	Gould & Gallagher 1990

Marennes-Oléron Bay, France	I	36.8–70.7	(127)	Te	O ₂	Gouleau et al. 1994
Nova Scotia, Canada	I	7.15	(19)	Te	O ₂	Grant et al. 1986b
Danish fjords	0.2–2.0	70	(189)	Te	¹⁴ C	Grøntved 1960
Wadden Sea, Denmark	I		(455)	Te	¹⁴ C	Grøntved 1962
Bay of Fundy, Canada	I		(58)	Te	O ₂	Hargrave et al. 1983
La Jolla, CA, USA	18.3	0–512	(414)	Te	O ₂	Hartwig 1978
Barbados	0.3	1030	(3760)	Tr	O ₂	Hawkins & Lewis 1982
Gulf of Trieste, Italy	7	211	(57)	Te	O ₂	Hemdl et al. 1989
	15	149	(40)			
	22	112	(30)			
Gray's Reef, GA, USA	20	22–97	(120)	Te	O ₂	Hopkinson et al. 1991
Beaufort Sea, AK, USA	7	0.01	(9)	Po	¹⁴ C	Horner & Schrader 1982
Long Is. Sound, NY, USA	0–1.8	0.9–8.0	(6.6)	Te	¹⁴ C	Iannuzzi et al. 1996
Georgia Bight, GA, USA	14–40	?			O ₂	Jahnke et al. 1996
Gt. Barrier Reef, Australia	1–7	570–1710	(333)	Tr	O ₂	Johnstone et al. 1990
SW England	I	5–115	143	Te	¹⁴ C	Joint 1978
SC, USA	I		(136)	Te	O ₂	Kelley et al. 1986
Westerschelde, Netherlands	I		(10)	Te	O ₂	Kromkamp et al. 1995
Ythan Estuary, Scotland	I	9–103	(20)	Te	¹⁴ C	Leach 1970
San Antonio Bay, TX, USA	2	0–90	(7.3)	Te	I×Chla	MacIntyre & Cullen 1996
S. New England, USA	I	20.1	(54)	Te	¹⁴ C	Marshall et al. 1971
Chukchi Sea, AK, USA	5	0.5–57	(16)	Po	¹⁴ C	Matheke & Horner 1974
Columbia River OR, USA	I	5–84	72	Te	O ₂	McIntire & Amspoker 1986
Mississippi Sound MS, USA	0–2		339	Te	¹⁴ C	Moncrieff et al. 1992
Great Barrier Reef, Australia	0–1	180–207	(696)	Tr	¹⁴ C/O ₂	Moriarty et al. 1985
Potter's Pond, RI, USA	0.7		150	Te	O ₂	Nowicki & Nixon 1985
False Bay, WA, USA	I		(108)	Te	O ₂	Pamatmat 1968

Table 3 Continued

Location	Depth m	Production			Location	Tech.	Reference
		$\text{mg C m}^{-2} \text{h}^{-1}$	$\text{mg C m}^{-2} \text{day}^{-1}$	$\text{g C m}^{-2} \text{yr}^{-1}$			
North River, SC, USA	I			(135)	Te	O ₂	Pinckney & Zingmark 1993
Côte-d'Ivoire	0-5	22.3		(81)	Tr	O ₂	Plante-Cuny 1977
Nosy-Bé, Madagascar	5	28.5		(104)	Tr	¹⁴ C	Plante-Cuny 1978
	15	23.2		(85)			
	25	11.5		(42)			
	35	4.66		(17)			
	60	3.33		(12)			
Golf de Fos, France	0.5	20		(54)	Te	O ₂	Plante-Cuny & Bodoy 1987
Sapelo Is., Georgia	I		0-578	(47)	Te	O ₂	Pomeroy 1959
Boca Ciega, FL, USA	0-5	0-52		(57)	Tr	O ₂	Pomeroy 1960
Vancouver, BC, Canada	I		170-910	(106)	Te	O ₂	Pomeroy & Stockner 1976
Woods Hole, MA, USA	I	5-75		(70)	Te	¹⁴ C	Van Raalte et al. 1974
Woods Hole, MA, USA	I	1-115		(95)	Te	¹⁴ C	Van Raalte et al. 1976
Bolsa Bay, CA, USA	I	26-59		(97)	Te	¹⁴ C	Riznyk et al. 1978
Chesapeake Bay, VA, USA	I			(234)	Te	O ₂	Rizzo & Wetzel 1985
	0-2			(196)			
AL, USA	1-1.4		220	(20)	Te	¹⁴ C	Schreiber & Pennock 1995
Barataria Bay LA, USA	I		0-1554	(121)	Te	O ₂	Shaffer 1988
S. Cal. lagoon, CA, USA	I	33-99		(143)	Te	O ₂	Shaffer & Onuf 1983
Marshall Is	0-5		800	300	Tr	O ₂	Sorokin 1973
Scott Reefs, Indian Ocean	1-10		1580-2160	(640)	Tr	O ₂	Sorokin 1986

Pacific Islands	1-10	140-352	(74)	Tr		
Vietnam	0-5	1660-8810	(1390)	Tr	O ₂	Sorokin 1990
Tuamotu Is, F. Polynesia	0-1	72-221	(426)	Tr	O ₂	Sourmia 1976b
Moorca, F. Polynesia	0.2-0.8	1100	(402)	Tr	O ₂	Sourmia 1976c
Santos Estuary, Brazil	I	45	(164)	Tr	¹⁴ C	De Souza 1983
Loch Ewe, Scotland	I-8		(5.8)	Te	¹⁴ C	Steele & Baird 1968
Mississippi Sound, MS, USA	I	1.4-163	(63)	Te	¹⁴ C	Sullivan & Moncrieff 1988
Laholm Bay, Sweden	5-8	10-750	7	Te	O ₂	Sundbäck 1986
	10-13		8			
	14-16		15			
	17-18		3.5			
	19-20		1			
Laholm Bay, Sweden	2-5		18.5	Te	¹⁴ C	Sundbäck & Jönsson 1988
Gray's Harbor, WA, USA	I		59	Te	O ₂	Thom 1984
Chapman Cove, WA, USA	I	12-55	(67)	Te	O ₂	Thom et al. 1994
NW Spain	I		79	Te	¹⁴ C	Varela & Penas 1985
Curacao	0-3.5	90-160	(405)	Tr	O ₂	Wanders 1976
Chesapeake Bay, VA, USA	I	1-90	(75)	Te	¹⁴ C	Wendker & Marshall 1993
Manukau Harbour, New Zealand	I		(476)	Te	IRGA ^d	Wilkinson 1981
Tijuana Bay, CA, USA	I		(232)	Te	O ₂	Zedler 1980

^a "O₂" denotes use of an oxygen exchange method to measure benthic microalgal production. Production values are reported in C units as the author(s) calculated them or are calculated from oxygen flux measurements using a conversion equation as follows: C flux=O fluxx0.32.

^b "¹⁴C" denotes use of a radiocarbon labelling technique to measure benthic microalgal production.

^c "¹⁴C/Chl_a" denotes use of the relationship between measures of light intensity, I, and benthic microalgal biomass as chlorophyll *a*, Chl_a, to estimate benthic microalgal production.

^d "IRGA" denotes use of an InfraRed Gas Analyzer to measure fluxes of gaseous carbon dioxide as a measure of benthic microalgal production.

Table 4 Summary of mean (\pm SD) reported and calculated annual benthic microalgal production estimates ($\text{g C m}^{-2} \text{ yr}^{-1}$) from Table 3 by region and depth range.

Region	Intertidal	Depth range m		
		0–5	5–20	>20
Polar (60°–90° N/S)	–	16 $n = 1$	28 \pm 26 $n = 3$	–
Temperate (30°–60° N/S)	111 \pm 99 $n = 41$	87 \pm 90 $n = 17$	62 \pm 116 $n = 12$	54 \pm 29 $n = 4$
Tropical (0°–30° N/S)	164 $n = 1$	576 \pm 894 $n = 17$	102 \pm 56 $n = 5$	53 \pm 33 $n = 7$
Total	$n = 42$	$n = 35$	$n = 20$	$n = 11$

that benthic microalgal production is supported across a greater depth range of shelf habitats than the presented data indicate. Also, production in intertidal habitats is not significantly greater than in shallow (0–5 m) subtidal habitats. Finally, the variability of the estimates is notable. Probable sources of variability include patchiness on all scales of time and space, variability in incident light flux and in P versus I responses, and to some extent the different methodologies employed.

Bearing in mind the limitations and caveats expressed above, I make a tentative calculation of global production by benthic microalgae in neritic habitats. Table 5 presents calculations using weighted average production values for each geographical zone, the area within each basin between 0–200 m, and an assumption that gross production is limited to approximately the top 60 m of that depth range. The results of these calculations derive an estimate of global benthic microalgal production on the order of 0.5 Gt C yr⁻¹. This estimate is about 50% greater than that derived by Charpy-Roubaud & Sournia (1990). However, there are several reasons why this estimate may be conservative. First, limited sampling of benthic production makes it likely that the real magnitude and depth distribution of production have been underestimated. Platt & Harrison (1985) have argued that undersampling tends to underestimate production, although their argument pertains to phytoplankton, which may show relatively more temporally variable productivity compared with benthic microalgae. Secondly, an extension of this argument is that some relatively large areas that ought to support significant benthic microalgal production have rarely or never been studied. For example, I have been unable to find any studies that measured benthic microalgal production in the Persian Gulf, the Red Sea, the eastern Mediterranean, the Black Sea, the East China Sea, the Indonesian seas, or most of the South China Sea, which encompass over $5.5 \times 10^6 \text{ km}^2$, or over 20% of total neritic zone area. Many of these areas are tropical and might be expected to support very high rates of production. Thirdly, the real depth distribution of productive benthic microalgae is unknown. No study has extended to water depths sufficient to define a point of zero gross production. Littler et al. (1985) have documented photosynthetic macroalgae growing at depths well below 200 m, so it is possible that significant benthic microalgal production occurs at depths well below those where it has yet been measured. In the next section of this review I consider information available on the depth distribution of benthic microalgal biomass.

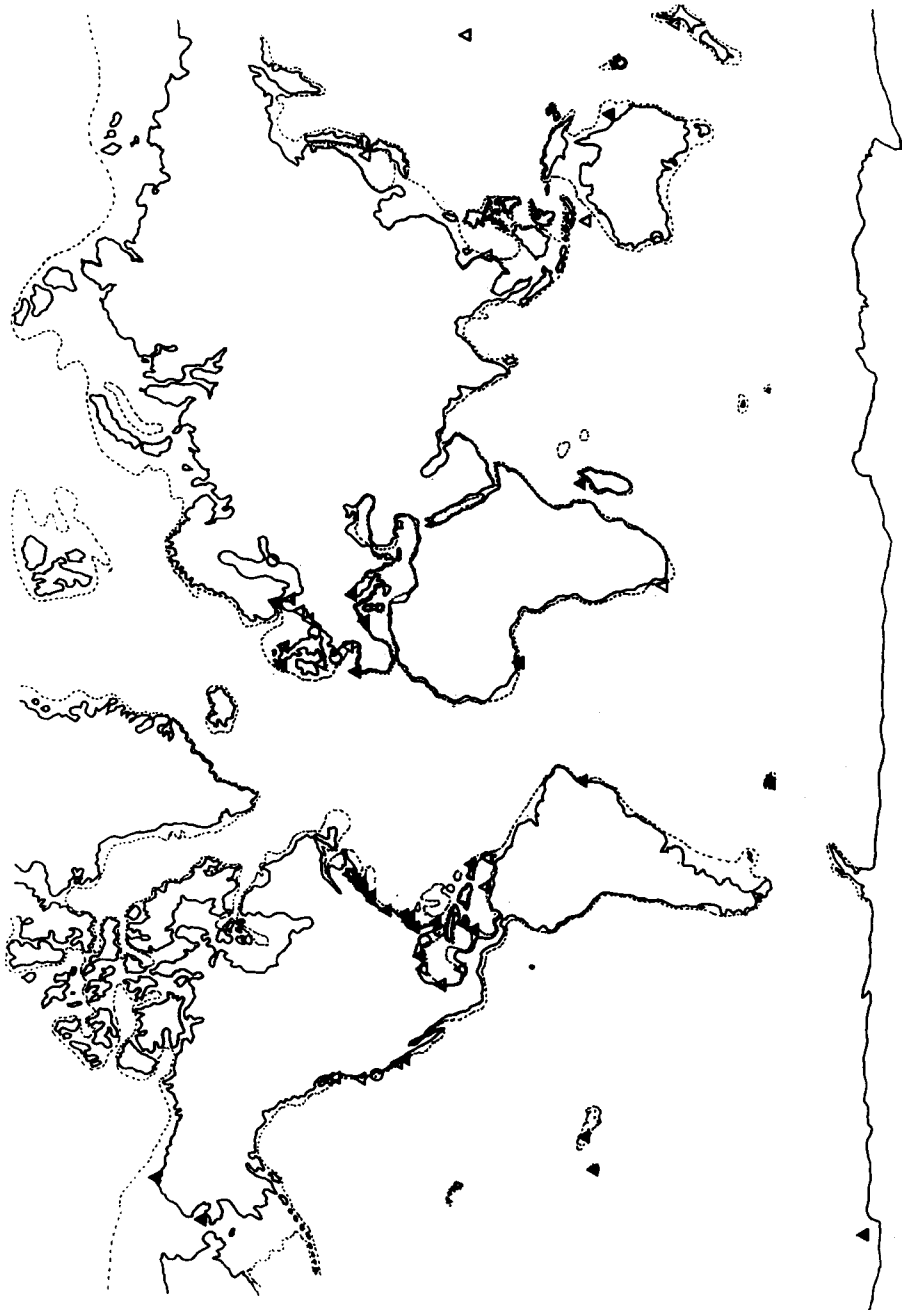


Figure 1 Map showing locations of studies measuring benthic microalgal production (open triangles) from Table 1 or biomass (open circles) from Table 3 or both (filled triangles). Some symbols correspond to more than one study in closely adjacent locations. Dashed line approximates 200 m isobath. This map is a modified Mercator projection that enlarges polar areas relative to equatorial regions.

Table 5 Calculation of global benthic microalgal production, 10^{12} g C yr⁻¹. Basin areas <200 m are from Menard & Smith (1966). Areas in each basin within tropical (Tr), temperate (Te) and polar (Po) zones are estimated very approximately. Production for each basin is calculated by multiplying basin area ($\text{km}^2=10^6\text{m}^2$) weighted by per cent in each geographical zone by average benthic microalgal production for each zone from Table 4. Average benthic microalgal production in each zone is 32.075 g C m^2 yr⁻¹ (Tr), 18.05 g C m^2 yr⁻¹ (Te), and 2.5 g C m^2 yr⁻¹ (Po), calculated as the weighted average of intertidal and 0–5 m production $\times 0.025\%$ of the area in depth zone 0–200 m plus 5–20 m production $\times 0.075\%$ of the area in depth zone 0–200 m plus >20 m production $\times 0.20\%$ (20–60 m area) in depth zone 0–200 m (0 for polar zone).

Basin	Area 10^6 km ²	% Tr	% Te	% Po	Production 10^{12} g C yr ⁻¹
Pacific Ocean	2.712	50	50	–	67.970
SE Asia-Aust.	4.715	100	–	–	151.23
Bering Sea	1.050	–	–	100	2.625
East Asian Seas	1.583	–	100	–	28.573
Gulf of California	0.071	90	10	–	0.149
Atlantic Ocean	6.080	20	60	20	107.89
Gulf of Mexico/Carib.	1.021	90	10	–	31.32
Mediterranean	0.513	–	100	–	9.260
Black Sea	0.177	–	100	–	3.195
Baltic Sea	0.381	–	100	–	6.877
Indian Ocean	2.622	80	20	–	76.745
Red Sea	0.188	100	–	–	6.030
Persian Gulf	0.238	100	–	–	7.634
Arctic Ocean	5.771	–	–	100	14.428
Total	27.122				513.926

Benthic microalgal biomass

Microalgal biomass is almost always measured and expressed in terms of chlorophyll *a* concentration. As with measurement of benthic microalgal production, there is no standard method for measuring this parameter and the different methods used have probably yielded somewhat different deviations from true values. Several studies have reviewed and compared the major methods for estimating benthic microalgal biomass, which include several spectrophotometric, fluorometric, and chromatographic (HPLC) methods, e.g. Whitney & Darley (1979), Varela (1981), Daemen (1986), Riaux-Gobin et al. (1987), Beretich (1992), and Plante-Cuny et al. (1993). In general HPLC methods are considered to be more accurate and to give somewhat lower chlorophyll *a* values than other methods, but HPLC is much more expensive and time-consuming. Spectrophotometric methods, particularly those that employ steps to eliminate interferences from pigment degradation products, especially chlorophyllides, e.g. Whitney & Darley (1979), yield relatively accurate results. The fluorometric techniques can yield overestimates of chlorophyll *a* if chlorophyllides are present, but this is not always so (Riaux-Gobin et al. 1987, Beretich 1992). Another bias is that benthic microalgae in low light flux habitats may accumulate relatively higher amounts

of chlorophyll *a* and/or accessory pigments per cell, so-called “shade adaptation” (Perry et al. 1981). Finally, settling phytoplankton may contribute to the chlorophyll *a* found in sediments (Sun et al. 1994). Consequently, many of the data available on benthic microalgal chlorophyll *a* biomass levels are probably slightly higher than actual values, but are still adequate for my purposes.

An analysis of the depth distribution of benthic microalgal biomass is useful in establishing the extent of neritic habitat inhabited by productive benthic microalgae, but several constraints must be acknowledged. Table 6 presents estimates of sediment (=benthic microalgal) chlorophyll *a* from subtidal locations in all areas of the world, along with notes on the methodologies used. Some of the values presented here come from habitats where light flux would not be sufficient to support production, e.g. Sun et al. (1994), while chlorophyll *a* values at deeper depths in other studies certainly included accumulated senescent phytoplankton in addition to productive microalgae, e.g. Plante-Cuny (1978), Cahoon et al. (1992). Loss of microalgae during sample retrieval might introduce a negative bias, while some of the values obtained by fluorometry may be high.

Table 7 summarizes the major geographic and depth distribution patterns of maximum sediment chlorophyll *a* values. (I use maximum values in this analysis to reduce the effects of seasonality and other biases, such as low estimates during low light seasons or caused by sampling artifacts.) There is a very uneven geographical distribution of sediment chlorophyll *a* measurements, with only 8 of 98 measurements from polar regions. There are also few (11 of 98) measurements from depths greater than 40 m, although the few data presented and the pattern in polar regions suggest that benthic microalgae may more often extend below 40 m. Mean maximum sediment chlorophyll *a* values in temperate and tropical regions, although highly variable, show a regular decline with depth. The lack of such a pattern in polar regions may reflect low sample numbers or different ecological constraints, such as regional differences in grazing pressure and population turnover rates, but clearly hints that productive benthic microalgal populations may extend below 40 m in these regions during the production season. This analysis does not establish a general depth limit for productive benthic microalgal populations, but nor does it invalidate the use of 60 m as a lower limit for benthic microalgal production in Table 5 and the discussion above. Of course, depth is a proxy for light flux to the bottom, which is one real constraint on the extent of benthic microalgal production. I review the state of knowledge from field and laboratory studies on the lower light limits for benthic microalgal production in the next section.

The average benthic microalgal biomass values presented in Table 7 may also be considered in comparison with integrated phytoplankton biomass in the overlying water-column. A few studies have directly compared sediment and water-column chlorophyll *a* values, e.g. Cahoon et al. (1990), Cahoon & Cooke (1992), but the broader comparisons possible using the values in Table 7 give a somewhat more comprehensive view of the relative significance of benthic microalgal biomass. Average sediment chlorophyll *a* values in the 0–5 m depth zone are equivalent to phytoplankton concentrations of at least 25 $\mu\text{g l}^{-1}$ (temperate region), which is much higher than typical phytoplankton concentrations in temperate neritic waters except for upwelling zones. Average sediment chlorophyll *a* values for deeper depth zones are smaller, but are still greater than most reported integrated phytoplankton chlorophyll *a* values from a wide variety of locations (Morel & Berthon 1989). Thus microalgal biomass is frequently very great compared with phytoplankton for most shallow areas and is essentially concentrated along a 2-dimensional surface rather than through the 3-dimensional water-column, which has several important ecological implications.

Table 6 Benthic microalgal biomass (as chlorophyll *a* (Chla)) estimates from subtidal habitats worldwide (refer to Fig. 1), with notes on method used. "Spec."=spectrophotometry, "Fluor."=fluorometry, "HPLC"=high performance liquid chromatography).

Reference	Location	Depth m	Chla		Method/Reference
			mg m ⁻²	µg g ⁻¹ sed	
Barranguet et al. 1994	Golfe de Fos, France	3.5–4	52–130		Spec./Lorenzen 1967; Riemann 1978
Barranguet et al. 1996	Golfe de Fos, France	0.5 13	28–45 30–60		HPLC/Barranguet 1994
Beretich 1992	Onslow Bay, NC	15	52–88		Spec./Whitney & Darley 1979
		19	88–104		
		22	22		
		31	20–53		
	Key Largo, FL	10	27–39		
		19	22–43		
		27	32–49		
		32	20–53		
	Cedar Key, FL	12	37–77		
Boucher & Clavier 1990	New Caledonia	9–16	134–171		Fluor./Holm-Hansen & Riemann 1978
Bodoy & Plante-Cuny 1984	Golfe de Fos, France	0.5	?–76		Spec./Plante-Cuny 1974
Bunt et al. 1972	Key Biscayne	3	63–73		Spec./Lorenzen 1967; Strickland & Parsons 1968
		60	27–39		
	Swan Island	9	30–62		
		16	30–79		
	Seranilla Bank	16	83–123		
		40	57–219		
	Pedro Bank	16	58–107		
		60	17		
	Discovery Bay	16	33–75		
60		17			
60		17			
Cahoon & Cooke 1992	Onslow Bay, NC, USA	15–20	16–54		Spec./Whitney & Darley 1979
		20–30	25–47		
		30–41	25–62		
Cahoon et al. 1990	Onslow Bay, NC, USA	13	41		Spec./Whitney & Darley 1979
		142	15		
Cahoon et al. 1992	Onslow Bay, NC, USA	45	19		Spec./Whitney & Darley 1979
		63	36		
		96	10.6		
		131	8.8		
		157	9.2		
		194	4.4		
Cahoon et al. 1993	Stellwagen Bank, MA, USA	21	49–79		Spec./Whitney & Darley 1979
		27	16–60		
Carpenter 1985	St Croix, Virgin Is	1.5–2	35–56		Spec./Jeffrey & Humphrey 1975

Table 6 continued

Reference	Location	Depth m	Chla		Method/Reference
			mg m ⁻²	µg g ⁻¹ sed	
Charpy & Charpy-Roubaud 1990	Tikehau, F. Polynesia	20	10		Spec./Plante-Cuny 1984
Charpy-Roubaud 1988	Tikehau, F. Polynesia	19	8.5		Spec./Plante-Cuny 1984
Dayton et al. 1986	McMurdo Sound, Antarctica	6	96-457		Spec./Lorenzen 1967
		18	47-913		
		25	139-325		
		40	60-360		
Delgado 1989	Ebro Bay, Spain	0-3	2-25		Spec./Lorenzen 1967; Whitney & Darley 1979
		5-6.5	6-30		
Gilbert 1991a	Signy Is., S. Orkney Is	8	6-510		Spec./Lorenzen 1967
Gilbert 1991b	Signy Is., S. Orkney Is	12	11-330		Spec./Lorenzen 1967
Hanson et al. 1981	GA Bight, GA, USA	13-18		0.47-2.76	Spec.
		25-31		1.13-2.01	
		39-68		0.55-1.09	
Herndl et al. 1989	G. Trieste, Adriatic Sea	15		3.2-13.1	Spec./Colijn & van Buurt 1975
		22		5-11.8	
Horner & Schrader 1982	Beaufort Sea, AK, USA	7	1-28		Spec./Matheke & Horner 1974
Hartwig 1978	La Jolla, CA, USA	18		6.2-23.4	Spec./Hartwig 1976
Hopkinson et al. 1991	Gray's Reef, GA, USA	20	197-869		Fluor./Strickland & Parsons 1972
Iannuzzi et al. 1996	Long Is. Sound, NY, USA	0.6-1.2	46-114		Fluor./Strickland & Parsons 1972
		1.2-1.8	67-136		
Jenness & Duineveld 1985	North Sea	26	4-14		Fluor.
Johnstone et al. 1990	G. B. Reef, Australia	1-7	44-65		Spec./Parsons et al. 1984
Kendrick et al. 1996	Marmion Lagoon, Australia	8-9		0.3-2.5	Spec./Whitney & Darley 1979
Lukatelich & McComb 1986	Peel-Harvey Estuary, Australia	0-1.5	45-391		Spec./Strickland & Parsons 1972; Whitney & Darley 1979
Matheke & Horner 1974	Chukchi Sea, AK, USA	5	35-321		Spec./Lorenzen 1967
Plante et al. 1986	Golfe de Fos, France	0.3	33-74		Spec./Lorenzen 1967
Plante-Cuny 1977	Côte d'Ivoire	0.2	170		Spec./Plante-Cuny 1974
		5	6		

Table 6 continued

Reference	Location	Depth m	Chla		Method/Reference
			mg m ⁻²	μg g ⁻¹ sed	
Plante-Cuny 1978	Nosy-Bé, Madagascar	5	219–602		Spec./Strickland & Parsons 1972
		15	142–237		
		25	39–118		
		35	19–52		
		40	9.9		
		55	10.4		
		60	16.4		
		83	30.4		
Plante-Cuny & Bodoy 1987	Golfe de Fos, France	0.5	30–215		Spec./Lorenzen 1967
Plante-Cuny et al. 1993	Golfe de Fos, France	4.5	9–82		Spec./Lorenzen 1967; Plante-Cuny 1978
Riaux-Gobin et al. 1987	Brittany, France	10		9.27–22.1	Spec./Fluor./HPLC (this paper)
		20		2.98–5.42	
Riaux-Gobin et al. 1989	Brittany, France	10		3.6–22.1	Fluor./Lorenzen 1967; Holm-Hansen et al. 1965
		20		1.56–6.74	
Rizzo & Wetzel 1985	Chesapeake Bay, VA, USA	0–2	5–52		Spec./Riemann 1978; Vollenweider 1974
Schreiber & Pennock 1995	Weeks Bay, AL, USA	1–1.4	0–31		Spec./Strickland & Parsons 1972
Sournia 1976b	Takapoto, F. Polynesia	0	211		Fluor./Yentsch & Menzel 1963; Lorenzen 1966
		1	236–907		
		10–17	56–140		
Sournia 1976c	Moorea, F. Polynesia	0.2–0.3	1270		Fluor./Lorenzen 1966
Sun et al. 1994	Long Is. Sound, NY, USA	10.8	18–43.5		HPLC
		41.3	6.4–15.3		
Sundbäck 1986	Laholm Bay, Sweden	5–8	8–19		Spec./Lorenzen 1967
		10–13	3–38		
		14–16	4–78		
		17–18	3–15		
		19–20	5–22		
Sundbäck & Jönsson 1988	Laholm Bay, Sweden	3.5	18		Spec./Lorenzen 1967
		6	13		
		12	12		
		15	19		
		17	9		
		19	8		
Steele & Baird 1968	Loch Ewe, Scotland	5		4–10	Fluor./Yentsch & Menzel 1963
		10		3–19	
		12.5		3–19	
Thompson et al. 1981	San Francisco Bay, CA, USA	0–6	30–270		?
Vilbaste 1992	Haapsalu Bay, Estonia	1–2	226–374		Spec./Lorenzen 1967
		4.5	179		
Zingmark 1986	Impoundments, SC, USA	0–1	16–225		Fluor./Yentsch & Menzel 1963

Table 7 Summary of mean (\pm SD) reported maximum estimates of sediment chlorophyll *a* values (mgm^{-2}) from Table 6 by depth range and region (as in Table 4).

Depth Range m	Geographical region		
	Polar	Temperate	Tropical
0–5	321 <i>n</i> = 1	128 \pm 101 <i>n</i> = 16	347 \pm 426 <i>n</i> = 11
5–20	448 \pm 320 <i>n</i> = 5	84 \pm 204 <i>n</i> = 17	94 \pm 71 <i>n</i> = 11
20–40	342 \pm 25 <i>n</i> = 2	44 \pm 24 <i>n</i> = 8	83 \pm 75 <i>n</i> = 6
40–60	–	19 <i>n</i> = 1	21 \pm 13 <i>n</i> = 4
60–100	–	10.6 <i>n</i> = 1	30.4 <i>n</i> = 1
100–200	–	9.6 \pm 4.3 <i>n</i> = 4	–
Total	<i>n</i> = 8	<i>n</i> = 47	<i>n</i> = 33

Light limitation

Light flux is a critical limiting factor for plants living at the bottom of a water-column, a situation in which some combination of depth and clarity must define compensation depth and, therefore, the limits of distribution of productive benthic microalgae. Given the importance of light and the ability of aquatic plants to adapt to variations in ambient light fluxes, physiological shade adaptation and selection for low-light adapted taxa are to be expected among benthic microalgae in subtidal habitats. Conversely, microalgae living in well-illuminated intertidal and shallow subtidal habitats might be expected to have very different P versus I responses.

A survey of studies examining P versus I responses of benthic microalgae shows that most have examined the responses of intertidal or shallow subtidal populations and have focused on defining the biomass-specific maximum rate of production, the saturating light intensity, and other properties of the production response at higher light intensities, e.g. Admiraal (1977), Mills & Wilkinson (1986), du Preez et al. (1990), Pinckney & Zingmark (1991), Blanchard & Montagna (1992), MacIntyre & Cullen (1996), Guarini et al. (1997). Several studies show that benthic microalgae can adjust their biomass-specific maximum rate of production and adapt to higher or lower maximum light levels, e.g. Whitney & Darley (1983), Blanchard et al. (1996). However, relatively few studies have defined compensation light intensity or depth, the lower limit for the distribution of benthic microalgae in aquatic ecosystems.

Information about the lower limits of photo-adaptation by benthic microalgae can help to define the depth distribution and areal extent of benthic microalgal production in neritic ecosystems. Table 8 summarizes the information available from published studies on the lowest light intensities or percent incident fluxes found to support detectable gross production by

Table 8 Minimum average light intensities at which benthic microalgal production has been measured.

Location	Intensity $\mu\text{Em}^{-2} \text{ s}^{-1}$	% Surface incident flux	Reference
Golfe de Fos, France	14	–	Barranguet et al. 1996
Stellwagen Bank, MA, USA	4.7	0.28	Cahoon et al. 1993
St. Croix, Virgin Is	37–119 ^a	–	Carpenter 1985
Nova Scotia, Canada	2.5	–	Grant 1986
Gulf of Trieste, Adriatic Sea	10	–	Herndl et al. 1989
Limfjorden, Denmark	7.5	–	Lassen et al. 1992
Chukchi Sea, AK, USA	–	0.8	Matheke & Horner 1974
Cape Fear River Estuary, NC, USA	7	–	Miller & Kamykowski 1986
McMurdo Sound, Antarctica	0.6	<0.04	Palmisano et al. 1985 ^b
McMurdo Sound, Antarctica	0.5	–	Palmisano et al. 1985b
McMurdo Sound, Antarctica	7	–	Palmisano et al. 1987 ^b
Nosy-Bé, Madagascar	–	0.2	Plante-Cuny 1978
McMurdo Sound, Antarctica	2.0	–	Rivkin & Putt 1987 ^b

^a reported compensation light intensities

^b studies of sea-ice microalgae

microalgae in the field, including several studies of sea-ice algae from the Antarctic, as sea-ice algae include many benthic pennate diatoms. The major conclusion that can be drawn from these data, aside from the relative paucity of them, is that benthic microalgae appear capable of sustaining growth at very low light intensities, in many cases well below average values of 5–10 $\mu\text{E m}^{-2} \text{ s}^{-1}$ and 1% surface incident radiation. There is some indication that microalgae in polar regions are particularly well adapted to low light levels. This may be an artifact of the numbers and focus of the studies, rather than the physiology of microalgae, but a reduction of compensation light intensity at low temperatures cannot be ruled out. Falkowski (1988) has estimated the theoretical minimum light intensity required to support growth to be on the order of 0.1% of surface incident flux. These data suggest that benthic microalgal production may closely approach that physiological limit.

If benthic microalgal production can extend to approximately the 0.1% light depth, then two approaches can be used to determine the probable depth distribution of productive benthic microalgae in neritic regions. Light extinction values calculated from Secchi depth data from 17 879 oceanographic stations in neritic areas of the world ocean (bottom depth <200 m) show that =0.1% of surface incident radiation would reach the bottom at 5425 of those locations, or approximately 30% of the total (NODC 1987). If the hypsometry of neritic waters is assumed to yield an approximately linear relationship of area versus depth, then 30% of total neritic zone area would generally encompass the depth zone 0–66 m, which is approximately the depth zone assumed to support benthic microalgal production in the calculation of global production above. Alternately, one can use an exponential light extinction equation of the form

$$I_d = I_0 e^{-kd}$$

to determine the depth to which 0.1% of surface incident radiation would penetrate assuming different light extinction coefficients. Penetration of 0.1% of surface incident radiation to a depth of 60 m requires an average light extinction coefficient, k , of approximately 0.115, corresponding to water somewhat clearer than Jerlov's (1970) "coastal" water types but not as clear as "oceanic" water types. Oligotrophic ocean waters frequently have light extinction coefficients of approximately 0.07, which would yield a 0.1% light depth of almost 100 m (Megard & Berman 1989). Consequently, the neritic areas most likely to support benthic microalgal production to deeper depths are those underlying clear waters, such as areas where river discharges and other sources of turbidity are minor, nutrient inputs are low and phytoplankton biomass is limited, or where oligotrophic ocean waters intrude.

The spectral quality of light reaching the bottom must also be considered, particularly in habitats where high water clarity permits light flux to relatively great depths, but where attenuation of longer wavelength light drives a shift towards dominance of green-blue light. In these circumstances it is possible that physiological adaptations, i.e. chromatic adaptation (Bold & Wynne 1985), or taxonomic shifts might result, but the data available on benthic microalgal pigment and species distributions with depth are too limited to resolve this question.

Microalgae and the sediment/water interface

Two important aspects of the ecology of benthic microalgae that distinguish them from planktonic microalgae are their concentration in the sediment/water interface microhabitat and their physical alteration of that microhabitat. Phytoplankton are, of course, dispersed by physical processes throughout the water-column and typically reach concentrations of the order of 0.1–1 μg chlorophyll a l^{-1} (or 0.0001–0.001 μg cm^{-3}) in neritic waters. Benthic microalgae are often 10^4 – 10^5 times as concentrated in sediments (assuming sediment bulk density of 2.0 g cm^{-3} and using values of microalgal biomass as μg chlorophyll a g sediment⁻¹ from Table 3, which yield values ranging from approximately 1 to 45 μg cm^{-3}). These very high concentrations of microalgal biomass in small volumes result from *in situ* production, settling of resuspended cells (Grant et al. 1986b), incorporation of phytoplankton or tychopelagic forms in settling material (Jenness & Duineveld 1985), and active migration of motile microalgae, e.g. monoraphic and biraphic pennate diatoms, from deeper in the sediment towards the interface (Joint et al. 1982, Paterson 1989, Wulff et al. 1997). What is even more remarkable is the maintenance of these high concentrations under physical conditions such as wave- and tidal current-induced sediment disturbance that would be expected to disperse or destroy living cells.

Sediment stabilization

A number of studies have now demonstrated that benthic microalgae and other sediment-associated micro-organisms can secrete extracellular polymeric substances (EPS) that act to bind sediments (Decho 1990, Underwood et al. 1995). Benthic diatoms are major producers of EPS (Grant et al. 1986b), which is a complex and still poorly described mix of polysaccharides and other compounds (Underwood et al. 1995). Some diatoms and cyanobacteria also form chains or colonies that can bind sediment particles by direct contact

and adhesion. Alteration of the mechanical properties of sediments by microalgal colonization and growth has been shown in many studies to reduce the credibility of these sediments under flow conditions that would otherwise cause substantial sediment erosion and resuspension, e.g. Holland et al. 1974, Grant et al. 1986a, Paterson 1989, Delgado et al. 1991a, Madsen et al. 1993, Underwood & Paterson 1993, Yallop et al. 1994). This stabilization of the sediment is one factor likely to be responsible for maintenance of very high microalgal biomass levels at the sediment/water interface.

Stabilization of the sediment at the interface by microalgal EPS secretion and growth forms may offer several adaptive advantages to microalgae themselves, and is likely, therefore, to be a key feature of their ecology. Stabilization allows benthic microalgae to resist displacement and resuspension, which may sometimes carry them into less desirable habitats or expose them to suspension feeders. Stabilization may reduce damage to microalgal cells by abrasion and collision with otherwise unconsolidated sediment grains (Delgado et al. 1991b, Miller 1989). Stabilization of the sediment, especially by sticky EPS, may reduce resuspension of very fine-grained sediment particles and the light-limiting turbidity that might then result (Roemer et al. 1984). Stabilization of the interface also allows benthic microalgae to remain fixed while overlying water flows past, which constantly replenishes their nutrient supply even at low ambient nutrient concentrations (Adey 1987) and reduces the thickness of the diffusive boundary layer adjacent to cells, which might otherwise limit production and nutrient uptake (Rodgers & Harvey 1976). Stabilization of the sediment/ water interface by a small but concentrated layer of benthic microalgae may also have important effects on exchanges of dissolved gases, nutrients, and organic substances through alteration of rates of sediment pore-water flushing and diffusion, permeability, and possibly changes in the composition and activities of the rest of the benthos, e.g. inhibition of macroalgal growth (Huang & Boney 1984). The biogeochemical effects of benthic microalgal production on the sediment-water microhabitat will be discussed later.

Physical processes also frequently create conditions in which sediment stabilization by benthic microalgae and other benthic forms is inadequate to prevent sediment displacement. To some degree, adaptations by benthic microalgae minimize the harmful effects of this displacement, i.e. attachment by small pennate diatoms to concavities on sand grains or mechanical robustness (Delgado et al. 1991b). However, suspension of benthic microalgae is not necessarily harmful, transforming them for some time into phytoplankton with enhanced access to light, which may permit accelerated growth rates. Release of nutrient-rich pore-water by suspension events would also enhance production. Simultaneous suspension of abundant fine particulates may also interfere with grazing on microalgae by suspension feeders. This alternation of benthic and planktonic life modes represents a "tychopelagic" life mode apparently typical of at least some taxa (Bold & Wynne 1985, Cahoon & Laws 1993). When benthic microalgal biomass and productivity are high, there may even be mechanisms that actively drive suspension of some microalgae in the water-column, such as formation of gas bubbles that lift cells and other material from the bottom (Durako et al. 1982). Several studies have shown the significant contribution to water-column production and total microalgal biomass by suspended benthic microalgae in estuarine ecosystems (Baillie & Welsh 1980, Gabrielson & Lukatelich 1985, Grant et al. 1986a, Shaffer & Sullivan 1988, de Jonge & van Beusekom 1992, 1995) and continental shelf waters (Roman & Tenore 1978, Kamykowski & Bird 1981). However, relatively few studies of water-column production have distinguished planktonic and resuspended benthic forms, and the processes driving resuspension are common. Consequently, it is highly probable that a significant portion of "phytoplankton" production in neritic waters is actually production by resuspended benthic microalgae.

Nutrient fluxes

The concentration of benthic microalgal biomass and production at the sediment/water interface drives a need for a large amount of nutrients to support that production. The physical stabilization of the sediment surface by microalgae also provides two ways to increase their access to nutrients. Microalgae attached at the sediment surface experience steady advection of water past them, which prevents local depletion. Even at low nutrient concentrations, the steady input of nutrients may permit adaptation of nutrient uptake kinetics to ensure adequate uptake rates, a biophysical strategy that works well for other benthic primary producers (Adey 1987). The nature of near-bottom water flows in neritic areas, which are driven by wave action, lunar and wind tides, internal waves, and other currents, ensures a frequently turbulent regime that also prevents nutrient depletion in the near-bottom zone.

The concentration of benthic microalgae at the sediment/water interface also allows them to take advantage of and sometimes alter the fluxes of nutrients regenerated by decomposition of organic matter in the sediments. Benthic microalgae typically represent a very small fraction of total organic matter in the sediments, usually <1–5% (assuming a C:Chl *a* ratio of 40:1 (de Jonge 1980), using sediment chlorophyll *a* values from Table 6, and comparing the resulting microalgal carbon equivalents to a typical low value of 0.1%, or 1 mg g⁻¹ sediment for neritic sediments (Walsh 1988)). The remaining organic material includes detrital matter and heterotrophic organisms, many of which consume and re-mineralize that organic material. Consequently, sediment pore-waters are often substantially enriched in dissolved organic matter and inorganic nutrients, driving strong concentration gradients and creating conditions favourable to high diffusive fluxes. A variety of laboratory and field studies have now established that benthic microalgae can take up substantial portions of the inorganic nutrients that flux from the sediments into the overlying water-column in shallow waters. For example, light-driven uptake of ammonium, phosphate, silicate, or nitrate, have been demonstrated by Sundbäck & Granéli (1988), Rizzo (1990), Sundbäck et al. (1991), Marinelli (1992), Reay et al. (1995), Bertuzzi et al. (1996), and Sigmon & Cahoon (1997), among others, by comparison of sediment-water fluxes in light and dark conditions. In some cases the magnitude of the effects by benthic microalgae on nutrient fluxes to overlying waters has been sufficient to create limiting nutrient regimes for planktonic microalgae, e.g. Fong et al. (1993), Bertuzzi et al. (1996), Sigmon & Cahoon (1997). A number of laboratory studies have also demonstrated the ability of some benthic microalgal taxa to take up dissolved organic compounds, e.g. Lewin & Lewin (1960), Hellebust & Lewin (1972), Antia et al. (1975), Lewin & Hellebust (1975, 1976), Darley et al. (1979), Admiraal et al. (1987), although it is difficult to assess the importance of this in terms of overall nutrient budgets. However, given the steady supply of high concentrations of dissolved organic substances from decomposition processes in sediment pore-waters and the energy advantage deriving from uptake of organic compounds, it is quite likely that benthic microalgae commonly utilize this source of nutrients and energy, particularly when low illumination levels may restrict light-driven uptake of inorganic nutrients.

The numbers of studies of benthic microalgal effects on nutrient fluxes in the field, particularly in subtidal waters, are too few to allow even approximate quantitative inferences to be drawn from them, given the many variables that affect uptake rates in the field. Furthermore, because microalgae can draw on either water-column or pore-water nutrient sources, specific nutrient budgets are more difficult to establish experimentally. However, one may generate approximate nutrient budget requirements for benthic microalgal communities using production rate estimates and assuming Redfield ratios of nutrient

utilization, which at least constrain the probable nutrient budgets. For example, estimated benthic microalgal productivity in the 0–5 m zone in the tropics of $576 \text{ g C m}^{-2} \text{ yr}^{-1}$ (from Table 4) would drive nitrogen uptake of approximately 102 g or $7.3 \text{ moles N m}^{-2} \text{ yr}^{-1}$. Similar calculations can be made for other depth zones, regions, and nutrients, although benthic diatoms, being rather heavily silicified in comparison with planktonic diatoms, may represent a much more significant sink for silicate than phytoplankton (Sigmon & Cahoon 1997).

Effects on other biogeochemical processes

Metabolic activities and physical alteration of the sediment/water interface through sediment stabilization by benthic microalgae may affect biogeochemical processes other than nutrient fluxes. The presence and activities of benthic microalgae can drive significant changes in vertical profiles across the interface of oxygen concentrations and carbon dioxide-bicarbonate-carbonate concentrations, thus affecting pH and redox potentials in this zone (Revsbech et al. 1981, Revsbech & Jørgensen 1983). These changes in vertical profiles can occur at short (minutes-days) and long (seasons) time scales (Ludden et al. 1985, Baillie 1986, Rizzo et al. 1992, Therkildsen & Lomstein 1993).

Temporal and spatial variability in oxygen and carbon cycling mediated by benthic microalgal metabolism may in turn drive changes in the cycling of other elements, although it is important to remember that microalgal metabolism is only one contributing set of processes in the sediment environment. Oxygenation of sediments by microalgal production may act to reduce the solubility of phosphorus compounds and thereby limit fluxes of this element from sediments (Sundbäck & Granéli 1988, Sundbäck et al. 1991). Conversely, net consumption of oxygen during dark periods coupled with restriction of the diffusion of oxygen from overlying waters by EPS-mediated reductions in sediment permeability may drive periodically higher phosphorus solubilities and fluxes. Cyanobacteria, particularly filamentous forms, can be important constituents of the benthic microflora; many species conduct nitrogen fixation. Conditions of nitrogen limitation and deoxygenation at night favour higher rates of nitrogen fixation, while inorganic nitrogen loading and photosynthetic oxygenation of the sediments lower fixation rates (Bebout et al. 1987, Pinckney et al. 1995). Alternating oxygenation and deoxygenation of pore-waters by microalgal photosynthesis and respiration have also been shown to affect rates of bacterially driven nitrification, denitrification, sulphate reduction and sulphur oxidation in sediment microhabitats (Triska & Oremland 1981, Canfield & Des Marais 1993, Chambers et al. 1994, Rysgaard et al. 1995, 1996). Although these studies have largely been conducted in intertidal and estuarine habitats, particularly in association with well-developed microalgal mat communities, the principles they have demonstrated are also likely to apply to deeper neritic ecosystems.

Grazing interactions

Plante-Cuny & Plante (1986) reviewed the literature on grazing of marine diatoms by benthos, classifying the grazers as microfauna, meiofauna, and macrofauna, and discussing primarily the diversity of grazers feeding on different functional groups of benthic diatoms. Without covering the same material, it is clear that many organisms are capable of feeding on benthic diatoms. Here I review the literature on grazing of benthic microalgae published subsequently and some of the major ideas from that literature.

Benthic microalgal production clearly supports a broad diversity of organisms, based on various traditional methods of measuring feeding, such as direct observations of feeding, gut content analyses, use of radiolabelling, or experimental comparisons of grazing and control treatments. Excretion of soluble organic matter by microalgae supports bacteria (and probably other heterotrophs) that take up dissolved organic compounds (Dobbs et al. 1989). Benthic protozoans, including ciliates (Epstein et al. 1992) and foraminiferans (Rivkin & DeLaca 1990), can graze microalgal cells. There has been considerable interest in the grazing relationships between metazoan meiofauna, especially harpacticoid copepods and nematodes, and benthic microalgae, (e.g. Decho 1988, Blanchard 1991, Montagna 1995, Montagna et al. 1995). Given the relative correspondence between the body sizes and population growth rates of microalgae and meiofauna, there has also been considerable interest in analyzing correlations among them in time (Alongi 1988) and at small spatial scales (Decho & Castenholz 1986, Decho & Fleeger 1988, Blanchard 1990, Pinckney & Sandulli 1990, Santos et al. 1995). However, the overall conclusion of these studies seems to be that spatial correlations between microalgae and meiofauna abundances are often weak and confounded by a variety of factors, although a strong grazing relationship usually exists. Another set of papers describes effects of grazing by gastropods and amphipods on benthic microalgae, including stimulation of microalgal growth rates, reduction of microalgal biomass, and selective grazing of certain microalgal taxa (Hargrave 1970, Connor & Edgar 1982, Connor et al. 1982, Juniper 1987). Benthic microalgal production has also been shown to support herbivorous anemones (Rivkin & DeLaca 1990), polychaetes (Asmus & Asmus 1985, Posey et al. 1995), deposit-feeding bivalves (Thompson & Nichols 1988, Page et al. 1992) and (probably) holothuroideans (Sloan & von Bodungen 1980). Interestingly, there is also evidence that the presence of benthic microalgae can deter recruitment to sediment microhabitats by at least a few species (Wennhage & Pihl 1994).

The use of stable isotope analyses to distinguish primary producers and trace their elemental signatures through higher trophic levels has provided additional insights to the importance of benthic microalgae in marine food webs. Some of these studies confirm earlier findings that benthic microalgae can be important foods for benthic bivalves (Incze et al. 1982, Riera & Richard 1996). Other studies, particularly those employing multiple stable isotope approaches, i.e. analysis of carbon, nitrogen and sulphur stable isotopes, have shown that, in addition to other primary producers, benthic microalgae frequently contribute significantly to food chains including gastropods, bivalves, shrimps, crabs, and fishes (Sullivan & Moncrieff 1990, Currin et al. 1995, Newell et al. 1995, Kwak & Zedler 1997, Stribling & Cornwell 1997). Most of these studies have focused on estuarine ecosystems. Information from offshore neritic ecosystems is more limited and inconsistent. Thomas & Cahoon (1993) found multiple stable isotope evidence indicating the existence of a benthic microalgae-supported food chain in a North Carolina (USA) continental shelf community, which implied that sediment geochemical processes altered the isotopic composition of benthic microalgae compared with phytoplankton and macroalgae in this ecosystem. However, Fry (1988) failed to find stable isotope evidence of a contribution by benthic microalgal production to the George's Bank ecosystem.

A new paradigm

The review of benthic microalgal ecology presented here attempts to evaluate the importance of benthic microalgae in neritic ecosystems with a focus on continental shelves. Quite clearly

the majority of studies published to date on all aspects of benthic microalgal ecology have resulted from work done in estuarine and other very shallow habitats, leaving substantial gaps in our knowledge. Nevertheless, there are enough studies from deeper, offshore habitats to suggest that the important aspects of microalgal ecology also apply to these habitats. A useful perspective on benthic microalgal ecology may be derived from considering the factors limiting benthic microalgal biomass and production and their probable responses to these factors. I offer here a synthesis of these ideas, partly to try to present a clearer picture of the roles benthic microalgae play in neritic ecosystems and partly to suggest hypotheses to address the gaps in our knowledge.

Light flux to the sediment/water interface is an obvious limiting factor that is a function of depth and turbidity. Possible responses by microalgae include physiological and genetic adaptation to low light intensities by increases in photosynthetic efficiency, increases in cellular pigment, facultative heterotrophy, and taxonomic changes. EPS production and stabilization of the sediment may also confer advantages in coping with light limitation. High rates of EPS production when light flux is high can stabilize the sediment and maintain microalgal populations in favourable conditions, balanced by low rates of EPS production when light levels and production are low, allowing easier displacement of microalgal cells into the water-column by physical processes. EPS production may also allow more effective binding of the smallest seston particles, which would otherwise increase turbidity. Certain species of benthic microalgae may also be suspended more easily than others by virtue of their growth modes, i.e. tychopelagic forms. At high overall biomass levels, “emigration” of these more easily transported cells may be advantageous to them and to less easily displaced cells that would otherwise be shaded by them.

Physical disturbance, especially resuspension events, may disperse microalgal cells, damage or kill them by abrasion, and expose them to suspension feeders. Although suspension may permit access to higher light levels in the water-column, displacement from the high-nutrient sediment microhabitat may offset this advantage. Furthermore, in shelf habitats, one frequent consequence of suspension may be transport offshore and downslope into unsuitably dark habitats, e.g. Cahoon et al. (1994). Resistance to physical displacement therefore is probably advantageous under most circumstances. The striking difference in EPS production by benthic microalgae and phytoplankton gives some evidence of the importance of resisting displacement. Not only does staying in place yield benefits for microalgae, stabilizing the sediment/water interface allows benthic microalgae to regulate nutrient fluxes by maintaining steep concentration gradients across the sediment/water interface, exposing them to steady advection of overlying water, and at least sometimes creating biogeochemical conditions favourable to maintaining a steady nutrient supply, such as nitrogen fixation and phosphorus dissolution. Microalgal regulation and interception of nutrients that might otherwise flux into the water-column may also limit phytoplankton growth, which then allows higher light flux to the benthic microalgae.

Grazing also poses the potential to reduce benthic microalgal biomass and production. The broad diversity of organisms eating microalgae and the abundant evidence of their importance in marine food chains suggests that microalgae probably do not frequently employ unpalatability, toxins, or other chemical defenses against grazing, although I am aware of no studies addressing this question. A more likely defensive response to grazing by generally single-celled organisms is high specific growth rates or morphological refuges, i.e. cells that attach and “hide” in crevices of sand grains. Specific growth rates appear to be low for some benthic microalgal populations (Gould & Gallagher 1990) but to increase when grazing pressure is higher, perhaps through selection for faster growing taxa (Connor

et al. 1982). Grazing by microscopic and meiofaunal grazers may be particularly well coupled with microalgal growth rates, posing the potential for strong grazing limitation. Suspension and dispersal of microalgae may be advantageous in this situation. In addition, it is conceivable that microalgal stabilization of the sediment may also be a strategy to limit diffusion of oxygen into the sediments at night, forcing emigration of obligately aerobic meiofauna and providing temporary relaxation of grazing pressure.

I postulate a spectrum of physical and biological conditions in neritic ecosystems based on the ability of benthic microalgae to overcome the factors limiting them. At one extreme are the conditions that most favour high benthic microalgal biomass and production: high light flux and minimal physical disturbance, allowing extensive microalgal stabilization of the sediments, high growth rates, and dominance by benthic microalgae over phytoplankton. These conditions are especially likely to occur in seas with low wind stress, such as the equatorial region, seasons with lower storm frequency and higher light fluxes, such as temperate and polar summers and, of course, in shallow waters. The other end member of this continuum would be characterized by a high frequency of strong physical disturbance and low light flux to the bottom, with frequent resuspension of benthic microalgae, and increased release of nutrients to the water-column, conditions favouring phytoplankton dominance. These conditions are most likely to occur at windier latitudes, during the stormier seasons, and in deeper waters.

Acknowledgements

I thank J.E.Nearhoof, D.Kamykowski and the editors for constructive criticism and comments, and the UNC Wilmington Center for Marine Science for a Summer Faculty Research Stipend. This is Contribution No. 202 of the UNCW Center for Marine Science Research.

References

- Adey, W.H. 1987. Food production in low-nutrient seas. *BioScience* **37**, 340–48.
- Admiraal, W. 1977. Influence of light and temperature on the growth rate of estuarine benthic diatoms in culture. *Marine Biology* **39**, 1–9.
- Admiraal, W. 1984. The ecology of sediment-inhabiting diatoms. In *Progress in phycological research*, Vol. 3, F.E.Round & D.J.Chapman (eds). Bristol: Biopress, 269–322.
- Admiraal, W., Riaux-Gobin, C. & Laane, R.W.P.M. 1987. Interactions of ammonium, nitrate, and D- and L-amino acids in the nitrogen assimilation of two species of estuarine benthic diatoms. *Marine Ecology Progress Series* **40**, 267–73.
- Alongi, D.M. 1988. Microbial-meiofaunal interrelationships in some tropical intertidal sediments. *Journal of Marine Research* **46**, 349–65.
- Antia, N.J., Berland, B.R., Bonin, D.J. & Maestrini, S.Y. 1975. Comparative evaluation of certain organic and inorganic sources of nitrogen for phototrophic growth of marine microalgae. *Journal of the Marine Biological Association of the United Kingdom* **55**, 519–39.
- Asmus, H. & Asmus, R. 1985. The importance of grazing food chain for energy flow and production in three intertidal sand bottom communities of the northern Wadden Sea. *Helgoländer Meeresuntersuchungen* **39**, 273–301.
- Asmus, R. 1982. Field measurements on seasonal variation of the activity of primary producers on a sandy tidal flat in the northern Wadden Sea. *Netherlands Journal of Sea Research* **16**, 389–402.
- Baillie, P.W. 1986. Oxygenation of intertidal estuarine sediments by benthic microalgal photosynthesis. *Estuarine, Coastal and Shelf Science* **22**, 143–59.

- Baillie, P.W. & Welsh, B.L. 1980. The effect of tidal resuspension on the distribution of intertidal epipellic algae in an estuary. *Estuarine and Coastal Marine Science* **10**, 165–80.
- Barranguet, C. 1994. *Rôle des microphytes benthiques dans l'oxygénation de l'interface eau-sédiment de deux systèmes conchylicoles méditerranéens: golfe de Fos, étang de Thau*. PhD thesis, Université d'Aix-Marseille II, France.
- Barranguet, C., Alliot, E. & Plante-Cuny, M.R. 1994. Benthic microphytic activity at two Mediterranean shellfish cultivation sites with reference to benthic fluxes. *Oceanologica Acta* **17**, 211–21.
- Barranguet, C., Plante-Cuny, M.R. & Alivon, E. 1996. Microphytobenthos production in the Gulf of Fos, French Mediterranean coast. *Hydrobiologia* **333**, 181–93.
- Bebout, B.M., Paerl, H.W., Crocker, K.M., & Prufert, L.E. 1987. Diel interactions of oxygenic photosynthesis and N₂ fixation (acetylene reduction) in a marine microbial mat community. *Applied and Environmental Microbiology* **53**, 2353–62.
- Beretch Jr, G.R. 1992. *Comparisons of water-column and benthic chlorophylls on the eastern U.S. continental shelf*. MS thesis, University of North Carolina Wilmington, Wilmington, NC, USA.
- Bertuzzi, A., Faganeli, J. & Brambati, A. 1996. Annual variation of benthic nutrient fluxes in shallow coastal waters (Gulf of Trieste, northern Adriatic Sea). *Marine Ecology PSZNI*. **17**, 261–78.
- Bigelow, G.W. 1977. *Primary productivity of benthic microalgae in the Newport River estuary*. MS thesis, North Carolina State University, Raleigh, NC, USA.
- Blanchard, G.F. 1990. Overlapping microscale dispersion patterns of meiofauna and microphytobenthos. *Marine Ecology Progress Series* **68**, 101–11.
- Blanchard, G.F. 1991. Measurement of meiofauna grazing rates on microphytobenthos: is primary production a limiting factor? *Journal of Experimental Marine Biology and Ecology* **147**, 37–46.
- Blanchard, G.F., Guarini, J.-M., Richard, P., Gros, P. & Mornet, F. 1996. Quantifying the short-term temperature effect on light-saturated photosynthesis of intertidal microphytobenthos. *Marine Ecology Progress Series* **134**, 309–13.
- Blanchard, G.F. & Montagna, P.A. 1992. Photosynthetic response of natural assemblages of marine benthic microalgae to short- and long-term variations of incident irradiance in Baffin Bay, Texas. *Journal of Phycology* **28**, 7–14.
- Bodoy, A. & Plante-Cuny, M.R. 1984. Relations entre révolution saisonnière des populations de palourdes (*Ruditapes decussatus*) et celle des microphytes benthiques et planctoniques (Golfe de Fos, France). *Haliotis* **14**, 71–8.
- Bold, H.C. & Wynne, M.J. 1985. *Introduction to the algae*. Englewood Cliffs, NJ: Prentice-Hall.
- Boucher, G. & Clavier, J. 1990. Contribution of benthic biomass to overall metabolism in New Caledonia lagoon sediments. *Marine Ecology Progress Series* **64**, 271–80.
- Brotas, V. & Plante-Cuny, M.R. 1996. Identification et quantification des pigments chlorophylliens et caroténoïdes des sédiments marins: un protocole d'analyse par HPLC. *Oceanologica Acta* **19**, 623–34.
- Bunt, J.S., Lee, C.C. & Lee, E. 1972. Primary productivity and related data from tropical and subtropical marine sediments. *Marine Biology* **16**, 28–36.
- Burkholder, P.R., Repak, A. & Sibert, J. 1965. Studies on some Long Island Sound littoral communities of micro-organisms and their primary productivity. *Bulletin of the Torrey Botanical Club* **92**, 378–402.
- Cadée, G.C. 1980. Reappraisal of the production and import of organic carbon in the western Wadden Sea. *Netherlands Journal of Sea Research* **14**, 305–22.
- Cadée, G.C. & Hegeman, J. 1974. Primary production of the benthic microflora living on tidal flats in the Dutch Wadden Sea. *Netherlands Journal of Sea Research* **8**, 260–91.
- Cadée, G.C. & Hegeman, J. 1977. Distribution of primary production of the benthic microflora and accumulation of organic matter on a tidal flat area, Balgzand, Dutch Wadden Sea. *Netherlands Journal of Sea Research* **11**, 24–41.
- Cahoon, L.B. 1988. Use of a whirling cup rotor to stir benthic chambers. *Hydrobiologia* **160**, 193–8.
- Cahoon, L.B. 1996. An instrumented lander for measurement of benthic microalgal production. In *Proceedings of the American Academy of Underwater Sciences Sixteenth Annual Scientific Diving Symposium: methods and techniques of underwater research*, M.A.Lang & C.C.Baldwin (eds). Nahant, MA: American Academy of Underwater Sciences, 45–51.
- Cahoon, L.B., Beretch Jr, G.R., Thomas, C.J. & McDonald, A. 1993. Benthic microalgal production at Stellwagen Bank, Massachusetts Bay, USA. *Marine Ecology Progress Series* **102**, 179–85.

- Cahoon, L.B. & Cooke, J.E. 1992. Benthic microalgal production in Onslow Bay, North Carolina, USA. *Marine Ecology Progress Series* **84**, 185–96.
- Cahoon, L.B. & Laws, R.A. 1993. Benthic diatoms from the North Carolina continental shelf: inner and mid shelf. *Journal of Phycology* **29**, 257–63.
- Cahoon, L.B., Laws, R.A. & Savidge, T.W. 1992. Characteristics of benthic microalgae from the North Carolina outer continental shelf and slope: preliminary results. In *Diving for Science. 1992, Proceedings of the American Academy of Underwater Sciences Twelfth Annual Scientific Diving Symposium*, L.B.Cahoon (ed.). La Jolla, CA: American Academy of Underwater Sciences, 61–8.
- Cahoon, L.B., Laws, R.A. & Thomas, C.J. 1994. Viable diatoms and chlorophyll *a* in continental slope sediments off Cape Hatteras, North Carolina. *Deep-Sea Research* **41**, 767–82.
- Cahoon, L.B., Redman, R.S. & Tronzo, C.R. 1990. Benthic microalgal biomass in sediments of Onslow Bay, North Carolina. *Estuarine, Coastal and Shelf Science* **31**, 805–16.
- Canfield, D.E. & Des Marais, D.J. 1993. Biogeochemical cycles of carbon, sulphur, and free oxygen in a microbial mat. *Geochimica et Cosmochimica Acta* **57**, 3971–84.
- Cariou-Le Gall, V. & Blanchard, G.F. 1995. Monthly HPLC measurements of pigment concentration from an intertidal muddy sediment of Marennes-Oléron Bay, France. *Marine Ecology Progress Series* **121**, 171–9.
- Carpenter, R. 1985. Relationship between primary production and irradiance for shallow algal communities on coral reefs. *Limnology and Oceanography* **30**, 784–93.
- Chambers, R.M., Hollibaugh, J.T. & Vink, S.M. 1994. Sulfate reduction and sediment metabolism in Tomales Bay, California. *Biogeochemistry* **25**, 1–18.
- Charpy-Roubaud, C.J. 1988. Production primaire des fonds meubles du lagon de Tikehau (atoll des Tuamotu, Polynésie française). *Oceanologica Acta* **11**, 241–8.
- Charpy-Roubaud, C. & Sournia, A. 1990. The comparative estimation of phytoplanktonic, microphytobenthic and macrophytobenthic primary production in the oceans. *Marine Microbial Food Webs* **4**, 31–57.
- Charpy, L. & Charpy-Roubaud, C.J. 1990. Trophic structure and productivity of the lagoonal communities of Tikehau atoll (Tuamotu Archipelago, French Polynesia). *Hydrobiologia* **207**, 43–52.
- Colijn, F. & Buurt, G.van. 1975. Influence of light and temperature on the photosynthetic rate of marine benthic diatoms. *Marine Biology* **31**, 209–14.
- Colijn, F. & de Jonge, V.N. 1984. Primary production of microphytobenthos in the Ems-Dollard Estuary. *Marine Ecology Progress Series* **14**, 185–96.
- Connor, M.S. & Edgar, R.K. 1982. Selective grazing by the mud snail *Ilyanassa obsoleta*. *Oecologia* **53**, 271–5.
- Connor, M.S., Teal, J.M. & Valiela, I. 1982. The effects of feeding by mud snails, *Ilyanassa obsoleta* (Say), on the structure and metabolism of a laboratory benthic algal community. *Journal of Experimental Marine Biology and Ecology* **65**, 29–45.
- Currin, C.A., Newell, S.Y. & Paerl, H.W. 1995. The role of standing dead *Spartina alterniflora* and benthic microalgae in salt marsh food webs: considerations based on multiple stable isotope analysis. *Marine Ecology Progress Series* **121**, 99–116.
- Cushing, D.H. 1988. The flow of energy in marine ecosystems, with special reference to the continental shelf. In *Ecosystems of the world, 27: continental shelves*, H.Postma & J.J.Zijlstra (eds). New York: Elsevier, 203–30.
- Daemen, E.A.M.J. 1986. Comparison of methods for the determination of chlorophyll in estuarine sediments. *Netherlands Journal of Sea Research* **20**, 21–8.
- Darley, W.M., Dunn, E.L., Holmes, K.S. & Larew III, H.G. 1976. A ¹⁴C method for measuring epibenthic microalgal productivity in air. *Journal of Experimental Marine Biology and Ecology* **25**, 207–17.
- Darley, W.M., Montague, C.L., Plumley, F.G., Sage, W.W. & Psalidas, A.T. 1981. Factors limiting edaphic algal biomass and productivity in a Georgia salt marsh. *Journal of Phycology* **17**, 122–8.
- Darley, W.M., Ohlman, C.T. & Wimpee, B.B. 1979. Utilization of dissolved organic carbon by natural populations of epibenthic salt marsh diatoms. *Journal of Phycology* **15**, 1–5.
- Davis, M.W. & McIntire, C.D. 1983. Effects of physical gradients on the production dynamics of sediment-associated algae. *Marine Ecology Progress Series* **13**, 103–14.
- Day, J.W., Day, R.H., Barreiro, M.T., Ley-Lou, F. & Madden, C.J. 1982. Primary production in the Laguna de Terminos, a tropical estuary in the Southern Gulf of Mexico. *Oceanologica Acta* **6**, 269–76.

- Dayton, P.K., Watson, D., Palmisano, A., Barry, J.P., Oliver, J.S. & Rivera, D. 1986. Distribution patterns of the benthic microalgal standing stock at McMurdo Sound, Antarctica. *Polar Biology* **6**, 207–13.
- Decho, A.W. 1988. How do harpacticoid grazing rates differ over a tidal cycle? Field verification using chlorophyll-pigment analyses. *Marine Ecology Progress Series* **45**, 263–70.
- Decho, A.W. 1990. Microbial exopolymer secretions in ocean environments: their role(s) in food webs and marine processes. *Oceanography and Marine Biology: an Annual Review* **28**, 73–153.
- Decho, A.W. & Castenholz, R.W. 1986. Spatial patterns and feeding of meiobenthic harpacticoid copepods in relation to microbial flora. *Hydrobiologia* **131**, 87–96.
- Decho, A.W. & Fleegeer, J.W. 1988. Microscale dispersion of meiobenthic copepods in response to food-resource patchiness. *Journal of Experimental Marine Biology and Ecology* **118**, 229–43.
- de Jonge, V.N. 1980. Fluctuations in the organic carbon to chlorophyll *a* ratios for estuarine benthic diatom populations. *Marine Ecology Progress Series* **2**, 345–53.
- de Jonge, V.N. & van Beusekom, J.E.E. 1992. Contribution of resuspended microphytobenthos to total phytoplankton in the Ems Estuary and its possible role for grazers. *Netherlands Journal of Sea Research* **30**, 91–105.
- de Jonge, V.N. & van Beusekom, J.E.E. 1995. Wind- and tide-induced resuspension of sediment and microphytobenthos from tidal flats in the Ems estuary. *Limnology and Oceanography* **40**, 766–78.
- Delgado, M. 1989. Abundance and distribution of microphytobenthos in the Bays of Ebro Delta (Spain). *Estuarine, Coastal and Shelf Science* **29**, 183–94.
- Delgado, M., de Jonge, V.N. & Peletier, H. 1991a. Experiments on resuspension of natural microphytobenthos populations. *Marine Biology* **108**, 321–8.
- Delgado, M., de Jonge, V.N. & Peletier, H. 1991b. Effect of sand movement on the growth of benthic diatoms. *Journal of Experimental Marine Biology and Ecology* **145**, 221–31.
- de Souza, E.C.P.M. 1983. Primary production of the benthic microflora living on intertidal flats in the Santos estuarine system (24°S, 46°W), São Paulo, Brazil. *Boletim do Instituto Oceanografica* **32**, 177–86.
- Dobbs, F.C., Guckert, J.B. & Carman, K.R. 1989. Comparison of three techniques for administering radiolabelled substrata to sediments for trophic studies: incorporation by microbes. *Microbial Ecology* **17**, 237–50.
- du Preez, D.R., Campbell, E.E. & Bate, G.C. 1990. Photoinhibition of photosynthesis in the surf diatom, *Anaulus australis* Drebes et Schulz. *Botanica Marina* **33**, 539–43.
- Durako, M.J., Medlyn, R.A. & Moffler, M.D. 1982. Particulate matter resuspension via metabolically produced gas bubbles from benthic estuarine microalgal communities. *Limnology and Oceanography* **27**, 752–7.
- Epstein, S.S., Burkovsky, I.V. & Shiaris, M.P. 1992. Ciliate grazing on bacteria, flagellates, and microalgae in a temperate zone sandy tidal flat: ingestion rates and food niche partitioning. *Journal of Experimental Marine Biology and Ecology* **165**, 103–23.
- Falkowski, P.G. 1988. Theoretical calculation of the depth of the euphotic zone in the sea. In *Biogeochemical cycling and fluxes between the deep euphotic zone and other ocean realms*, C. Agegian (ed.). Rockville, MD: National Undersea Research Program Report No. 88–1, 47–60.
- Fielding, P.J., Damstra, K.St J. & Branch, G.M. 1988. Benthic diatom biomass, production and sediment chlorophyll in Langebaan Lagoon, South Africa. *Estuarine, Coastal and Shelf Science* **27**, 413–26.
- Fitzwater, S.E., Knauer, G.A., & Martin, J.H. 1982. Metal contamination and primary production: field and laboratory methods of control. *Limnology and Oceanography* **27**, 544–51.
- Fong, P., Donohoe, R.M. & Zedler, J.B. 1993. Competition with macroalgae and benthic cyanobacterial mats limits phytoplankton abundance in experimental microcosms. *Marine Ecology Progress Series* **100**, 97–102.
- Fry, B. 1988. Food web structure on Georges Bank from stable C, N, and S isotopic compositions. *Limnology and Oceanography* **33**, 1182–90.
- Fuji, A., Watanabe, H., Ogura, K., Noda, T. & Goshima, S. 1991. Abundance and productivity of microphytobenthos on a rocky shore in southern Hokkaido. *Bulletin of the Faculty of Fisheries of Hokkaido University* **42**, 136–46.
- Gabrielson, J.O. & Lukatelich, R.J. 1985. Wind-related resuspension of sediments in the Peel-Harvey estuarine system. *Estuarine, Coastal and Shelf Science* **20**, 135–45.

- Gallagher, J.L. & Daiber, F.C. 1974. Primary production of edaphic algal communities in a Delaware salt marsh. *Limnology and Oceanography* **19**, 390–95.
- Garcia-Baptista, M. & Baptista, L.R.M. 1992. Algas psâmicas de Jardim Beira-Mar, Capão da Canoa, Rio Grande do Sul. *Revista Brasileira de Biologia* **52**, 325–42.
- Gargas, E. 1970. Measurements of primary production, dark fixation and vertical distribution of the microbenthic algae in the Øresund. *Ophelia* **8**, 231–53.
- Gargas, E. 1972. Measurements of microalgal primary production (phytoplankton and microbenthos) in the Smålandshavet (Denmark). *Ophelia* **10**, 75–89.
- Gargas, E. 1980. Production and photosynthetic efficiency of microalgae (phytoplankton and microbenthos) in a shallow Danish fjord. *Vatten* **36**, 125–38.
- Gilbert, N.S. 1991a. Primary production by benthic microalgae in nearshore marine sediments of Signy Island, Antarctica. *Polar Biology* **11**, 339–46.
- Gilbert, N.S. 1991b. Microphytobenthic seasonality in near-shore sediments at Signy Island, South Orkney Islands, Antarctica. *Estuarine, Coastal and Shelf Science* **33**, 89–104.
- Gould, D.M. & Gallagher, E.D. 1990. Field measurement of specific growth rate, biomass, and primary production of benthic diatoms of Savin Hill Cove, Boston. *Limnology and Oceanography* **35**, 1757–70.
- Gouleau, D., Blanchard, G. & Cariou-Le Gall, V. 1994. Production potentielle et consommation d'oxygène sur une vasière intertidale au cours d'une émerision. *Vie Milieu* **44**, 109–15.
- Grant, J. 1986. Sensitivity of benthic community respiration and primary production to changes in temperature and light. *Marine Biology* **90**, 299–306.
- Grant, J., Bathmann, U.V. & Mills, E.L. 1986a. The interaction between benthic diatom films and sediment transport. *Estuarine, Coastal and Shelf Science* **23**, 225–38.
- Grant, J., Mills, E.L. & Hopper, C.M. 1986b. A chlorophyll budget of the sediment-water interface and the effect of stabilizing biofilms on particle fluxes. *Ophelia* **26**, 207–19.
- Grøntved, J. 1960. On the productivity of microbenthos and phytoplankton in some Danish fjords. *Meddelelser fra Danmarks Fiskeri- og Havundersøgelser* **3**, 55–92.
- Grøntved, J. 1962. Preliminary report on the productivity of microbenthos and phytoplankton in the Danish Wadden Sea. *Meddelelser fra Danmarks Fiskeri- og Havundersøgelser* **3**, 347–78.
- Guarini, J.-M., Blanchard, G.F., Gros, P. & Harrison, S.J. 1997. Modelling the mud surface temperature on intertidal flats to investigate the spatio-temporal dynamics of the benthic microalgal photosynthetic capacity. *Marine Ecology Progress Series* **153**, 25–36.
- Hackney, J.M., Carpenter, R.C. & Adey, W.H. 1989. Characteristic adaptations to grazing among algal turfs on a Caribbean coral reef. *Phycologia* **28**, 109–19.
- Hanson, R.B., Tenore, K.R., Bishop, S., Chamberlain, C., Pamatmat, M.M. & Tietjen, J. 1981. Benthic enrichment in the Georgia Bight related to Gulf Stream intrusions and estuarine outwelling. *Journal of Marine Research* **39**, 417–41.
- Hargrave, B.T. 1970. The utilization of benthic microflora by *Hyalella azteca* (Amphipoda). *Journal of Animal Ecology* **39**, 427–37.
- Hargrave, B.T., Prouse, N.J., Phillips, G.A. & Neame, P.A. 1983. Primary production and respiration in pelagic and benthic communities at two intertidal sites in the upper Bay of Fundy. *Canadian Journal of Fisheries and Aquatic Sciences* **40** (Suppl. 1), 229–43.
- Hartwig, E.O. 1976. Nutrient cycling between the water-column and a marine sediment. I. Organic carbon. *Marine Biology* **34**, 285–95.
- Hartwig, E.O. 1978. Factors affecting respiration and photosynthesis by the benthic community of a subtidal siliceous sediment. *Marine Biology* **46**, 283–93.
- Hawkins, C.M. & Lewis, J.B. 1982. Benthic primary production on a fringing coral reef in Barbados, West Indies. *Aquatic Botany* **12**, 355–63.
- Hellebust, J.A. & Lewin, J.C. 1972. Transport systems for organic acids induced in the marine pennate diatom, *Cylindrotheca fusiformis*. *Canadian Journal of Microbiology* **18**, 225–33.
- Herndl, G.J., Peduzzi, P. & Fanuko, N. 1989. Benthic community metabolism and microbial dynamics in the Gulf of Trieste (Northern Adriatic Sea). *Marine Ecology Progress Series* **53**, 169–78.
- Holland, A.F., Zingmark, R.G. & Dean, J.M. 1974. Quantitative evidence concerning the stabilization of sediments by marine benthic diatoms. *Marine Biology* **27**, 191–6.
- Holm-Hansen, O., Lorenzen, C.J., Holmes, R.W. & Strickland, J.D.H. 1965. Fluorometric determination of chlorophyll. *Journal du Conseil, Conseil International pour l'Exploration de la Mer* **30**, 3–15.

- Holm-Hansen, O. & Riemann, B. 1978. Chlorophyll *a* determination: improvements in methodology. *Oikos* **30**, 438–47.
- Hopkinson Jr, C.S., Fallen, R.D., Jansson, B.-O. & Schubauer, J.P. 1991. Community metabolism and nutrient cycling at Gray's Reef, a hard bottom habitat in the Georgia Bight. *Marine Ecology Progress Series* **73**, 105–20.
- Horner, R. & Schrader, G.C. 1982. Relative contributions of ice algae, phytoplankton, and benthic microalgae to primary production in nearshore regions of the Beaufort Sea. *Arctic* **35**, 485–503.
- Huang, R. & Boney, A.D. 1984. Growth interactions between littoral diatoms and juvenile marine algae. *Journal of Experimental Marine Biology and Ecology* **81**, 21–45.
- Huettel, M. & Gust, G. 1992. Solute release mechanisms from confined sediment cores in stirred benthic chambers and flume flows. *Marine Ecology Progress Series* **82**, 187–97.
- Hunding, C. & Hargrave, B.T. 1973. A comparison of benthic microalgal production measured by C^{14} and oxygen methods. *Journal of the Fisheries Research Board of Canada* **30**, 309–12.
- Hustedt, F. 1955. Marine littoral diatoms of Beaufort, North Carolina. *Bulletin of the Duke University Marine Laboratory*, No. 6.
- Iannuzzi, T.J., Weinstein, M.P., Sellner, K.G. & Barrett, J.C. 1996. Habitat disturbance and marina development: an assessment of ecological effects. I. Changes in primary production due to dredging and marina construction. *Estuaries* **19**, 257–71.
- Incze, L.S., Mayer, L.M., Sherr, E.B. & Macko, S.A. 1982. Carbon inputs to bivalve mollusks: a comparison of two estuaries. *Canadian Journal of Fisheries and Aquatic Sciences* **39**, 1348–52.
- Jahnke, R.A. & Christiansen, M.B. 1989. A free vehicle benthic chamber instrument for sea floor studies. *Deep-Sea Research* **36**, 625–37.
- Jahnke, R.A., Marinelli, R.L., Nelson, J.R. & Eckman, J.E. 1996. The role of benthic primary production on the cycling of carbon, oxygen and nutrients on continental shelves. *Transactions of the American Geophysical Union* **76**, 202 only.
- Jeffrey, S.W. & Humphrey, G.F. 1975. New spectrophotometer equations for determining chlorophylls *a*, *b*, *c*₁, *c*₂, in higher plants, algae, and natural phytoplankton. *Biochimie und Physiologic der Pflanzen* **167**, 191–4.
- Jenness, M.I. & Duineveld, G.C.A. 1985. Effects of tidal currents on chlorophyll *a* content of sandy sediments in the southern North Sea. *Marine Ecology Progress Series* **21**, 283–7.
- Jerlov, N.G. 1970. Light. In *Marine ecology*, O.Kinne (ed.). London: Wiley Interscience, 95–102.
- Johnstone, R.W., Koop, K. & Larkin, A.W.D. 1990. Physical aspects of coral reef lagoon sediments in relation to detritus processing and primary production. *Marine Ecology Progress Series* **66**, 273–83.
- Joint, I.R. 1978. Microbial production of an estuarine mudflat. *Estuarine and Coastal Marine Science* **7**, 185–95.
- Joint, I.R., Gee, J.M. & Warwick, R.M. 1982. Determination of fine-scale vertical distribution of microbes and meiofauna in an intertidal sediment. *Marine Biology* **72**, 157–64.
- Juniper, S.K. 1987. Deposit feeding ecology of *Amphibola crenata* I. Long-term effects of deposit feeding on sediment micro-organisms. *New Zealand Journal of Marine and Freshwater Research* **21**, 235–46.
- Kamykowski, D. & Bird, J.L. 1981. Phytoplankton associations with the variable nepheloid layer on the Texas continental shelf. *Estuarine, Coastal and Shelf Science* **13**, 317–26.
- Kelley, B.J., McKellar, H.N. & Zingmark, R.G. 1986. Summary and comparison of component productivities. In *South Carolina coastal wetland impoundments: ecological characterization, management, status and use. Vol. II. Technical synthesis*, R.Devoe & D.Baughman (eds). South Carolina Sea Grant Publication #SC-SG-TR-86–2.
- Kendrick, G.A., Jacoby, C.A. & Heinemann, D. 1996. Benthic microalgae: comparisons of chlorophyll *a* in mesocosms and field sites. *Hydrobiologia* **326/327**, 283–9.
- Kennett, D.M. & Hargraves, P.E. 1984. Subtidal benthic diatoms from a stratified estuarine basin. *Botanica Marina* **27**, 169–83.
- Klein, B. & Riaux-Gobin, C. 1991. Algal pigment diversity in coastal sediments from Kerguelen (sub-Antarctic Islands) reflecting local dominance of green algae, euglenoids and diatoms. *Polar Biology* **11**, 439–48.
- Kromkamp, J., Peene, J., van Rijswijk, P., Sandee, A. & Goosen, N. 1995. Nutrients, light and primary production by phytoplankton and microphytobenthos in the eutrophic, turbid Westerschelde estuary (The Netherlands). *Hydrobiologia* **311**, 9–19.

- Kwak, T.J. & Zedler, J.B. 1997. Food web analysis of southern California coastal wetlands using multiple stable isotopes. *Oecologia* **110**, 262–77.
- Lassen, C., Ploug, H. & Jørgensen, B.B. 1992. Microalgal photosynthesis and spectral scalar irradiance in coastal marine sediments of Limfjorden, Denmark. *Limnology and Oceanography* **37**, 760–72.
- Laws, R.A. 1988. Diatoms (Bacillariophyceae) from surface sediments in the San Francisco Bay estuary. *Proceedings of the California Academy of Sciences* **45**, 133–254.
- Leach, J.H. 1970. Epibenthic algal production in an intertidal mudflat. *Limnology and Oceanography* **15**, 514–21.
- Lewin, J.C. & Hellebust, J.A. 1975. Heterotrophic nutrition of the marine pennate diatom *Navicula pavillardii* Hustedt. *Canadian Journal of Microbiology* **21**, 1335–42.
- Lewin, J.C., & Hellebust, J.A. 1976. Heterotrophic nutrition of the marine pennate diatom *Nitzschia angularis* var. *affinis*. *Marine Biology* **36**, 313–20.
- Lewin, J.C. & Lewin, R.A. 1960. Auxotrophy and heterotrophy in marine littoral diatoms. *Canadian Journal of Microbiology* **6**, 127–34.
- Littler, M., Littler, D., Blair, S.M. & Norris, J.N. 1985. Deepest known plant life discovered on an uncharted seamount. *Science* **227**, 57–9.
- Longhurst, A., Sathyendrenath, S., Platt, T. & Caverhill, C. 1995. An estimate of global production in the ocean from satellite radiometer data. *Journal of Plankton Research* **17**, 1245–71.
- Lorenzen, C.J. 1966. A method for the continuous measurement of *in vivo* chlorophyll concentration. *Deep-Sea Research* **13**, 223–7.
- Lorenzen, C.J. 1967. Determination of chlorophyll and phaeopigments: spectrophotometric equations. *Limnology and Oceanography* **12**, 343–6.
- Ludden, E., Admiraal, W. & Colijn, F. 1985. Cycling of carbon and oxygen in layers of marine microphytes; a simulation model and its eco-physiological implications. *Oecologia* **66**, 50–59.
- Lukatelich, R.J. & McComb, A.J. 1986. Distribution and abundance of benthic microalgae in a shallow southwestern Australian estuarine system. *Marine Ecology Progress Series* **27**, 287–97.
- MacIntyre, H.L. & Cullen, J.J. 1996. Primary production by suspended and benthic microalgae in a turbid estuary: time-scales of variability in San Antonio Bay, Texas. *Marine Ecology Progress Series* **145**, 245–68.
- MacIntyre, H.L., Geider, R.J. & Miller, D.C. 1996. Microphytobenthos: The ecological role of the “secret garden” of unvegetated, shallow-water marine habitats. I. Distribution, abundance, and primary production. *Estuaries* **19**, 186–201.
- Madsen, K.N., Nilsson, P. & Sundbäck, K. 1993. The influence of benthic microalgae on the stability of a subtidal sediment. *Journal of Experimental Marine Biology and Ecology* **170**, 159–77.
- Marinelli, R.L. 1992. Effects of polychaetes on silicate dynamics and fluxes in sediments: importance of species, animal activity and polychaete effects on benthic diatoms. *Journal of Marine Research* **50**, 745–81.
- Marra, J. & Heinemann, K. 1984. A comparison between noncontaminating and conventional incubation procedures in primary production measurements. *Limnology and Oceanography* **29**, 389–92.
- Marshall, N., Oviatt, C.A. & Skauen, D.M. 1971. Productivity of the benthic microflora of shoal estuarine environments in southern New England. *Internationale Revue der gesamten Hydrobiologie* **56**, 947–56.
- Martin, J.H., Knauer, G.A., Karl, D.M. & Broenkow, W.W. 1987. VERTEX: carbon cycling in the northeast Pacific. *Deep-Sea Research* **34**, 267–85.
- Matheke, G.E.M. & Horner, R. 1974. Primary productivity of the benthic microalgae in the Chukchi Sea near Barrow, Alaska. *Journal of the Fisheries Research Board of Canada* **31**, 1779–86.
- McIntire, C.D. & Ampoker, M.C. 1986. Effects of sediment properties on benthic primary production in the Columbia River Estuary. *Aquatic Botany* **24**, 249–67.
- McIntire, C.D. & Moore, W.W. 1977. Marine littoral diatoms: Ecological considerations. In *Botanical Monographs, Vol. 13. The biology of diatoms*, D.Werner (ed.). Berkeley: University of California Press, 333–71.
- Meadows, P.S. & Anderson, J.G. 1968. Microorganisms attached to marine sand grains. *Journal of the Marine Biological Association of the United Kingdom* **48**, 161–75.
- Megard, R.O. & Berman, T. 1989. Effects of algae on the Secchi transparency of the southeastern Mediterranean Sea. *Limnology and Oceanography* **34**, 1640–55.
- Menard, H.W. & Smith, S.M. 1966. Hypsometry of ocean basin provinces. *Journal of Geophysical Research* **71**, 4305–325.

- Miller, D.C. 1989. Abrasion effects on microbes in sandy sediments. *Marine Ecology Progress Series* **55**, 73–82.
- Miller, D.C., Geider, R.J. & MacIntyre, H.L. 1996. Microphytobenthos: The ecological role of the “secret garden” of unvegetated, shallow-water marine habitats. II. Role in sediment stability and shallow-water food webs. *Estuaries* **19**, 202–12.
- Miller, R.L. & Kamykowski, D.L. 1986. Effects of temperature, salinity, irradiance and diurnal periodicity on growth and photosynthesis in the diatom *Nitzschia americana*: light-saturated growth. *Journal of Phycology* **22**, 339–48.
- Mills, D.K. & Wilkinson, M. 1986. Photosynthesis and light in estuarine benthic microalgae. *Botanica Marina* **29**, 125–9.
- Moncrieff, C.A., Sullivan, M.J. & Daehnick, A.E. 1992. Primary production dynamics in seagrass beds of Mississippi Sound: the contributions of seagrass, epiphytic algae, sand microflora, and phytoplankton. *Marine Ecology Progress Series* **87**, 161–71.
- Montagna, P.A. 1995. Rates of metazoan meiofaunal microbivory: a review. *Vie Milieu* **45**, 1–9.
- Montagna, P.A., Blanchard, G.F. & Dinert, A. 1995. Effect of production and biomass of intertidal microphytobenthos on meiofaunal grazing rates. *Journal of Experimental Marine Biology and Ecology* **185**, 149–65.
- Morel, A. & Berthon, J.-F. 1989. Surface pigments, algal biomass profiles, and potential production of the euphotic layer: relationships reinvestigated in view of remote-sensing applications. *Limnology and Oceanography* **34**, 1545–62.
- Moriarty, D.J.W., Pollard, P.C., Hunt, W.G., Moriarty, C.M. & Wassenberg, T.J. 1985. Productivity of bacteria and microalgae and the effect of grazing by holothurians in sediments on a coral reef flat. *Marine Biology* **85**, 293–300.
- Newell, R.I.E., Marshall, N., Sasekumar, A. & Chong, V.C. 1995. Relative importance of benthic microalgae, phytoplankton, and mangroves as sources of nutrition for penaeid prawns and other coastal invertebrates from Malaysia. *Marine Biology* **123**, 595–606.
- NODC 1987. *World-wide ocean water color/water transparency data*. Washington, DC 20235: National Oceanographic Data Center, National Environmental Satellite, Data, and Information Service.
- Nowicki, B.L. & Nixon, S.W. 1985. Benthic community metabolism in a coastal lagoon ecosystem. *Marine Ecology Progress Series* **22**, 21–30.
- Page, H.M., Dugan, J.E. & Hubbard, D.M. 1992. Comparative effects of infaunal bivalves on an epibenthic microalgal community. *Journal of Experimental Marine Biology and Ecology* **157**, 247–62.
- Palmisano, A.C., SooHoo, J.B. & Sullivan, C.W. 1985a. Photosynthesis-irradiance relationships in sea-ice microalgae from McMurdo Sound, Antarctica. *Journal of Phycology* **21**, 341–6.
- Palmisano, A.C., SooHoo, J.B. & Sullivan, C.W. 1987. Effects of four environmental variables on photosynthesis-irradiance relationships in Antarctic sea-ice microalgae. *Marine Biology* **94**, 299–306.
- Palmisano, A.C., SooHoo, J.B., White, D.C., Smith, G.A., Stanton, G.R. & Burckle, L.H. 1985b. Shade adapted benthic diatoms beneath Antarctic sea-ice. *Journal of Phycology* **21**, 664–7.
- Pamatmat, M.M. 1968. Ecology and metabolism of a benthic community on an intertidal sandflat. *Internationale Revue der gesamten Hydrobiologie* **53**, 211–98.
- Parsons, T.R., Maita, Y. & Lalli, C.M. 1984. *A manual of chemical and biological methods of seawater analysis*. New York: Pergamon.
- Paterson, D.M. 1989. Short-term changes in the erodibility of intertidal cohesive sediments related to the migratory behavior of epipellic diatoms. *Limnology and Oceanography* **34**, 223–34.
- Perry, M.J., Talbot, M.C. & Alberte, R.S. 1981. Photoadaptation in marine phytoplankton: response of the photosynthetic unit. *Marine Biology* **62**, 91–101.
- Pinckney, J., Paerl, H.W. & Fitzpatrick, M. 1995. Impacts of seasonality and nutrients on microbial mat community structure and function. *Marine Ecology Progress Series* **123**, 207–16.
- Pinckney, J. & Sandulli, R. 1990. Spatial autocorrelation analysis of meiofaunal and microalgal populations on an intertidal sandflat: Scale linkage between consumers and resources. *Estuarine, Coastal and Shelf Science* **30**, 341–53.
- Pinckney, J. & Zingmark, R.G. 1991. Effects of tidal stage and sun angles on intertidal benthic microalgal productivity. *Marine Ecology Progress Series* **76**, 81–9.
- Pinckney, J.L. & Zingmark, R.G. 1993. Modeling the annual production of intertidal benthic microalgae in estuarine ecosystems. *Journal of Phycology* **29**, 396–407.

- Plante, R., Plante-Cuny, M.R. & Reys, J.-P. 1986. Photosynthetic pigments of sandy sediments on the north Mediterranean coast: their spatial distribution and its effect on sampling strategies. *Marine Ecology Progress Series* **34**, 133–41.
- Plante-Cuny, M.R. 1974. Evaluation par spectrophotométrie des teneurs en chlorophylle *a* fonctionnelle et en phéopigments des substrats meubles marins. *Documents Scientifiques de Mission ORSTOM. Nosy-Bé* **45**, 1–76.
- Plante-Cuny, M.R. 1977. Pigments photosynthétiques et production primaire du microphytobenthos d'une lagune tropicale, la Lagune Ébrié (Abidjan, Côte d'Ivoire). *Cahiers ORSTOM, series Oceanographique* **15**, 3–25.
- Plante-Cuny, M.R. 1978. Pigments photosynthétiques et production primaire des fonds meubles néritiques d'une région tropicale (Nosy-Bé, Madagascar). *Travaux et Documents de L'ORSTOM* **96**, Paris.
- Plante-Cuny, M.R. 1984. Le microphytobenthos et son rôle à l'échelon primaire dans le milieu marin. *Oceanis* **10**, 417–27.
- Plante-Cuny, M.R. & Boday, A. 1987. Biomasse et production primaire du phytoplancton de deux biotopes sableux (Golfe de Fos, France). *Oceanologica Acta* **10**, 223–37.
- Plante-Cuny, M.R. & Plante, R. 1986. Benthic marine diatoms as food for benthic marine animals. In *Proceedings of the Eighth International Diatom Symposium*, M.Ricard (ed.) Koenigstein, Germany: Koeltz Scientific Books, 525–37.
- Plante-Cuny, M.R., Salen-Picard, C., Grenz, C., Plante, R., Alliot, E. & Barranguet, C. 1993. Experimental field study of the effects of crude oil, drill cuttings and natural biodeposits on microphytoand macrozoobenthic communities in a Mediterranean area. *Marine Biology* **117**, 355–66.
- Platt, T. & Harrison, W.G. 1985. Biogenic fluxes of carbon and nitrogen in the ocean. *Nature* **318**, 55–68.
- Pomeroy, L.R. 1959. Algal productivity in Georgia salt marshes. *Limnology and Oceanography* **4**, 386–97.
- Pomeroy, L.R. 1960. Primary productivity of Boca Ciega Bay, Florida. *Bulletin of Marine Science of the Gulf and Caribbean* **10**, 1–10.
- Pomeroy, W.G. & Stockner, J.G. 1976. Effects of environmental disturbance on the distribution and primary production of benthic algae on a British Columbia estuary. *Journal of the Fisheries Research Board of Canada* **33**, 1175–87.
- Posey, M., Powell, C., Cahoon, L. & Lindquist, D. 1995. Top down versus bottom up control of benthic community composition on an intertidal tideflat. *Journal of Experimental Marine Biology and Ecology* **185**, 19–31.
- Reay, W.G., Gallagher, D.L. & Simmons Jr, G.M. 1995. Sediment-water-column oxygen and nutrient fluxes in nearshore environments of the lower Delmarva Peninsula, USA. *Marine Ecology Progress Series* **118**, 215–27.
- Revsbech, N.P. & Jørgensen, B.B. 1983. Photosynthesis of benthic microflora measured with high spatial resolution by the oxygen microprofile method: Capabilities and limitations of the method. *Limnology and Oceanography* **28**, 749–57.
- Revsbech, N.P., Jørgensen, B.B. & Brix, O. 1981. Primary production of microalgae in sediments measured by oxygen microprofile, $H^{14}CO_3$ fixation, and oxygen exchange methods. *Limnology and Oceanography* **26**, 717–30.
- Riaux, C. 1983. Structure d'un peuplement estuarien de diatomées épipeliques du Nord-Finistère. *Oceanologica Acta* **6**, 173–83.
- Riaux-Gobin, C., Douchement, C. & Tréguer, P. 1989. Microphytobenthos de deux sédiments subtidaux de Nord Bretagne. *Hydrobiologia* **178**, 11–20.
- Riaux-Gobin, C., Llewellyn, C.A. & Klein, B. 1987. Microphytobenthos from two subtidal sediments from North Brittany. II. Variations of pigment compositions and concentrations determined by HPLC and conventional techniques. *Marine Ecology Progress Series* **40**, 275–83.
- Riemann, B. 1978. Carotenoid interference in the spectrophotometric determination of chlorophyll degradation products from natural populations of phytoplankton. *Limnology and Oceanography* **23**, 1059–66.
- Riera, P. & Richard, P. 1996. Isotopic determination of food sources of *Crassostrea gigas* along a trophic gradient in the estuarine bay of Marennes-Oléron. *Estuarine, Coastal and Shelf Science* **42**, 347–60.

- Rivkin, R.B. & DeLaca, T.E. 1990. Trophic dynamics in Antarctic benthic communities. I. In situ ingestion of microalgae by Foraminifera and metazoan meiofauna. *Marine Ecology Progress Series* **64**, 129–36.
- Rivkin, R.B. & Putt, M. 1987. Photosynthesis and cell division by Antarctic microalgae: comparison of benthic, planktonic and ice algae. *Journal of Phycology* **23**, 223–9.
- Riznyk, R.Z., Edens, J.L. & Libby, R.C. 1978. Production of epibenthic diatoms in a southern California impounded estuary. *Journal of Phycology* **14**, 273–9.
- Rizzo, W.M. 1990. Nutrient exchange between the water-column and a subtidal benthic microalgal community. *Estuaries* **13**, 219–26.
- Rizzo, W.M., Lackey, G.J. & Christian, R.R. 1992. Significance of euphotic, subtidal sediments to oxygen and nutrient cycling in a temperate estuary. *Marine Ecology Progress Series* **86**, 51–61.
- Rizzo, W.M. & Wetzel, R.L. 1985. Intertidal and shoal benthic community metabolism in a temperate estuary: studies of spatial and temporal scales of variability. *Estuaries* **8**, 342–51.
- Rodgers, J.H. & Harvey, R.S. 1976. The effect of current on periphytic productivity as determined using carbon-14. *Water Resources Bulletin* **12**, 1109–18.
- Roemer, S.C., Hoagland, K.D. & Rosowski, J.R. 1984. Development of a freshwater periphyton community as influenced by diatom mucilages. *Canadian Journal of Botany* **62**, 1799–813.
- Roman, M.R. & Tenore, K.R. 1978. Tidal resuspension in Buzzards Bay, Massachusetts. I. Seasonal changes in the resuspension of organic carbon and chlorophyll *a*. *Estuarine and Coastal Marine Science* **6**, 37–46.
- Round, F.E. 1971. Benthic marine diatoms. *Oceanography and Marine Biology: an Annual Review* **9**, 83–139.
- Round, F.E. 1979. A diatom assemblage living below the surface of intertidal sand flats. *Marine Biology* **54**, 219–23.
- Rysgaard, S., Christensen, P.B. & Nielsen, L.P. 1995. Seasonal variation in nitrification and denitrification in estuarine sediment colonized by benthic microalgae and bioturbating infauna. *Marine Ecology Progress Series* **126**, 111–21.
- Rysgaard, S., Risgaard-Petersen, N. & Sloth, N.P. 1996. Nitrification, denitrification, and nitrate ammonification in sediments of two coastal lagoons in Southern France. *Hydrobiologia* **329**, 133–41.
- Sabbe, K. & Vyverman, W. 1991. Distribution of benthic diatom assemblages in the Westerschelde (Zeeland, The Netherlands). *Belgian Journal of Botany* **124**, 91–101.
- Santos, P.J.P., Castel, J. & Souza-Santos, L.P. 1995. Microphytobenthic patches and their influence on meiofaunal distribution. *Cahiers Biologie Marine* **36**, 133–9.
- Schreiber, R.A. & Pennock, J.R. 1995. The relative contribution of benthic microalgae to total microalgal production in a shallow sub-tidal estuarine environment. *Ophelia* **42**, 335–52.
- Shaffer, G.P. 1988. A comparison of benthic microfloral production on the West and Gulf coasts of the United States: an introduction to the dynamic K-systems model. *Marine Ecology Progress Series* **43**, 55–62.
- Shaffer, G.P. & Onuf, C.P. 1983. An analysis of factors influencing the primary production of the benthic microflora in a southern California lagoon. *Netherlands Journal of Sea Research* **17**, 126–44.
- Shaffer, G.P. & Onuf, C.P. 1985. Reducing the error in estimating annual production of benthic microflora: hourly to monthly rates, patchiness in space and time. *Marine Ecology Progress Series* **26**, 221–31.
- Shaffer, G.P. & Sullivan, M.J. 1988. Water-column productivity attributable to displaced benthic diatoms in well-mixed shallow estuaries. *Journal of Phycology* **24**, 132–40.
- Sharp, G.D. 1988. Fish populations and fisheries: their perturbations, natural and man-induced. In *Ecosystems of the world, 27: continental shelves*, H.Postma & J.J.Zijlstra (eds). New York: Elsevier, 155–202.
- Sigmon, D.E. & L.B.Cahoon. 1997. Comparative effects of benthic microalgae and phytoplankton on dissolved silica fluxes. *Aquatic Microbial Ecology* **13**, 275–84.
- Sloan, N.A. & von Bodungen, B. 1980. Distribution and feeding of the sea cucumber *Isostichopus badionotus* in relation to shelter and sediment criteria of the Bermuda Platform. *Marine Ecology Progress Series* **2**, 257–64.
- Sorokin, Yu.I. 1973. Production characteristics of microflora, periphyton and phytoplankton of the coral biomasses on Majuro Atoll (Marshall Islands). *Okeanologija* **13**, 487–92.

- Sorokin, Yu.I. 1986. Parameters of productivity of some components of coral reef ecosystems. *Polskie Archiwum Hydrobiologii* **33**, 33–68.
- Sorokin, Yu.I. 1990. Aspects of trophic relations, productivity and energy balance on coral-reef ecosystems. In *Coral reefs*, Z.Dubinsky (ed.). Amsterdam: Elsevier, 401–10.
- Sournia, A. 1976a. Ecologie et productivité d'une Cyanophycée en milieu corallien: *Oscillatoria limosa* Agardh. *Phycologia* **15**, 363–6.
- Sournia, A. 1976b. Primary production of sands in the lagoon of an atoll and the role of foraminiferan symbionts. *Marine Biology* **37**, 29–32.
- Sournia, A. 1976c. Oxygen metabolism of a fringing reef in French Polynesia. *Helgoländer Wissenschaftliche Meeresuntersuchungen* **28**, 401–10.
- Steele, J.H. & Baird, I.E. 1968. Production ecology of a sandy beach. *Limnology and Oceanography* **13**, 14–25.
- Stribling, J.M. & Cornwell, J.C. 1997. Identification of important primary producers in a Chesapeake Bay tidal creek system using stable isotopes of carbon and sulphur. *Estuaries* **20**, 77–85.
- Strickland, J.D.H. & Parsons, T.R. 1968. A practical handbook of seawater analysis. *Bulletin of the Fisheries Research Board of Canada* No. 167, 1–311.
- Strickland, J.D.H. & Parsons, T.R. 1972. *A practical handbook of seawater analysis*, 2nd edn, *Bulletin of the Fisheries Research Board of Canada* No. 167, 1–310.
- Sullivan, M.J. & Moncrieff, C.A. 1988. Primary production of edaphic algal communities in a Mississippi salt marsh. *Journal of Phycology* **24**, 49–58.
- Sullivan, M.J. & Moncrieff, C.A. 1990. Edaphic algae are an important component of salt marsh food-webs: evidence from multiple stable isotope analyses. *Marine Ecology Progress Series* **62**, 149–59.
- Sun, M.-Y., Aller, R.C. & Lee, C. 1994. Spatial and temporal distributions of sedimentary chloropigments as indicators of benthic processes in Long Island Sound. *Journal of Marine Research* **52**, 149–76.
- Sundbäck, K. 1986. What are the benthic microalgae doing on the bottom of Laholm Bay? *Ophelia Suppl.* **4**, 273–86.
- Sundbäck, K., Enoksson, V., Granéli, W. & Pettersson, K. 1991. Influence of sublittoral microphytobenthos on the oxygen and nutrient flux between sediment and water: a laboratory continuous-flow study. *Marine Ecology Progress Series* **74**, 263–79.
- Sundbäck, K. & Granéli, W. 1988. Influence of microphytobenthos on the nutrient flux between sediment and water: a laboratory study. *Marine Ecology Progress Series* **43**, 63–9.
- Sundbäck, K. & Jönsson, B. 1988. Microphytobenthic productivity and biomass in sublittoral sediments of a stratified bay, southeastern Kattegat. *Journal of Experimental Marine Biology and Ecology* **122**, 63–81.
- Sverdrup, H.U., Johnson, M.W. & Fleming, R.H. 1962. *The oceans: their physics, chemistry and general biology*. Englewood Cliffs, NJ: Prentice-Hall.
- Therkildsen, M.S. & Lomstein, B.A. 1993. Seasonal variation in net benthic C-mineralization in a shallow estuary. *FEMS Microbiology Ecology* **12**, 131–42.
- Thom, R.M. 1984. Primary production in Gray's Harbor Estuary, Washington. *Bulletin of the Southern California Academy of Science* **83**, 99–105.
- Thom, R.M., Parkwell, T.L., Niyogi, D.K. & Shreffler, D.K. 1994. Effects of graveling on the primary productivity, respiration and nutrient flux of two estuarine tidal flats. *Marine Biology* **118**, 329–41.
- Thomas, C.J. & Cahoon, L.B. 1993. Stable isotope analyses differentiate between different trophic pathways supporting rocky-reef fishes. *Marine Ecology Progress Series* **95**, 19–24.
- Thompson, J.K. & Nichols, F.H. 1988. Food availability controls seasonal cycle of growth in *Macoma balthica* (L.) in San Francisco Bay, California. *Journal of Experimental Marine Biology and Ecology* **116**, 43–61.
- Thompson, J.K., Nichols, F.H., Wienke, S.M. & Wong, R.L.J. 1981. A comparison of benthic microalgae and phytoplankton biomass in San Francisco Bay. *Estuaries* **4**, 299 only.
- Triska, F.J. & Oremland, R.S. 1981. Denitrification associated with periphyton communities. *Applied and Environmental Microbiology* **42**, 745–8.
- Underwood, G.J.C. & Paterson, D.M. 1993. Seasonal changes in diatom biomass, sediment stability and biogenic stabilization in the Severn estuary. *Journal of the Marine Biological Association of the United Kingdom* **73**, 871–87.

- Underwood, G.J.C., Paterson, D.M. & Parkes, R.J. 1995. The measurement of microbial carbohydrate exopolymers from intertidal sediments. *Limnology and Oceanography* **40**, 1243–53.
- Van Es, F.B. 1982. Community metabolism of intertidal flats in the Ems Dollard Estuary. *Marine Biology* **66**, 95–108.
- van Raalte, C., Stewart, W.C. & Valiela, I. 1974. A ¹⁴C technique for measuring salt marsh productivity in salt marsh muds. *Botanica Marina* **17**, 186–8.
- van Raalte, C., Valiela, I. & Teal, J.M. 1976. Production of salt marsh algae: Light and nutrient limitation. *Limnology and Oceanography* **21**, 862–72.
- Varela, M. 1981. El problema de la determinación de clorofila *a* en el fitomicrobentos: discusión sobre la metodología. *Oecologia aquatica* **5**, 7–19.
- Varela, M. 1985. Medida de la producción primaria de la microflora bentónica. Revisión metodológica. *Boletín del Instituto Español de Oceanografía* **2**, 53–68.
- Varela, M. & Penas, E. 1985. Primary production of benthic microalgae in an intertidal sand flat of the Ria de Arosa, NW Spain. *Marine Ecology Progress Series* **25**, 111–19.
- Vilbaste, S. 1992. Microphytobenthos—a part of the ecosystem of Haapsalu Bay, the Baltic Sea. *Proceedings of the Estonian Academy of Science and Ecology* **2**, 119–26.
- Vollenweider, R.A. 1974. *A manual of methods for measurement of primary production in aquatic ecosystems*. IBP Handbook No. 12. Oxford: Blackwell Scientific Publications.
- Walsh, J.J. 1984. The role of the ocean biota in accelerated ecological cycles: a temporal view. *BioScience* **34**, 499–507.
- Walsh, J.J. 1988. *On the nature of continental shelves*, San Diego, CA: Academic Press.
- Wanders, J.B.W. 1976. The role of benthic algae in the shallow reef of Curacao (Netherlands Antilles): primary productivity in the coral reef. *Aquatic Botany* **2**, 235–70.
- Wendker, S. & Marshall, H.G. 1993. Primary productivity of benthic microalgae in the lower Chesapeake Bay. *Virginia Journal of Science* **44**, 125 only.
- Wennhage, H. & Pihl, L. 1994. Substratum selection by juvenile plaice (*Pleuronectes platessa* L.): impact of benthic microalgae and filamentous macroalgae. *Netherlands Journal of Sea Research* **32**, 343–51.
- Whitney, D.E. & Darley, W.M. 1979. A method for the determination of chlorophyll *a* in samples containing degradation products. *Limnology and Oceanography* **24**, 183–6.
- Whitney, D.E. & Darley, W.M. 1983. Effect of light intensity upon salt marsh benthic microalgal photosynthesis. *Marine Biology* **75**, 249–52.
- Wilkinson, V. 1981. *Production ecology of microphytobenthos populations in the Manukau Harbour*. MS thesis, University of Auckland, New Zealand.
- Wollast, R. 1991. The coastal organic carbon cycle: fluxes, sources, and sinks. In *Ocean margin processes in global change*, R.F.C. Mantoura et al. (eds). New York: John Wiley, 365–81.
- Wollast, R. & Billen, G. 1981. The fate of terrestrial organic carbon in the coastal area. In *Carbon dioxide effects research and assessment program*, G.E. Likens et al. (eds). Washington: US Department of Energy, CONF 8009140, 331–59.
- Wulff, A., Sundbäck, K., Nilsson, C., Carlson, L. & Jönsson, B. 1997. Effect of sediment load on the microbenthic community of a shallow-water sandy sediment. *Estuaries* **20**, 547–58.
- Yallop, M.L., de Winder, B., Paterson, D.M. & Stal, L.J. 1994. Comparative structure, primary production and biogenic stabilization of cohesive and non-cohesive marine sediments inhabited by microphytobenthos. *Estuarine, Coastal and Shelf Science* **38**, 565–82.
- Yentsch, C.S. & Menzel, D.W. 1963. A method for the determination of phytoplankton chlorophyll and phaeophytin by fluorescence. *Deep-Sea Research* **10**, 221–31.
- Zedler, J.B. 1980. Algal mat productivity: comparisons in a salt marsh. *Estuaries* **3**, 122–31.
- Zedler, J.B. 1982. Salt marsh algal mat composition: spatial and temporal comparisons. *Bulletin of the Southern California Academy of Science* **81**, 41–50.
- Zingmark, R.G. 1986. Production of the microbenthic algae. In *South Carolina Coastal wetlands and impoundments: ecological characteristics, management, status, and use. Vol. II. Technical synthesis*, R. Devoe & D. Baughman (eds). SC Sea Grant Publication No. SC-SG-TR-86–2, Charleston, SC, 179–94.

MESOTHERBIVORE-MACROALGAL INTERACTIONS: FEEDING ECOLOGY OF SACOGLOSSAN SEA SLUGS (MOLLUSCA, OPISTHOBRANCHIA) AND THEIR EFFECTS ON THEIR FOOD ALGAE

S.I. WILLIAMS & D.I. WALKER

Botany Department, The University of Western Australia, WA, 6907, Australia

Abstract The feeding interactions between sacoglossan (= ascoglossan) sea slugs and their algal prey are discussed. Many of these gastropod molluscs are capable of kleptoplasty—a process whereby the slugs photosynthesize using chloroplasts ingested from their algal diet. Despite extensive study, the importance of kleptoplasty in sacoglossan (slug) feeding ecology remains poorly defined. The effects of slug grazing on marine algae, particularly in tropical-subtropical regions are also unclear. We extend the scope of previous reviews and synthesize the disparate areas of sacoglossan feeding ecology. The review is in three parts: first, the diet of sacoglossans is discussed; secondly, the role of kleptoplasty in slug feeding ecology is examined and thirdly, the effects of grazing by the slugs on their food algae are considered. Further research is required to clarify sacoglossan feeding ecology, in particular slug food choice in the field, the importance of kleptoplasty to the range of slug diets and the effects of slug grazing on tropical marine algae.

Introduction

Despite extensive study of sacoglossan (slug)—algal interactions and a number of reviews (Trench 1975 on kleptoplasty in the group, Jensen 1980 on diet, Clark & DeFreese 1987 on population ecology, Clark 1992 and Jensen 1993b on feeding ecology, Williams & Cobb 1992 on endosymbiosis and Jensen 1996, 1997a,b on slug systematics and phylogeny), slug feeding ecology remains poorly defined. A comprehensive understanding of the intricate relationship between these marine mesograzers and their food plants has yet to be developed (Jensen 1993b). Since these reviews were published, a number of researchers have published studies that help to elucidate the role of kleptoplasty in slug feeding ecology and the effects of slug grazing on food algae. Our review synthesizes this recent ecological work with earlier physiological studies, summarizing the current state of knowledge of slug feeding ecology and highlighting areas where further work is required.

Three areas relevant to slug feeding ecology are discussed. First, the diet of sacoglossans is examined, with a critical examination of the methods used in obtaining dietary information. Many studies have been based on slug-algal associations in the field, with only a few rigorous food choice experiments conducted. Secondly, the role of kleptoplasty in slug feeding ecology is discussed. Very few studies in this area exist, particularly for slugs feeding on the green alga *Caulerpa*, the most widespread diet within the group. Finally, the effects of slug grazing on their algal host are investigated. A number of studies in the

area have been carried out on temperate shores. Again, there is a paucity of data for slug-*Caulerpa* associations.

What are sacoglossans?

Sacoglossan sea slugs are a diverse order of marine molluscs in the subclass Opisthobranchia (Class Gastropoda). The term “opisthobranch” means “rearward gills” (Yonge & Thompson 1976)—most opisthobranchs have gills at the rear end of the body. Opisthobranchs usually have two pairs of tentacles on the head (one pair of rhinophores and one pair of oral tentacles), with an eye located at the base of the tentacles. The eyes are not highly developed and mostly function in orientation rather than object discrimination. Opisthobranchs are hermaphroditic and are a very diverse group, ranging from bubble shells to sea butterflies, sea hares and various types of sea slugs (Yonge & Thompson 1976).

Sacoglossans display a remarkable diversity in shape, ranging from shelled burrowing species (*Ascobulla*) and the bivalved *Julia* to epifaunal, nudibranch-like species (*Stiliger*, *Polybranchia*) and flattened leaf-like *Elysia* (Burn 1998). The shelled sacoglossans possess gills, but in the non-shelled slugs gills are absent, with gas exchange instead occurring through the body surface. Many of these slugs have a high surface area to volume ratio through extensions of the body such as parapodia or cerata. Sacoglossans are generally small—from less than 1 cm to 4 cm in length (Wells & Bryce 1993). They can be difficult to see as their colour is generally green, like that of the algae upon which they are usually found, with the slug coloration provided by algal chloroplasts retained in the digestive gland.

The two characteristics common to the order are their almost exclusively herbivorous habit and their highly modified uniseriate radula. The vast majority of sacoglossans are herbivorous with many species feeding on green algae, although a few species are carnivorous, feeding on opisthobranch egg masses (Clark 1992). The radula of sacoglossans is highly modified, with a continuous single row of teeth (Fig. 1). The blade-like tooth is very distinctive and is often used in identification of genera (Burn 1972).

Gascoigne (1985) reports that the order Sacoglossa was proposed in 1876 by Ihering, and almost simultaneously the term Ascoglossa was proposed by Bergh. Both names for the order are still used, referring to the feature common throughout the order—a small sac (or ascus) ventral to the buccal mass, in which worn radular teeth are stored (Gascoigne 1985). Although the terms Sacoglossa and Ascoglossa are both in current usage, Sacoglossa is used throughout this review, as suggested by Jensen (1992).

Another distinctive feature of the sacoglossans is their digestive gland, which tends to be highly branched, particularly in the shell-less species (Fig. 2). The digestive gland may be divided into many branches, which extend into the cerata and parapodia, covering much of the slug’s dorsal surface. These branches may be involved in the circulation of blood (e.g. in *Alderia modesta*) as well as digestive function (Yonge & Thompson 1976).

Approximately 250 to 300 species of sacoglossan have been described (Jensen 1997b). According to Clark (1992), there may be as many as 400 species of sacoglossans worldwide. The slugs described to date tend to inhabit near-shore subtidal and intertidal areas, including splash zone rockpools on open-coast shores (Trowbridge 1993a), coral reef flats and mangroves (Clark & DeFreese 1987), sheltered sandy bays (Jensen 1990), mudflats (Trowbridge 1993c), salt marsh (Gascoigne 1985, Theisen & Jensen 1991) and exposed

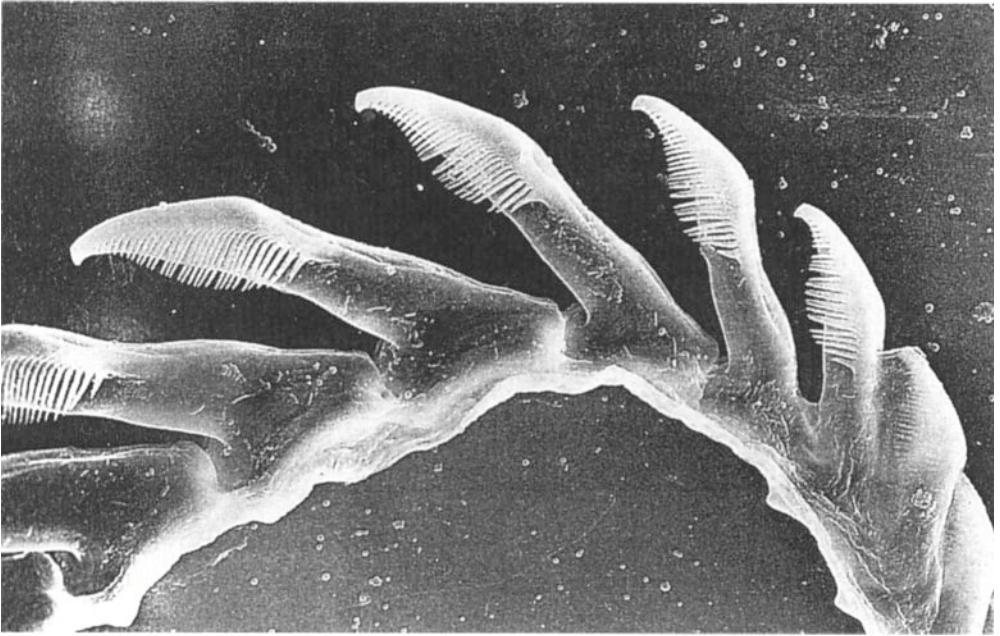


Figure 1 Radula of the sacoglossan *Ascobulla fischeri* (from Wells & Bryce 1993).

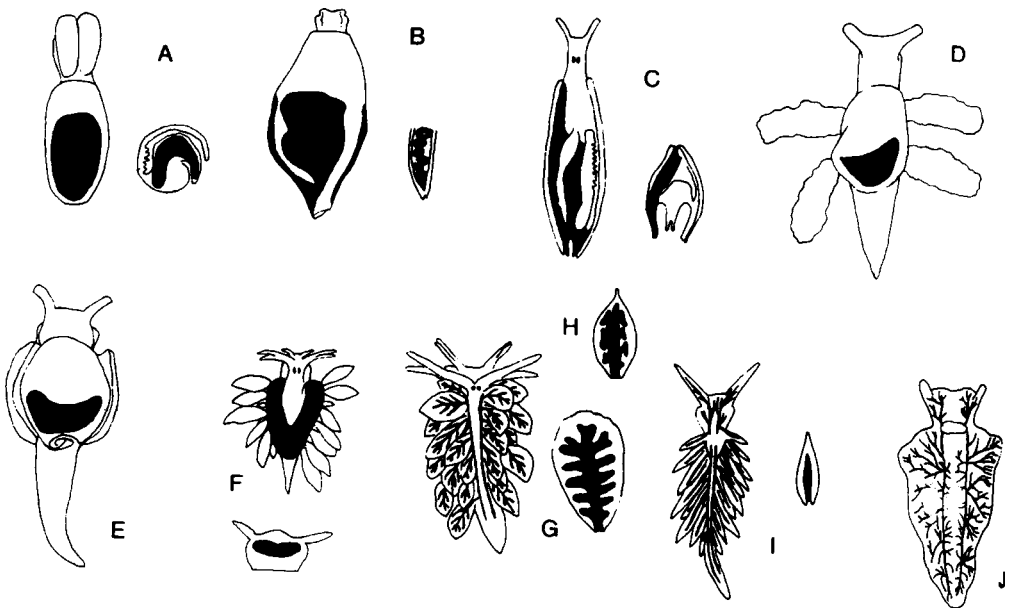


Figure 2 Extension of digestive gland (shaded area) in Sacoglossa (not drawn to scale). A, *Ascobulla*, transverse section shown to the right. B, *Volvatella*, section through the mantle shown to the right. C, *Berthelina*, transverse section shown to the right. D, *Lobiger*. E, *Oxynoe*. F, *Cyerce*, transverse section shown below. G, *Mourgona*, enlargement of ceras shown to right. H, Ceras of *Costasiella*. I, *Stiligeridae*, enlargement of ceras shown to right. J, Elysiidae. (After Jensen 1991, Fig. 6).

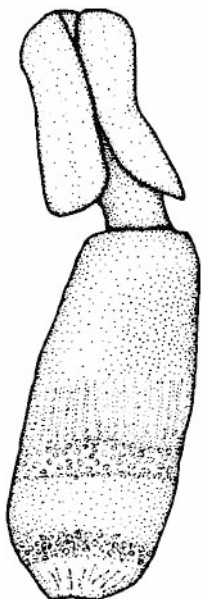


Figure 3 *Ascobulla fischeri* (Volvatellidae)
Dorsal view of live specimen.
Shell length of animal=7 mm.
(After Jensen & Wells 1990, Fig. 2).

ointertidal reef platforms (Wells & Bryce 1993). Clark & DeFreese (1987) note that slug population density is higher in eutrophic near-shore areas such as mangroves than in oligotrophic areas such as coral reefs. In terms of species richness, the group is mainly tropical and subtropical, with fewer species in temperate and boreal waters (Gascoigne 1985). However, population densities tend to be far higher in temperate regions than in tropical areas, with slug density increasing with latitude on a logarithmic scale (Clark & DeFreese 1987).

There is still some debate over the taxonomy of sacoglossans, with classification somewhat unstable. The classification used here is that of Jensen (1997a), which is used over the more recent system of Burn (1998). The system of Jensen (1997a) is used as it is based on a phylogenetic analysis. However, it seems likely that further refinements will be made in future (Burn 1998). Jensen (1997a) divides the Sacoglossa into two suborders (the shelled and non-shelled slugs) and then into five morphologically distinct groups, corresponding to family or superfamily levels. The brief descriptions below are based on this system with additional notes from Jensen (1980, 1996), Gascoigne (1985), Wells & Bryce (1993) and Burn (1998):

1. Shelled sacoglossans (Suborder: Oxynoacea) Approximately 60 species have been described within this suborder, comprising 20% of described sacoglossans (Jensen 1997b).

(a) Family: Volvatellidae (Fig. 3)

These slugs have a large pear-shaped or cylindrical shell into which the slug can withdraw completely. Rhinophores and parapodia are absent, the foot is short, the body usually unpigmented although the mantle fold of some species is green. The slugs are often

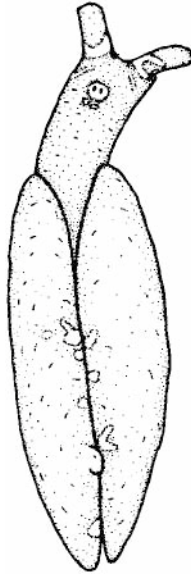


Figure 4 *Berthelinia rotnesti* n.sp. (Juliidae)
Length of live animal=6 mm.
(After Jensen 1993a, Fig. 2).

found at the base of the green alga, *Caulerpa*, where they burrow in sand around the alga's stolon.

(b) Family: Juliidae (Fig. 4)

These species are termed bivalved gastropods as they appear to have a bivalve shell, although it is actually a gastropod shell with a single valve. The shell develops as two lateral plates, the right one of which fractures lengthways to form a false hinge (Burn 1972). The periostracum thickens over the fracture to create a ligament and very simple hinge teeth develop as the shell grows (Burn 1972). The slug has an adductor muscle, allowing it to withdraw into the shell, which covers the slug's body completely. Rolled rhinophores are present and the body is usually green.

(c) Family: Oxynoidae (Fig. 5)

Oxynoids have a greatly reduced shell, which may be flattened. The shell covers only the visceral mass and most of the head of the retracted slug. Rolled rhinophores are present and much of the shell is covered by parapodia. There is a long muscular tail and the body is usually green.

2. Sacoglossans without a shell (Suborder: Plakobranchacea) The majority of sacoglossans are within this suborder, with approximately 250 species described, representing 80% of described sacoglossans (Jensen 1997b).

(a) Superfamily: Plakobranchioidea (=Plakobranchidae; =Elysiioidea) (Fig. 6)

This superfamily contains the parapodia-bearing slugs, although not all species in this group have parapodia. The feature uniting this superfamily is the presence of an anus and oviducal opening close together in a lateral groove on the right side of the body. This is the largest superfamily of sacoglossans. The largest family in this group is the Plakobranchidae (=Elysiidae) which contains the genus *Elysia*, with at least 70 species described (Jensen 1997a). Species in the genus *Elysia* have a narrow foot and a pair of

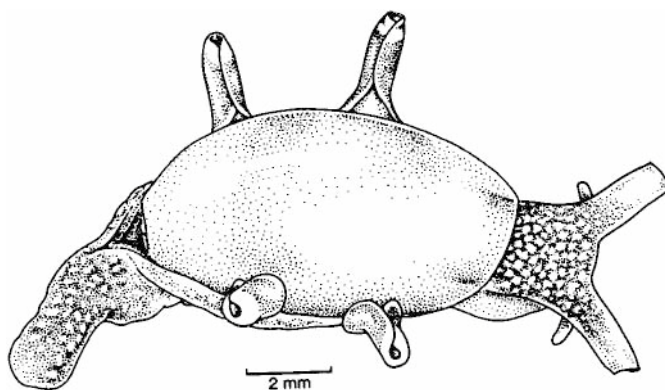


Figure 5 *Roburnella wilsoni* (Oxynoidae)
dorsal view. (After Burn 1998, Fig. 16.45).

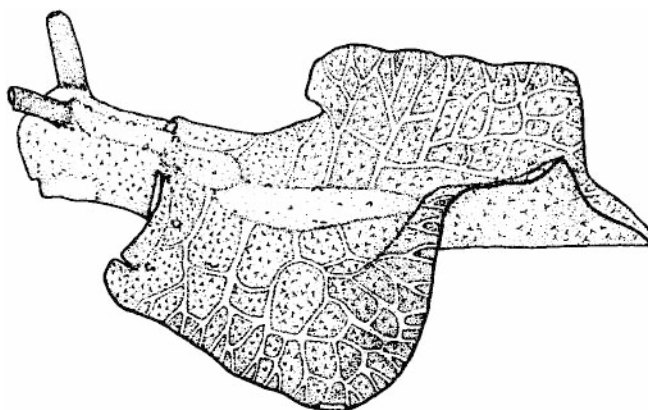


Figure 6 *Elysia expansa* (Plakobranchidae)
Length of animal approx 3 cm.
(After Jensen 1993a, Fig. 14).

lateral, leaf-like parapodia that wrap along the body or form elongate wings. The slugs are often green, with this colour provided by ingested algal chloroplasts, and may have a coloured margin along the parapodia. Many species live in association with *Caulerpa* but some species include other algae and even seagrass in their diet,

(b) Superfamily: Limapontioidea (= Polybranchioidea;=Stiligerioidea) (Figs 7 and 8) This superfamily contains the cerata-bearing slugs. The largest family in this group is the Limapontiidae (=Stiligeridae), with approximately 70 species described (Jensen 1997b). The Limapontioidea also includes the genus *Hermaea*, which are generally found in association with red algae (Jensen 1997a), unlike other sacoglossans which are generally found in association with green algae. Species of the genus *Hermaea* are often pink to red in colour, with rhodoplasts from their host algae providing this coloration.

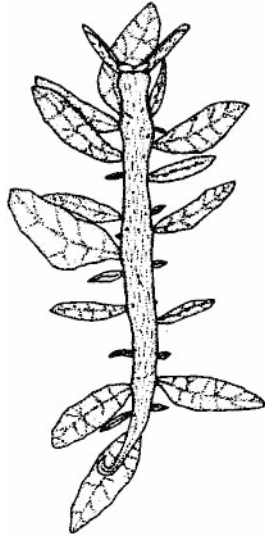


Figure 7 *Hermaea evelinemarkusae* n. sp. (Hermaeidae)
ventral view. Length of animal=12 mm.
(After Jensen 1993a, Fig. 35).



Figure 8 *Stiliger aureomarginatus* n. sp. (Limapontiidae)
Length of animal=16 mm.
(After Jensen 1993a, Fig. 21).

Diet of sacoglossans

Sacoglossans are thought to be one of the few groups of specialist herbivores in the marine environment (Hay & Fenical 1988, Hay & Steinberg 1992). These slugs feed suctorially on the cell sap of macroalgae and seagrasses, with all shelled slugs feeding only on the siphonaeal green algal genus *Caulerpa* (Jensen 1993b). Jensen (1983) suggests that two functional groups of slug food plants can be distinguished—filamentous algae and planar algae—with very few slugs including both food types in their diet. In a detailed study of feeding methods in sacoglossans, Jensen (1981) notes that feeding has two phases—rasping and sucking. During rasping, the radular teeth actively pierce the algal cell wall; while sucking, the muscular pharynx pumps in the cell sap of the food plant. Buccal regurgitation also occurs, which may allow the slug's saliva to mix with the sap, reducing viscosity and assisting suction (Jensen 1981).

Jensen (1980) produced a comprehensive list of the diet of 60 sacoglossan species drawing together data from a number of studies. Table 1 below is based on her detailed work, updated for diet studies published since 1980.

All shelled slugs tested for diet feed on the genus *Caulerpa* (Table 1). Some of the slugs without a shell also feed on *Caulerpa* (Table 1) but the diet of the Plakobranchea is generally wider than that of the shelled slugs. The most narrow food spectra are found in the bivalved species and the broadest dietary range is found in the genus *Elysia* (Jensen 1980). Of the approximately 70 sacoglossan species for which diet has been tested, 60 include green algae in their diet and 24 include *Caulerpa* (Table 2). Much of the dietary work has

Table 1 Sacoglossan food spectra.

Sacoglossan suborder and family	Diet of slug family ¹	No. of slug species tested for diet ¹	Total no. of described slug species ²
Oxynoacea:			
Volvatellidae	<i>Caulerpa</i>	3	20–26
Juliidae	<i>Caulerpa</i>	8	17–25
Oxynoidae	<i>Caulerpa</i>	7	11–13
Plakobranchea:			
Plakobranchoidea	<i>Caulerpa</i> Other green algae Brown algae Diatoms <i>Vaucheria</i> Seagrasses	25	102–116
Limapontioidea	<i>Caulerpa</i> Other green algae Red algae Diatoms <i>Vaucheria</i> Molluscan eggs	30	110–142
Total		73	260–322

¹ From Table 2.

² From Jensen (1997b).

Table 2 Sacoglossan diet spectra (adapted from Jensen 1980; Table 5 and updated).

Sacoglossan superfamily/ family	Species name	Diet of slug	References
Volvatellidae	<i>Ascobulla fischeri</i>	<i>Caulerpa</i>	Jensen (1980)
Volvatellidae	<i>Ascobulla ulla</i>	<i>Caulerpa racemosa</i> , <i>Caulerpa</i> spp.	Jensen (1980, 1981)
Volvatellidae	<i>Volvatella pyriformis</i>	<i>Caulerpa</i>	Jensen (1980)
Juliidae	<i>Julia japonica</i>	<i>Caulerpa ambigua</i>	Jensen (1980)
Juliidae	<i>Berthelinia australis</i>	<i>Caulerpa simpliciuscula</i>	Jensen (1980)
Juliidae	<i>Berthelinia babai</i>	<i>Caulerpa scalpelliformis</i> , <i>C. geminata</i>	Jensen (1980)
Juliidae	<i>Berthelinia caribbea</i>	<i>Caulerpa verticillata</i>	Jensen (1980)
Juliidae	<i>Berthelinia ganapati</i>	<i>Caulerpa racemosa</i>	Jensen (1980)
Juliidae	<i>Berthelinia limax</i>	<i>Caulerpa okamurai</i>	Jensen (1980)
Juliidae	<i>Berthelinia rotnesti</i>	<i>Caulerpa racemosa</i>	S. I. Williams (unpubl. data)
Juliidae	<i>Berthelinia typica</i>	<i>Caulerpa brownii</i>	Jensen (1980)
Oxynoidae	<i>Oxynoe antillarum</i>	<i>Caulerpa racemosa</i> , <i>C. sertularioides</i>	Jensen (1980)
Oxynoidae	<i>Oxynoe panamensis</i>	<i>Caulerpa sertularioides</i>	Jensen (1980)
Oxynoidae	<i>Oxynoe viridis</i>	<i>Caulerpa</i> , <i>C. racemosa</i>	Jensen (1980), S. I. Williams (unpubl. data)
Oxynoidae	<i>Oxynoe azuropunctata</i>	<i>Caulerpa racemosa</i> , <i>C. sertularioides</i>	Jensen (1981)
Oxynoidae	<i>Oxynoe</i> n. sp.	<i>Caulerpa paspaloides</i> , <i>C. cupressoides</i> , <i>C. sertularioides</i>	Jensen (1980)
Oxynoidae	<i>Lobiger serradifalci</i>	<i>Caulerpa prolifera</i>	Jensen (1980)
Oxynoidae	<i>Lobiger souverbiei</i>	<i>Caulerpa racemosa</i>	Jensen (1980)
Plakobranchidae (=Elysiidae)	<i>Elysia atroviridis</i>	<i>Codium fragile</i>	Jensen (1980)
Plakobranchidae (=Elysiidae)	<i>Elysia australis</i>	<i>Polyphysa peniculus</i> , <i>Chaetomorpha</i> , <i>Rhizoclonium</i> , <i>Enteromorpha</i>	Hinde (1983), Jensen (1990)
Plakobranchidae (=Elysiidae)	<i>Elysia canguzua</i>	<i>Codium</i> , <i>Bryopsis plumosa</i>	Jensen (1980, 1983)
Plakobranchidae (=Elysiidae)	<i>Elysia catulus</i>	<i>Zostera marina</i>	Jensen (1980)
Plakobranchidae (=Elysiidae)	<i>Elysia chlorotica</i>	<i>Cladophora</i> , <i>Vaucheria</i>	Jensen (1980)
Plakobranchidae (=Elysiidae)	<i>Elysia evelinae</i>	<i>Biddulphia</i>	Jensen (1980, 1981)

Table 2 continued

Sacoglossan superfamily/ family	Species name	Diet of slug	References
Plakobrachidae (=Elysiidae)	<i>Elysia expansa</i>	<i>Caulerpa racemosa</i> , <i>C. cupressoides</i>	S. I. Williams (unpubl. data)
Plakobrachidae (=Elysiidae)	<i>Elysia filicauda</i>	<i>Polyphysa peniculus</i>	Jensen (1990)
Plakobrachidae (=Elysiidae)	<i>Elysia fusca</i>	<i>Codium</i>	Jensen (1980)
Plakobrachidae (=Elysiidae)	<i>Elysia hedgpethi</i>	<i>Codium fragile</i> , <i>C. setchellii</i> , <i>Bryopsis corticulans</i>	Jensen (1980), Trowbridge (pers. comm.)
Plakobrachidae (=Elysiidae)	<i>Elysia maoria</i>	<i>Codium</i> , <i>C. convolutum</i> , <i>C. fragile</i> ssp. <i>tomentosoides</i>	Jensen (1980), Trowbridge (1995)
Plakobrachidae (=Elysiidae)	<i>Elysia ornata</i>	<i>Bryopsis plumosa</i>	Jensen (1981)
Plakobrachidae (=Elysiidae)	<i>Elysia papillosa</i>	<i>Penicillus capitatus</i> , <i>Halimeda tuna</i>	Jensen (1980, 1983)
Plakobrachidae (=Elysiidae)	<i>Elysia punctata</i>	<i>Codium</i>	Jensen (1980)
Plakobrachidae (=Elysiidae)	<i>Elysia serca</i>	<i>Halodule wrightii</i> (seagrass), <i>Halophila engelmanni</i> , <i>Thalassia testudinum</i> , <i>Syringodium filiforme</i> , <i>Ulva lactuca</i>	Jensen (1980, 1983)
Plakobrachidae (=Elysiidae)	<i>Elysia subornata</i> (= <i>E. cauze</i>)	<i>Caulerpa ashmeadii</i> , <i>C. racemosa</i> , <i>C. sertularioides</i> , <i>C. cupressoides</i> , <i>C. mexicana</i> , <i>C. paspaloides</i>	Jensen (1980)
Plakobrachidae (=Elysiidae)	<i>Elysia timida</i>	<i>Acetabularia acetabulum</i>	Marín & Ros (1992)
Plakobrachidae (=Elysiidae)	<i>Elysia tuca</i>	<i>Halimeda discoidea</i> , <i>H. incrassata</i> , <i>Caulerpa sertularioides</i> , <i>C. mexicana</i> , <i>C. racemosa</i> , <i>C. cupressoides</i> , <i>Avrainvillea nigricans</i> , <i>Udotea</i>	Jensen (1980, 1983)
Plakobrachidae (=Elysiidae)	<i>Elysia viridis</i>	<i>Codium</i> , <i>Bryopsis plumosa</i> , <i>Chaetomorpha linum</i> , <i>Cladophora rupestris</i>	Jensen (1980), C. D. Trowbridge & C. D. Todd (unpubl. data)
Plakobrachidae (=Elysiidae)	<i>Elysiella pusilla</i> (= <i>Elysia halimeda</i>)	<i>Halimeda cuneata</i> , <i>H. macroloba</i> , <i>Codium</i>	Jensen (1980), Paul & Van Alstyne (1988)
Plakobrachidae (=Elysiidae)	<i>Plakobranthus ocellatus</i>	<i>Udotea</i> , <i>Chlorodesmis</i>	Jensen (1980)

Table 2 continued

Sacoglossan superfamily/ family	Species name	Diet of slug	References
Plakobranchidae (=Elysiidae)	<i>Tridachia crispata</i>	<i>Halimeda</i> , <i>Bryopsis plumosa</i> , <i>Penicillus</i> , <i>Ratophora</i> , <i>Caulerpa verticillata</i>	Jensen (1980)
Plakobranchidae (=Elysiidae)	<i>Tridachiella diomedea</i>	<i>Padina</i>	Jensen (1980)
Bosellidae	<i>Bosellia mimetica</i>	<i>Halimeda tuna</i>	Jensen (1980, 1981)
Polybranchiidae	<i>Caliphylla mediterranea</i>	<i>Bryopsis</i>	Jensen (1980)
Polybranchiidae	<i>Cyerce antillensis</i>	<i>Penicillus dametosis</i> , <i>P. capitatus</i> , <i>Halimeda</i> , <i>Udotea flabellum</i>	Jensen (1980, 1981, 1983)
Polybranchiidae	<i>Cyerce nigra</i>	<i>Chlorodesmis comosa</i>	Jensen (1980)
Polybranchiidae	<i>Mourgonia germaineae</i>	<i>Cymplia barbata</i>	Jensen (1981)
Polybranchiidae	<i>Polybranchia viride</i>	<i>Caulerpa</i>	Jensen (1980)
Hermacidae	<i>Aplysiopsis enteromorphae</i> (<i>A. smithi</i> , = <i>Hermaea smithi</i>)	<i>Rhizoclonium</i> , <i>Cladophora</i> , <i>Chaetomorpha</i> , <i>Urospora</i>	Jensen (1980), Trowbridge (1993a)
Hermacidae	<i>Aplysiopsis zebra</i>	<i>Cladophora fuliginosa</i> , <i>Chaetomorpha</i>	Jensen (1983)
Hermacidae	<i>Hermaea bifida</i>	<i>Griffithsia flocculosa</i>	Jensen (1980)
Hermacidae	<i>Hermaea cruciata</i>	<i>Griffithsia</i> , <i>Dasya</i>	Jensen (1983)
Hermacidae	<i>Hermaea vancouverensis</i>	<i>Isthmia nervosa</i>	Jensen (1980)
Limapontiidae (=Stiligeridae)	<i>Alderia modesta</i>	<i>Vaucheria</i>	Jensen (1980)
Limapontiidae (=Stiligeridae)	<i>Calliopaera oophaga</i>	eggs of <i>Philine denticulata</i> and <i>Reticula truncatula</i>	Jensen (1980)
Limapontiidae (=Stiligeridae)	<i>Costasiella ocillata</i> (= <i>C. lilianae</i>)	<i>Ayamvillea nigricans</i> , <i>Caulerpa fastigiata</i> , <i>Cladophora</i>	Jensen (1980, 1981, 1983)
Limapontiidae (=Stiligeridae)	<i>Placida capensis</i>	<i>Codium stephensiae</i>	Jensen (1980)
Limapontiidae (=Stiligeridae)	<i>Placida demibranchia</i>	<i>Codium</i> spp., <i>Bryopsis plumosa</i> , <i>B. verticillans</i>	Jensen (1980), Trowbridge (1991a, 1992, 1995)
Limapontiidae (=Stiligeridae)	<i>Placida kingstoni</i>	<i>Bryopsis</i> , <i>Cladophora</i>	Jensen (1980, 1981)
Limapontiidae (=Stiligeridae)	<i>Placida viridis</i>	<i>Bryopsis plumosa</i>	Jensen (1980)
Limapontiidae (=Stiligeridae)	<i>Stiliger fuscivittatus</i>	<i>Polysiphonia pacifica</i>	Jensen (1980)

Table 2 continued

Sacoglossan superfamily/ family	Species name	Diet of slug	References
Limapontiidae (=Stiligeridae)	<i>Stiliger vesiculosus</i>	eggs of <i>Favorinus branchialis</i>	Jensen (1980)
Limapontiidae (=Stiligeridae)	<i>Olea hansineensis</i>	eggs of <i>Haminoea virescens</i> , <i>Aglaja diomedea</i> , <i>Gastropteron pacificum</i> , <i>Archidoris montereyensis</i> , <i>Hermisenda crassicornis</i> , <i>Dendronotus iris</i>	Jensen (1980)
Limapontiidae (=Stiligeridae)	<i>Ercolania boodlea</i>	<i>Chaetomorpha aerea</i> , <i>C. moniligera</i> , <i>Cladophora</i>	Jensen (1980)
Limapontiidae (=Stiligeridae)	<i>Ercolania coerulea</i>	<i>Valonia</i> , <i>Dictyosphaeria cavernosa</i> , <i>Cladophoropsis</i>	Jensen (1980, 1981, 1983)
Limapontiidae (=Stiligeridae)	<i>Ercolania funerea</i>	<i>Chaetomorpha</i> , <i>Cladophora</i> , <i>Cladophoropsis</i>	Jensen (1980, 1981, 1983)
Limapontiidae (=Stiligeridae)	<i>Ercolania fuscata</i>	<i>Cladophora</i> , <i>Chaetomorpha linum</i> , <i>Caulerpa verticillata</i> , <i>Cladophoropsis</i>	Jensen (1980, 1983)
Limapontiidae (=Stiligeridae)	<i>Ercolania gopalai</i>	<i>Chaetomorpha</i>	Jensen (1980)
Limapontiidae (=Stiligeridae)	<i>Ercolania nigra</i>	<i>Chaetomorpha linum</i>	Jensen (1980)
Limapontiidae (=Stiligeridae)	<i>Ercolania vanellus</i>	<i>Caulerpa verticillata</i>	Jensen (1980)
Limapontiidae (=Stiligeridae)	<i>Ercolania viridis</i>	<i>Chaetomorpha</i>	Jensen (1980)
Limapontiidae (=Stiligeridae)	<i>Limapontia capitata</i>	<i>Cladophora</i> , <i>Chaetomorpha linum</i> , <i>Bryopsis plumosa</i>	Jensen (1980)
Limapontiidae (=Stiligeridae)	<i>Limapontia cocksi</i>	<i>Cladophora rupestris</i>	Jensen (1980)
Limapontiidae (=Stiligeridae)	<i>Limapontia depressa</i>	<i>Vaucheria</i> , <i>Rhizoclonium riparium</i>	Jensen (1980)

been carried out on tropical-subtropical slugs given the greater species diversity in these regions.

Food choice experiments

These patterns, however, should be treated with some caution. Few slugs, particularly species in the Plakobranchacea, have been tested for diet, with only approximately 25% of the Plakobranchacea examined to date (Table 1). Additionally, much of the dietary data in Table

1 is based on “repeated associations” (Clark & Busacca 1978) in the field between the slug and alga, with few rigorous food choice experiments conducted.

The design of food preference experiments is fraught with difficulty (for reviews, see Peterson & Renaud 1989 and Brawley 1992). It is not surprising therefore, that there is scope for improvement in the few slug food choice experiments that have been conducted to date. Because of the difficulty inherent in directly observing slug feeding, researchers have concluded that the slug is expressing a dietary preference by moving onto a particular algal species and remaining there for an unspecified period of time (e.g. Jensen 1981), 1–2 h (e.g. Jensen 1990) or as little as 30 min (e.g. Paul & Van Alstyne 1988). In Jensen (1981), feeding tracks were observed on the alga, but grazing was not quantified. In such experiments, it is not clear whether the slugs are expressing a dietary preference. They may, for example, be expressing a choice not related to the alga’s nutritional quality, but to habitat—for example, the alga may offer protection from predation and/or wave action (Nicotri 1980). Only a small number of food preference studies appear to have accounted for this possibility—for example, Jensen (1983) and Trowbridge (1991b) in which growth and survival in the slugs maintained on different diets was examined. Note however, that in the study by Jensen (1983), food was presented to groups of slug individuals, rather than to one slug. This procedure means that feeding biases may have been introduced by positive or negative interactions between the slugs (Peterson & Renaud 1989). In fact, intraspecific interactions have been shown to occur between individuals of the slug *Placida dendritica* (Trowbridge 1991a). Trowbridge (1991b) used plugs of algae, rather than whole thalli, which may have also introduced a bias into the experiment by influencing the condition of the alga (Brawley 1992).

In addition, most of the sacoglossan food choice experiments published to date have offered the slugs few algal species, and generally those offered have been the species on which the slugs were observed in the field. Jensen (1981) appears to have offered the slugs a wider range of potential food items than most studies of this nature. Interestingly, this study found that many slug species will associate with a range of Chlorophyta species in the laboratory, including algae that the slugs have not been observed upon in the field—this study increased the dietary width of six slug species. The lack of broader diet studies in the literature may be an artifact of the tendency in science to publish only surprising or unexpected results. For example, unpublished studies of the slug *Placida dendritica* exist in which a wide range of diets have been offered, including species of *Codium*, *Spongomorpha*, *Acrosiphonia* and *Bryopsis* (C.D.Trowbridge, pers. comm.).

There is some evidence, although conflicting, of the ability of sacoglossans to switch between diets. The slug *Elysia viridis* is able to switch between two algal diets with a learning period (Jensen 1989) whereas *Placida dendritica* (Trowbridge 1991b) and *Elysia hedgpethi* (C.D.Trowbridge, pers. comm.) are generally unable to survive on “unfamiliar” host algal species. Further work in this area may help to clarify the width of sacoglossan diets.

Few long-term studies of sacoglossan diet have been conducted, so that possible seasonal/life cycle variations in diet have not generally been considered. One of the few long-term studies of slug diet/kleptoplasty was conducted by Brandley (1984). The study found that the slug *Elysia furvacauda* could be observed on green algae during some months of the year, and on the brown alga *Sargassum* at other times. Although feeding by the slugs was not examined directly, the slugs were found to retain functional chloroplasts from three different algal species (two green, one red) during different seasons, implying that diet varied seasonally. Interestingly, the presence of rhodoplasts in the slugs suggests they may feed on red algae epiphytic on the host alga.

A further improvement that could be made to food preference experimental design would be to consider diurnal cycles in sacoglossan behaviour. Field observations of some Florida slugs indicate that some species may feed nocturnally (Weaver & Clark 1981). None of the food preference studies performed to date appears to have considered this aspect of slug behaviour, with no mention of feeding differences between light and dark, particularly in studies lasting only several hours. In unpublished food choice experiments, however, no diurnal feeding pattern has been observed (C.D.Trowbridge, pers. comm.).

The use of more rigorous laboratory food choice experiments may help to clarify the diet spectra of Sacoglossa. Given the pitfalls in designing such experiments there would be clear advantages in using additional techniques to give an indication of diet in the field (i.e. more than the simple observation of substratum). One such method would be the use of stable isotope ratios as natural tracers of diet.

Stable isotope ratios as “natural tracers” of diet

Stable isotope analysis has become an alternative tool for food web analysis in recent years, supplementing more traditional approaches such as direct observations in laboratory and field, gut and faeces analysis, radiolabelling and immunological techniques (Michener & Schell 1994). It is particularly useful where more traditional approaches are difficult—for example, where gut contents are difficult to identify owing to the speed of digestion or where direct observation of feeding is not possible. The use of stable isotope techniques, particularly stable carbon and nitrogen isotopes, has therefore become widespread in elucidating a range of marine food chains from arctic and subarctic regions (e.g. Parsons & Lee Chen 1995) to the tropics (e.g. Risk et al. 1994, Yamamuro et al. 1995).

Stable carbon and nitrogen isotope ratios have become useful tracers of diet because of the way they behave as a natural “signature” of diet. The stable isotopic composition of the carbon in an animal tends to reflect that of its diet with slight enrichment (e.g. DeNiro & Epstein 1978, Macko et al. 1982, Tieszen et al. 1983). A similar relationship exists for stable nitrogen isotopes, although enrichment occurs to a greater extent (e.g. DeNiro & Epstein 1981, Macko et al. 1982). Michener & Schell (1994) concluded that the ^{13}C content of an animal tends to be enriched by 0.5‰ to 1‰ relative to diet. Owens (1987) concluded that the ^{15}N content of an animal is enriched by approximately 3.0‰ relative to diet, which was confirmed more recently by Rau et al. (1991) who found an increase in biomass $\delta^{15}\text{N}$ of 3.5‰ per trophic step in Weddell Sea invertebrates.

Background to stable isotopes

Nitrogen exists naturally as two stable isotopes of which ^{14}N constitutes 99.6% and ^{15}N about 0.4% (Owens 1987). Carbon also exists as two stable isotopes—98.9% in the form of ^{12}C and 1.1% in the form of ^{13}C (Maberly et al. 1992). The isotopic compositions of natural materials can be measured with great precision by a mass spectrometer. Isotopic compositions are generally expressed as δ values which represent the difference between the ratio of heavy isotope to light isotope in the sample compared with this ratio for a standard reference material and is expressed in parts per thousand (refer equations 1 and 2 below). An increase in the δ value indicates an increase in the abundance of heavy isotope to light isotope in the sample. The standard reference material for carbon is PDB carbonate and for nitrogen, atmospheric N_2 . These standards are assigned a value of 0‰ on the δ scale.

$$\delta^{15}\text{N} = ((R_{\text{sample}}/R_{\text{standard}}) - 1) * 10^3$$

where R=ratio of ^{15}N to ^{14}N (Equ. 1)

$$\delta^{13}\text{C} = ((R_{\text{sample}}/R_{\text{standard}}) - 1) * 10^3$$

where R=ratio of ^{13}C to ^{12}C (Equ. 2)

The enrichment in animal $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ relative to diet results from isotope effects, which can be divided into physical isotope effects and chemical isotope effects (Owens 1987). Physical fractionation occurs, for example, during diffusion, resulting from the lighter isotope moving more rapidly than the heavier isotope. Chemical fractionation occurs during the formation and destruction of chemical bonds where the heavier isotope is discriminated against because of the lower vibrational frequency of a bond involving the heavier isotope, such that slightly more energy is required to break a bond to, for example, ^{13}C than to ^{12}C . Isotope effects are denoted by α (refer equation 3 below). Isotope effects are also called fractionation factors because they result in fractionation of isotopes. The process of fractionation leads to an unequal partitioning of heavy and light isotope between the substrate and product of a reaction. The result is that the product is depleted in the heavier isotope relative to the substrate.

$$\alpha = R_r/R_p$$

where $R_r = ^{13}\text{C}/^{12}\text{C}$ molar ratio of reactant
and $R_p = ^{13}\text{C}/^{12}\text{C}$ molar ratio of product (Equ. 3)

An example of an isotope effect is the fact that in plants, the enzyme Rubisco fixes $^{12}\text{CO}_2$ faster than $^{13}\text{CO}_2$ (Raven 1996). The $^{13}\text{C}/^{12}\text{C}$ ratio in plant organic carbon is thus generally lower than that in the inorganic carbon from which it was derived. In animals, the result of the isotope effect is that products such as respiration and excretion are depleted in the heavier isotope relative to diet. Consequently the animal's tissue tends to be enriched in the heavier isotope (e.g. DeNiro & Epstein 1978, Macko et al. 1982, Tieszen et al. 1983). The isotope effect may occur in a number of biochemical processes in an animal. Its magnitude in metabolism is not yet completely understood. It is likely that fractionation during processes such as glycolysis and the citric acid cycle contributes to the slight enrichment in animal $\delta^{13}\text{C}$ relative to diet. DeNiro & Epstein (1978) found that the enrichment in ^{13}C of laboratory grown animals was balanced by a depletion in ^{13}C of respired CO_2 . Fractionation during other processes may also contribute to animal $\delta^{13}\text{C}$ enrichment—such as preferential uptake of ^{13}C compounds during digestion and metabolic fractionation during the synthesis of different tissue types (Michener & Schell 1994).

When $\delta^{15}\text{N}$ enrichment occurs in animal tissue, excreted urea or ammonium has been found to be depleted in ^{15}N (Minagawa & Wada 1984), implying that isotope fractionation during deamination and (in the case of terrestrial animals) during the conversion of NH_4 to excretory product contributes to tissue ^{15}N enrichment. The magnitude of fractionation in these processes is not clearly understood. Fractionation during transamination is also likely to play a role in tissue $\delta^{15}\text{N}$ enrichment. For example, Macko et al. (1986) investigated the degree of fractionation of nitrogen isotopes during transamination. They concluded that $^{14}\text{NH}_2$ reacts 1.0017 to 1.0083 times faster than $^{15}\text{NH}_2$ during transamination reactions catalyzed by one of the many transaminases.

Animal tissue $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values may also be influenced by a range of factors additional to dietary $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and metabolic fractionation, including the calorific value of diet (Tieszen et al. 1983, Stephenson et al. 1986, Wada et al. 1987, Rau et al. 1991), age

of the animal (DeNiro & Epstein 1981, Rau et al. 1981), seasonal variations in growth and assimilation efficiencies (Minagawa & Wada 1984).

In plants, tissue $\delta^{13}\text{C}$ is commonly depleted relative to atmospheric CO_2 , indicating that carbon isotope discrimination occurs in the incorporation of CO_2 into plant biomass, with a number of models having been developed to explain how this occurs (Farquhar et al. 1989).

Using stable isotope techniques to determine diet of sacoglossans

Because of their ability to act as a “signature” of diet, stable C and N isotopes may be a useful supplement to laboratory food choice experiments in elucidating the diet of slugs. It may be possible to measure the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of a range of potential diet algae and compare these with the d^{13}C and d^{15}N of the animals. The d^{15}N of some slug species in southwestern Australia has been shown to reflect that of their suspected host alga (Raven et al. 1999). Further work is clearly needed in this area. For this to be a useful method, the various potential diets would need to have quite distinct signatures and analysis would be complicated if the slugs feed on a range of diets. It would also be further complicated if the slug is kleptoplastic (see pp. 105–17). The fixation, transport and assimilation of photosynthetic carbon in the animal cell may be subject to different $^{13}\text{C}/^{12}\text{C}$ discrimination to that in the algal cell, which could result in a different d^{13}C signature.

Nitrogen uptake by sacoglossans

Sacoglossans may be able to take up dissolved free amino acids (DFAAS) from sea water via direct transport across the epidermis. Using DFAAS labelled with ^{14}C , DeFreese & Clark (1991) demonstrated uptake and incorporation of the carbon skeleton from DFAAS in several sacoglossan species. The process appears to be independent of kleptoplasty as it occurs in species with or without functional kleptoplasty. DFAA uptake also appears to be independent of photosynthetic carbon fixation, occurring in light and dark conditions (DeFreese & Clark 1991). The ability to take up DFAAS appears to be widespread among soft-bodied marine invertebrates (Stephens 1988).

It is not clear what contribution DFAA uptake makes to slug nitrogen requirements or in fact, whether the nitrogen is taken up at all. Strictly speaking, in order to demonstrate uptake of nitrogen from DFAAS, the nitrogen in DFAAS should be labelled. DeFreese & Clark (1991) suggest DFAAS may be an important nutrient source for the slugs, helping compensate for a diet of algal cytoplasm high in carbohydrate and low in nitrogen. This idea has some support from work that shows Western Australian species of *Caulerpa* and *Codium* have C:N ratios of around 20 compared with 6 for slugs found on these algae (Raven 1996, Raven et al. 1999). DeFreese & Clark (1991) also speculate that the importance of DFAA uptake as a nitrogen supplement may vary throughout the year, with seasonal variations in the nutritional content of macroalgae.

Algae with which sacoglossans associate

The majority of sacoglossans are thought to feed on green macroalgae (Table 3). This algal division, Chlorophyta, covers a wide range of species with a broad spectrum of morphology,

Table 3 Diet of sacoglossans by algal functional group.

Algal functional group	No. of sacoglossan spp. feeding on the algal group ¹	Dominant sacoglossan group feeding on the algal group ¹
<i>Caulerpa</i>	26	Shelled species—69% of spp.; Plakobrachidae—15% of spp.
Green filamentous algae	28	Limapontiidae—50%; Plakobrachidae—36%
Green calcified coenocytic algae	13	Plakobrachidae—62%; Polybranchiidae—15%
<i>Codium</i>	10	Plakobrachidae—80%; Limapontiidae—20%
Other diets (red algae, brown algae, egg masses, diatoms)	14	Limapontiidae—42%; Plakobrachidae—36%
Total ²	91	

¹ From Table 2.

² Total is higher than for Tables 1 and 2 as some slugs feed on >1 algal group.

population dynamics and habitat. Many species are coenocytic (the algal thallus is one cell) (e.g. *Caulerpa*), some are also calcified (e.g. *Halimeda*), and some have a filamentous (e.g. *Chaetomorpha*) or globular (e.g. *Valonia*) morphology. Some of the algae are highly seasonal (e.g. many of the filamentous algae), others are pseudoperennial (e.g. many of the calcified algal species). Some of the algae occur in highly eutrophic conditions (e.g. many of the filamentous algae), others in mesotrophic to oligotrophic conditions (e.g. many of the calcified algal species). These variations are likely to influence the feeding effort required for slug grazers (Clark & DeFreese 1987). In an attempt to classify these algae in a way meaningful to slug feeding ecology, the algae were categorized into three functional groups by Clark & DeFreese (1987). These groups of mainly coenocytic algae do not include *Codium*, a common alga with which sacoglossans associate in temperate regions (see Table 3). Clark & DeFreese (1987) suggest that this alga is transitional between the groups as it is uncalcified, filamentous and coenocytic. The Clark & DeFreese (1987) study concentrated on algae and slugs in the Caribbean and thus does not expand on sacoglossans and their host algae in temperate regions. For the purpose of this review, *Codium* is classified as a fourth group, given its importance as an algal host for slugs in temperate regions: ten slug species feed on this algal genus (Table 3).

These groups are not exhaustive—they do not include all of the green algae with which slugs are associated or the other diets such as red algae, brown algae, seagrasses, diatoms or molluscan egg masses. However, the classification provides at least a starting point for categorizing sacoglossan diets:

- (a) *Caulerpa*;
- (b) filamentous green algae such as *Cladophora*, *Chaetomorpha*, *Bryopsis* and *Cladophoropsis*;
- (c) calcified green algae such as *Halimeda*, *Penicillus*, *Udotea*, *Cympolia* and *Avrainvillea*;
- (d) the green alga *Codium*.

Caulerpa

The chlorophyte Order Caulerpales is thought to be the most common food of sacoglossans, with the Oxynoacea feeding exclusively on the genus *Caulerpa* (Jensen 1980). Two-thirds of the slugs feeding on this algal genus are in the group Oxynoacea (Table 3). *C. racemosa* is probably the most widespread food of sacoglossans (Jensen 1980).

The genus *Caulerpa* has a horizontal stolon attached by rhizoidal outgrowths and bearing branched photosynthetic fronds. The alga is coenocytic, i.e. the thallus is a single multinucleate cell with cell wall ingrowths (trabeculae) providing structural support (Womersley 1984). Species of *Caulerpa* are pseudoperennial—individual thalli live for less than 1 yr, but the alga as a whole is long-lived. Clark & DeFreese (1987) state that species of *Caulerpa* have an intermediate ash content (15–60%), indicating an intermediate level of nutrients for grazers per unit of feeding effort. *Caulerpa* species occur mostly in mesotrophic habitats on a range of substrata, including rock, silty to well-oxidized sediment and mangrove roots (Clark & DeFreese 1987). *Caulerpa* species rapidly form wound plugs when injured (Dawes & Goddard 1978) which limits cytoplasmic loss in such circumstances. It has been suggested that wound-plug formation may increase feeding effort for sacoglossans (Clark 1992).

Caulerpa species appear to undergo rhythmic changes in chloroplast distribution (Dawes & Barilotti 1969). The algae exhibit basipetal migration of chloroplasts (= movement of chloroplasts from the upper parts of the thallus towards the basal region of the alga) associated with darkness during 12 h light/12 h dark cycles. It is not clear whether this has any relevance to slug feeding behaviour (e.g. whether the slugs feed in a way that targets chloroplasts) as published studies of feeding in slugs do not appear to discuss this issue.

It is a large and common genus, with 73 species described worldwide (Jacobs 1994). It tends to occur in tropical and subtropical regions, but is particularly diverse on the coasts of southern Australia, with 22 species described (Womersley 1984). This means that 30% of the world's species of *Caulerpa* are found in this region, leading Womersley (1984) to suggest that southern Australia may be the geographic origin of this genus.

Filamentous green algae

This group of algae, which includes *Cladophora*, *Chaetomorpha*, *Bryopsis* and *Cladophoropsis* is associated with a wide range of substrata ranging from drift algae to mangrove roots to high intertidal rockpools on temperate coasts. These algae are typically filamentous, uniseriate and septate (except for *Bryopsis* which is a coenocytic alga). They are highly seasonal in occurrence (Croley & Dawes 1970). Growth of these algae is associated with high concentrations of dissolved nutrients, which are extracted directly from the water column. Species such as *Ulva*, *Enteromorpha* and *Cladophora* grow luxuriantly in eutrophic waters (Clayton & King 1990). These algae have a relatively low ash content (16–40%), which may indicate that slugs grazing on this algal group can gain more nutrients per unit feeding effort than those feeding on *Caulerpa* (Clark & DeFreese 1987). The slugs associated with these seasonal algae also tend to have highly seasonal and irruptive populations (Clark 1975, Trowbridge 1993a).

Dawes & Barilotti (1969), reporting findings by workers early this century, note that *Bryopsis* exhibits migration of chloroplasts associated with shading, i.e. the chloroplasts move away from areas of the alga that are shaded.

Clark & DeFreese (1987) argue that the slugs associated with these algae are generally stiligerids (now the Limapontiidae) and hermaeids. However, a review of the literature on slug diets does not completely support this view. Certainly the Limapontiidae account for 50% of slug species feeding on these algae (Table 3), but the Plakobranchidae are also a large group—accounting for 36% of slugs feeding on filamentous algae (Table 3).

Calcified coenocytic algae

This group contains species such as *Halimeda*, *Penicillus*, *Udotea*, *Cymplia* and *Avrainvillea*. These algae are coenocytic, pseudoperennial and have moderate to high ash level (35–95%)—which includes an external layer of carbonate (Clark & DeFreese 1987). They often occur in mesotrophic to oligotrophic habitats and as for *Caulerpa*, they have nutrient-absorbing rhizoids which penetrate the sediment or adhere to rock surfaces. Clark & DeFreese (1987) also note another similarity with *Caulerpa*—these algae also form wound plugs when damaged. The slugs associated with these algae are generally those without a shell, i.e. plakobranchids, limapontiids, polybranchiids and hermaeids (Clark & DeFreese 1987). This view is supported by a review of the relevant literature, summarized in Table 3.

Like *Caulerpa* species, some calcified algae, such as *Halimeda* and *Acetabularia* appear to undergo rhythmic changes in chloroplast distribution (*Halimeda*, Drew & Abel 1992; *Acetabularia*, Koop et al. 1978). The algae exhibit basipetal migration of chloroplasts associated with darkness during 12 h light/12 h dark cycles. The chloroplasts are thought to move along networks of microtubules/actin filaments (Drew & Abel 1992).

Codium

The coenocytic genus *Codium* contains approximately 100 described species and is one of the most diverse genera of marine algae (Silva 1992). *Codium fragile*, a common host of slugs, has an extremely wide distribution from 26° to 70° latitude in both the northern and southern hemispheres and occurs over a wide range of exposure, tidal and nutrient regimes (Trowbridge 1998a). The slugs associated with *Codium* are generally plakobranchids and limapontiids (Table 3).

Kleptoplasty

History of kleptoplasty research

One of the most interesting aspects of sacoglossan-algal interactions is the fact that the slugs “steal” chloroplasts from the food algae and retain these intact plastids intracellularly. In some slugs, the chloroplasts continue to photosynthesize for up to 9 months (Pierce et al. 1996). The retained chloroplasts often release photosynthetic products into the slug cells, which has been traced to polysaccharides and amino acids in the slugs (Greene & Muscatine 1972, Trench 1973, 1975).

This subject has clearly captured the imagination of many researchers (and funding organizations) as it has been the focus of at least 30 research publications in as many years. A number of reviews have also been carried out (Trench 1975, Hinde 1980, 1983, Clark 1992). This ability of slugs to retain chloroplasts has been given many names: “chloroplast symbiosis” (Trench 1975), “chloroplast farming” (Hinde 1983), “chloroplast retention” (Marín & Ros 1992) and “kleptoplasty” (Gilyarov (1983), cited by Waugh & Clark 1986). The latter authors coined the term “kleptoplast” from the Greek “kleptein” meaning “borrowed”. The terms “chloroplast retention” and “kleptoplasty” are both used today (Marín & Ros 1992, Clark 1992). The phrase “enslavement of algal chloroplasts” has also been used in relation to a similar process carried out by ciliates (Stoecker et al. 1988–9). The term “kleptoplasty” will be used in this review as it is concise and appropriate given that the chloroplasts are sequestered from the alga and their existence in the slug is finite and non-reproductive.

The plant-like appearance of sacoglossans is reflected in the names given to the slugs by researchers in the nineteenth century—species names such as “*viridis*” and “*chloris*” (green) and generic names such as “*Caliphylla*” (beautiful leaves) and “*Tridachia*” (lettuce). However, it was not until early in the twentieth century that the basis for this green colour was recognized as being due to the retention of algal symbionts/chloroplasts. With the advent of the electron microscope and improvements in sample preparation, Kawaguti & Yamasu (1965) were able to describe this phenomenon more clearly. These authors identified the green bodies in the digestive gland of the opisthobranch mollusc *Elysia atroviridis* as chloroplasts which were indistinguishable from those of *Codium fragile*. This was the first time that organelles from one species had been shown to be able to survive in the cells of another. To date, no other group of metazoans has been shown to retain functional chloroplasts intracellularly, although this phenomenon has been recorded from unicellular animals such as ciliates and Foraminifera (Lopez 1979, Stoecker et al. 1987).

A number of studies were then carried out on the physiology of kleptoplasty in sacoglossans in the UK and USA. In the UK, work was focused on *Elysia viridis* (Taylor 1968, Hinde & Smith 1972, 1974, 1975, Trench et al. 1973a,b, Gallop 1974, Gallop et al. 1980, Williams & Cobb 1989). In the USA, studies were carried out on *Tridachia crispata* (Trench 1969, 1973, Taylor 1971). A great deal of work followed in the USA and Canada, surveying a range of slug species for evidence of chloroplast retention and in some cases attempting to examine the role of kleptoplasty in the feeding ecology of the slugs (Greene 1970, Clark & Busacca 1978, Clark et al. 1979, 1981, 1990, Stirts & Clark 1980, Weaver & Clark 1981, Waugh & Clark 1986, Gibson et al. 1986).

A number of studies have also been conducted in Australia, with four sacoglossan species surveyed for evidence of kleptoplasty—*Elysia australis*, *Oxynoe viridis* and *Placida dendritica* (Hinde 1983) and *Elysia furvacauda* (Brandley 1984). Hinde (1983) also included two unnamed *Elysia* species. The ultrastructural aspects of chloroplasts taken up by *Elysia maoria* have been the subject of a study by Brandley (1981).

More recently, studies of kleptoplasty in sacoglossans have been conducted in Spain on *Elysia timida* (Marín & Ros 1992) relating kleptoplasty to the slug’s feeding strategy. Recent molecular studies have also been carried out in the USA showing that algal chloroplast genes are transcribed and translated in both kleptoplasts and animal cytoplasm in the slug *Elysia chlorotica* (Mujer et al. 1996, Pierce et al. 1996).

Despite the fact that at least 30 studies on kleptoplasty have been conducted over the past 30 years and 15% of described sacoglossans have been tested for kleptoplasty (Table 4), little is known about its role in sacoglossan feeding ecology. One of the main researchers in this field admits that “the specific contribution of photosynthate to the animal’s energy budget

Table 4 Kleptoplasty in sacoglossans—by sacoglossan family.

Sacoglossan family	No. of spp. with functional kleptoplasty ¹	No. of spp. tested for kleptoplasty ¹	No. of spp. described ²	% of described spp. tested for kleptoplasty
Volvatellidae	0	1	20–26	5
Juliidae	0	2	17–25	12
Oxynoidae	0	5	11–13	45
Plakobranchidae (=Elysiidae)	12	15	97–111	15
Bosellidae	1	1	5	20
Polybranchiidae	2	4	24–28	17
Hermaeidae	1	4	19–25	21
Limapontiidae (=Stiligeridae)	4	8	67–89	12
Total	20	39	260–322	15

¹ Source—Table 7. ² From Jensen (1997b).

remains poorly defined” (Clark 1992). The focus of many of the studies has been to determine how long the kleptoplasts remain functional under starvation conditions (i.e. their physiological limits), rather than considering the importance of kleptoplasty to the slug under ecologically realistic conditions. In particular, two questions have not been addressed in detail:

1. What contribution does kleptoplasty make to the slug’s energy budget?
 2. What role does kleptoplasty play (if any) in reducing the alga’s biomass loss from grazing?
- A description of how kleptoplasty is thought to occur is given below, drawing on the results of the many studies over the past 30 years. An examination of trends in kleptoplasty follows in an attempt to find clues to help answer the questions above. Following this is a description of the methods used to observe kleptoplasty, together with suggestions of new methods.

How kleptoplasty occurs

The extent to which kleptoplasty occurs is very variable throughout the Sacoglossa—in starved slugs, the ingested chloroplasts may continue to photosynthesize for periods ranging from a few hours to a few days in some species (e.g. *Oxynoe* sp.: Clark & Busacca 1978, Hinde 1980), between 6 and 12 wk in others (e.g. *Elysia viridis*: Hinde & Smith 1972, *Elysia australis*: Hinde 1980), and for periods of up to 9 months in some species (e.g. *Elysia chlorotica*: Pierce et al. 1996). In slugs that are permitted to continue to feed, the chloroplasts are retained for much shorter periods. Gallop et al. (1980) estimated that in *E. viridis* with free access to *Codium fragile* one-third to one-half of the chloroplasts may be turned over each week.

The physiological studies of the 1960s and 1970s have helped to elucidate how the process of kleptoplasty occurs, with a helpful review by Trench (1975). The digestive tract of the non-shelled slugs is a highly branched tubular system which extends into the cerata or parapodia (Fig. 2). The epithelium of the digestive tract is highly folded and ciliated and is lined with phagocytic digestive cells which are thought to engulf the plastids taken in via the slug’s suctorial mode of feeding. In species that carry out carbon fixation, it appears the chloroplasts are taken up in an intact state. Electron micrographs show that the plastid

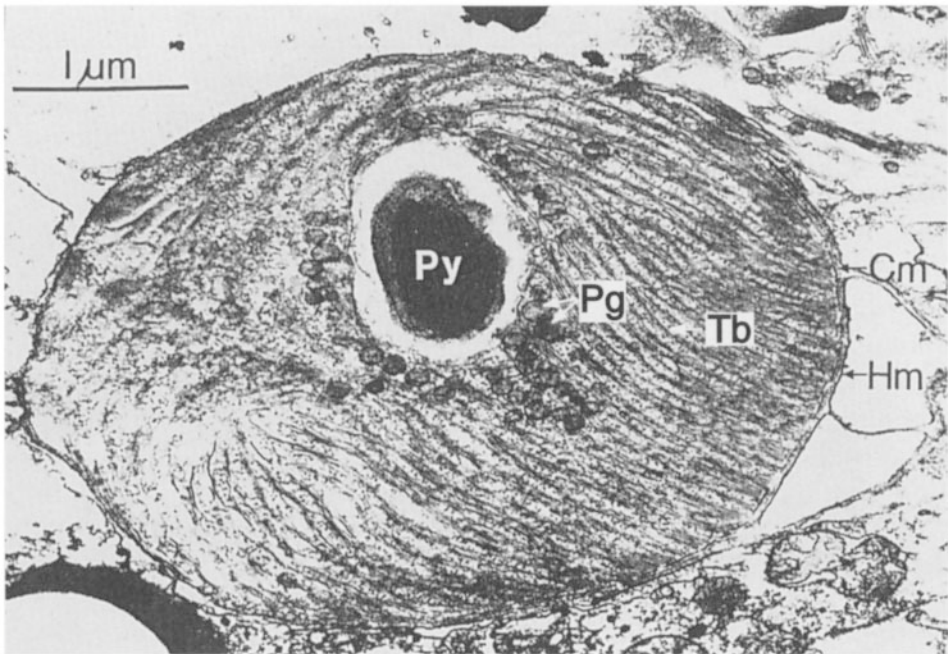


Figure 9 Symbiotic chloroplast from digestive gland cell of fed *Costasiella liliana*. Cm—chloroplast membrane; Hm—host membrane; Pg—plastoglobuli; Py—pyrenoid; Tb—Thylakoid band. (After Clark et al. 1981, Fig. 7).

envelope remains intact and that the thylakoid membranes and starch grains all appear identical to those found in the plastids of the seaweed from which they were derived (Figs 9–11). Other algal organelles such as nuclei have not been observed in the slug digestive cells. It also seems that the slug is somehow able to sort between photosynthetic plastids and amylogenic plastids as Trench (1975) notes that *Elysia cauzescops* feeding on *Caulerpa sertularioides* contains only chloroplasts in its digestive cells, although this alga also contains amylogenic plastids.

Trench (1975) was unclear on whether the chloroplasts are contained within animal cell vacuoles or free in the cytoplasm as it is difficult to accurately recognize intracellular membranes. However, more recent work by Brandley (1981), Hinde (1983), and Marín & Ros (1993) suggests that active chloroplasts are in direct contact with the slug's cytoplasm and that only when they become defunct are the plastids enveloped by slug vacuoles.

Sacoglossans appear to produce a “host factor” that causes the products of photosynthesis to leak from the chloroplasts (Gallop 1974). Gallop found that homogenates of *Elysia viridis* strongly stimulated the movement of fixed ^{14}C from chloroplasts, with as much as 73% of fixed ^{14}C being released. She found that only homogenates of the animal's digestive gland were involved in this release (Gallop 1974).

It is thought that the slugs take up the chloroplasts by phagocytosis—this has been observed in one species—*Placida dendritica* (McLean 1976). It is unlikely that the slugs pass on chloroplasts to offspring as ^{14}C labelling experiments have shown that kleptoplasts do not synthesize chlorophyll (Trench et al. 1973a, Trench 1975). No slug eggs or veliger larvae have been found to contain chlorophyll, and it is therefore believed that the slugs acquire chloroplasts *de novo* with each new generation (Trench 1975, Marín & Ros 1993). *Elysia*

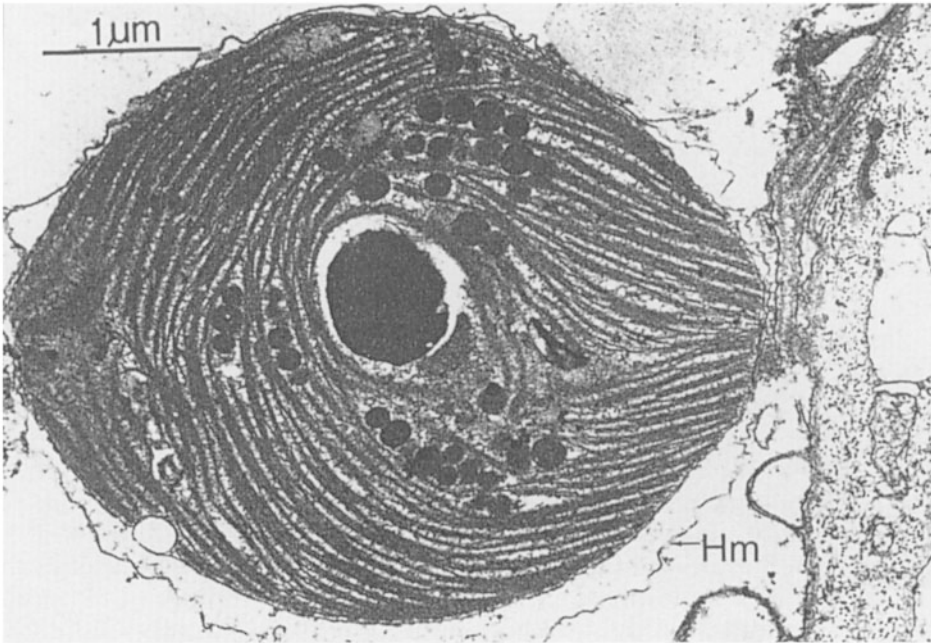


Figure 10 Intact chloroplast from digestive gland cell of 2-week starved *Costasiella liliana*. Hm-host membrane (After Clark et al. 1981, Fig. 8).

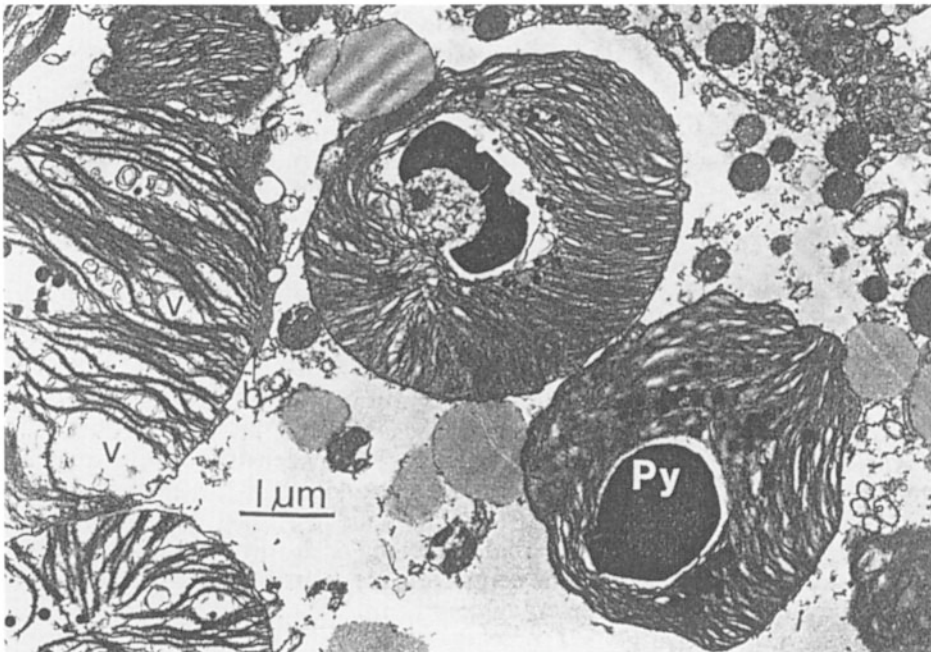


Figure 11 Chloroplasts from digestive gland cell of 2-week starved *Costasiella liliana*, showing early degenerative changes, b-cytoplasmic bleb enclosed within plastid membranes; Py-pyrenoid; v-interthylakoid vesicle. (After Clark et al. 1981, Fig. 9).

viridis slugs reared from egg masses in laboratory experiments do not contain chloroplasts until after feeding on the algae commences (C.D.Trowbridge, pers. comm.).

Trends in kleptoplasty among the Sacoglossa

Taxonomic trends

Shelled versus non-shelled sacoglossans Clark (1992) notes that functional kleptoplasty is most common among more “primitive” elysiids (now the Plakobranchidae) and stiligerids (now the Limapontiidae), which feed on algae in the order Caulerpales. As diet has radiated out from Caulerpales and other algae in the now obsolete order Siphonales (families Derbesiaceae, Caulerpaceae, Bryopsidaceae and Codiaceae), the more “advanced” plakobranchids and limapontiids are unable to fix carbon as the chloroplasts of their food algae or plants are less robust and are mechanically disrupted during ingestion.

This argument is supported by a review of the literature on kleptoplasty in sacoglossans, which indicates that most slug species that fix carbon are plakobranchids (Table 4) and the most common diet of carbon-fixing slugs is algae in the order Caulerpales and other green algae (Table 5). Thirty-nine species of slug have been examined for evidence of functional kleptoplasty (Table 4). Table 4 only includes studies where the slug has been tested for the ability to fix carbon photosynthetically, i.e. where the slug has been shown to fix significantly more ^{14}C in the light than in the dark or where oxygen production in the light has been observed. Table 4 shows that of the 39 species surveyed, 20 use plastids for photosynthesis and 19 do not. Most of the carbon fixing slugs are plakobranchids—12 of the 20 species that photosynthesize. None of the shelled slugs has been shown to fix carbon.

Calcification of food algae It can be seen from Table 5 that the green algae are the most common diet of the slugs that fix carbon, accounting for 14 of the 20 carbon-fixing slug species. Six of the carbon-fixing slugs feed on algae in the order Caulerpales, and eight on other green algae. It has been suggested by Clark (1992) that kleptoplasty may have played a role in enabling sacoglossans to radiate out to algae other than *Caulerpa*. He argues that kleptoplasty would be of great benefit to slugs feeding on highly calcified algae, where carbon fixation may help to compensate for high feeding effort. Waugh & Clark (1986) found that sacoglossans feeding on the highly calcified *Halimeda incrassata* had a higher chlorophyll content than those feeding on the less calcified *H.discoidea*, even though the two algal species had similar chlorophyll concentrations.

More recently, Marín & Ros (1992) also suggested a link with calcification. They found that as the food alga *Acetabularia acetabulum* becomes more calcified during the year, grazing by the slug *Elysia timida* eventually ceases, but carbon fixation by the slug continues as the chloroplasts are retained for up to 45 days. They also found the population density of the slug to be linked with the seasonal life cycle of the algal population. In an earlier publication, Marín & Ros (1989) reported that well-fed slugs turn over their kleptoplast population at a high rate, replacing around 10% of plastids after 4 days. The fact that the slugs can retain kleptoplasts for 45 days when food is less plentiful suggests that starved slugs have a slower rate of kleptoplast turnover. Marín & Ros (1992) concluded that kleptoplasty may provide the slugs with a buffer energy source, alleviating the effects of seasonal changes in the abundance and density of their food source, and being particularly important during the months when the alga is calcified, and therefore unavailable for grazing by the slugs.

Table 5 Kleptoplasty in sacoglossans—by diet.

Diet of sacoglossan	No. of spp. with functional kleptoplasty ¹	No. of spp. without functional kleptoplasty ¹	Spp. with functional kleptoplasty as a % of total spp. tested
<i>Caulerpa</i> sp.	1	7	13
<i>Caulerpa</i> + other Caulerpales	3	0	100
Non-caulerpan Caulerpales (<i>Halimeda</i> , <i>Avrainvillea</i> , <i>Udotea</i> , <i>Chlorodesmis</i>)	2	1	67
Other green algae (<i>Cladophora</i> , <i>Codium</i> , <i>Bryopsis</i> , <i>Acetabularia</i> , <i>Chaetomorpha</i> , <i>Rhizoclonium</i>)	8	6	62
Brown algae (<i>Padina</i>)	1	0	100
Chrysophyta (<i>Vaucheria</i> , diatoms)	1	1	50
Red algae	1	1	50
Seagrass	0	2	0
Mixed plastid source	2	0	100
Unknown diet	1	1	33
Total	20	19	51

¹ Source—Table 7.

Review of the literature however, indicates that calcification of food algae does not fully explain the role of kleptoplasty in sacoglossan feeding ecology. It can be seen in Table 6 that 9 of the 20 slugs that fix carbon include calcified algae in their diet, i.e. 45% of the carbon-fixing species. The next largest group of carbon-fixing slugs are those that include filamentous green algae in their diet, with eight such species feeding on this algal group (Table 6). Many of the filamentous algae are thought to have highly seasonal population dynamics (Clark & DeFreese 1987). Kleptoplasty may therefore be a strategy that allows

Table 6 Kleptoplasty in sacoglossans—by algal functional group.

Algal functional group ¹	No. of spp. with functional kleptoplasty ²	No. of spp. without functional kleptoplasty ²	Spp. with functional kleptoplasty as a % of total spp. tested
<i>Caulerpa</i>	4	7	36
Filamentous green algae	8	4	67
Calcified coenocytic green algae	9	2	82
<i>Codium</i>	1	1	50
Other diet (brown algae, Chrysophyta, red algae, seagrass, molluscan eggs)	5	5	50
Unknown diet	1	1	50
Total³	28	20	

¹ Algal functional groups are as defined by Clark & DeFreese (1987).

² Source—Table 7.

³ Total is higher than for Tables 4, 5 and 7 as some slugs feed on >1 algal group.

the slugs to utilize a food source which is highly seasonal. This does not, however, explain the role of kleptoplasty for slugs that feed on *Caulerpa* spp., which are not calcified and are pseudoperennial. Clark & Busacca (1978) may offer a better explanation, arguing that kleptoplasty may be correlated with a patchy distribution of the slug's food algae.

These conclusions are somewhat speculative, however, given that very few studies of kleptoplasty have rigorously examined the source of the kleptoplastids, with the dietary information given in Tables 5 to 7 generally coming from separate diet studies. Many of the publications on kleptoplasty have assumed that the source of the kleptoplastids is the alga on which the slug is found.

Seasonal trends

Seasonal trends may have a more important correlation with kleptoplasty than has been considered in the literature. Very few studies of kleptoplasty have been conducted throughout the life cycle of the slugs, with most publications giving no indication of the time of year of collection of slugs. Hinde & Smith (1975) noted that *Elysia viridis* shows seasonal variations in behaviour, with greater activity and growth in the autumn and winter, suggesting that these seasonal differences in the slug's energy requirements may mean seasonal variations in kleptoplasty. However, few of the later studies appear to have taken this into account. One of the few is that of Brandley (1984) which showed, interestingly, that *Elysia furvacauda*, in Botany Bay, Australia, retains functional chloroplasts from three different algal species (two green, one red) at different times of the year. Between each shift in plastid type, the slugs appear to have a non-photosynthetic stage, indicating that an adjustment period may be required when a new chloroplast type is acquired. Brandley (1984) found large variations in the slugs' level of carbon fixation during the year. These results have been supported recently by Marín & Ros (1992), who found seasonal variations in the carbon fixation rate of *Elysia timida* in the Mediterranean, with peak photosynthetic activity in the autumn.

These results may cast doubt on earlier surveys for kleptoplasty where the slugs have been examined for photosynthetic ability during only one season. For example, the results for 18 of the 39 species listed in Table 5 come from a study by Clark et al. (1990) which does not indicate whether seasonal variations in photosynthetic ability were considered. An earlier study by Waugh & Clark (1986) had indicated that the level of chlorophyll in sacoglossans in this region (Florida, USA) varies seasonally, peaking in the autumn, which may suggest seasonal variations in the slugs' ability to fix carbon. The sampling design of Clark et al. (1990) may have resulted in an understatement of the extent to which functional kleptoplasty occurs within the order.

To obtain a clearer understanding of the role of kleptoplasty in the feeding ecology of sacoglossans, further work is required to examine the incidence of kleptoplasty in the slugs during different seasons. Such studies need to ensure the source of the plastids is identified in order to make real comparisons between the feeding ecology of slugs with different dietary sources. In order to obtain an understanding of the contribution carbon fixation makes to the energy budget of the slugs, experiments should be carried out under ecologically realistic conditions, i.e. rather than obtaining measures of carbon fixation under starvation conditions, it would be useful to obtain such measures for slugs with free access to food. Finally, a comparison of the incidence of kleptoplasty in sacoglossans feeding on *Caulerpa* and other *Caulerpales* may help to throw light on the role (if any) of kleptoplasty in diet radiation among the Sacoglossa.

Table 7 Kleptoplasty in sacoglossans—by species.

Species	Family ¹	Kleptoplasty ²	References	Diet ³	Diet References
<i>Ascobulla ulla</i>	Volvatellidae	No	Clark et al. (1990)	<i>Caulerpa racemosa</i>	Jensen (1980)
<i>Berthelinia caribbea</i>	Juliidae	No	Clark et al. (1990)	<i>Caulerpa verticillata</i>	Grahame (1969) cited in Jensen (1980)
<i>Berthelinia chloris</i>	Juliidae	No	Muscattine & Greene (1973)	Diet not tested	
<i>Oxynoe antillarum</i>	Oxynoidea	No	Muscattine & Greene (1973)	<i>Caulerpa</i>	Clark & Busacca (1978)
<i>Oxynoe panamensis</i>	Oxynoidea	Unclear	Muscattine & Greene (1973)	<i>Caulerpa sertularioides</i>	Lewin (1970) cited in Jensen (1980)
<i>Oxynoe azuropunctata</i>	Oxynoidea	No	Clark et al. (1990)	<i>Caulerpa racemosa</i> , <i>C. sertularioides</i>	Jensen (1981)
<i>Oxynoe viridis</i>	Oxynoidea	No	Hinde (1980)	<i>Caulerpa filiformis</i>	Hinde (1980)
<i>Lobiger souverbiei</i>	Oxynoidea	No	Clark et al. (1990)	<i>Caulerpa racemosa</i>	Jensen (1980)
<i>Elysia australis</i>	Plakobranchidae (=Elysiidae)	Yes	Hinde (1980)	<i>Enteromorpha intestinalis</i>	Hinde (1980)
<i>Elysia catulus</i>	Plakobranchidae (=Elysiidae)	No	Clark et al. (1990)	Seagrasses	Clark (1975) cited in Jensen (1980)
<i>Elysia cauze</i>	Plakobranchidae (=Elysiidae)	Yes	Clark et al. (1979)	<i>Caulerpa</i>	Clark & Busacca (1978)
<i>Elysia chlorotica</i>	Plakobranchidae (=Elysiidae)	Yes	Gibson et al. (1986)	<i>Cladophorales</i> and <i>Vaucheria</i>	Clark (1975) cited in Jensen (1980)
<i>Elysia evelinae</i>	Plakobranchidae (=Elysiidae)	No	Clark et al. (1990)	Diatoms	Jensen (1980)
<i>Elysia furvacauda</i>	Plakobranchidae (=Elysiidae)	Yes	Brandley (1984)	<i>Codium, Microdictyon</i> red epiphytic algae on <i>Sargassum</i>	Brandley (1984)
<i>Elysia hedgpethi</i>	Plakobranchidae (=Elysiidae)	Yes	Greene & Muscattine (1972)	Codiales	Greene (1970a) cited in Jensen (1980)

Table 7 continued

Species	Family ¹	Kleptoplasty ²	References	Diet ³	Diet References
<i>Elysia serca</i>	Plakobranchidae (=Elysiidae)	No	Clark et al. (1990)	Seagrasses	Jensen (1980)
<i>Elysia timida</i>	Plakobranchidae (=Elysiidae)	Yes	Marin & Ros (1992)	Dasycladales	Schmekel (1968) cited in Jensen (1980)
<i>Elysia tuca</i>	Plakobranchidae (=Elysiidae)	Yes	Stirts & Clark (1980)	Caulerpa, <i>Halimeda</i> , <i>Avrainvillea</i>	Clark & Busacca (1978)
<i>Elysia viridis</i>	Plakobranchidae (=Elysiidae)	Yes	Hinde & Smith (1974, 1975)	Codiiales, Derbesiales, Cladophorales	Fretter (1941) and Rasmussen (1973) cited in Jensen (1980)
<i>Plakobranchus ocellatus</i>	Plakobranchidae (=Elysiidae)	Yes	Greene & Muscatine (1972)	Non-caulerpan Caulerpales (<i>Udotea</i> , <i>Chlorodesmis</i>)	Switzer-Dunlap (1975) cited in Jensen (1980)
<i>Plakobranchus ianthobapsus</i>	Plakobranchidae (=Elysiidae)	Yes	Trench et al. (1969)	diet not tested	
<i>Tridachia crispata</i>	Plakobranchidae (=Elysiidae)	Yes	Trench et al. (1969)	Caulerpales incl. <i>Caulerpa verticillata</i> and <i>Halimeda</i> Derbesiales	Clark & Busacca (1978)
<i>Tridachia diomedea</i>	Plakobranchidae (=Elysiidae)	Yes	Trench et al. (1969)	Brown algae	Bertsch & Smith (1973) cited in Jensen (1980)
<i>Bosellia mimetica</i>	Bosellidae	Yes	Clark et al. (1990)	Non-caulerpan Caulerpales (<i>Halimeda</i>)	Portmann (1958) cited in Jensen (1980)
<i>Caliphylla mediterranea</i>	Polybranchiidae	Yes	Clark et al. (1990)	Derbesiales	Brüel (1904) cited in Jensen (1980)
<i>Cyerce antillensis</i>	Polybranchiidae	No	Clark et al. (1990)	Non-caulerpan Caulerpales (<i>Penicillus</i> , <i>Halimeda</i>)	Jensen (1980)
<i>Mourgona germaineae</i>	Polybranchiidae	Yes	Clark et al. (1990)	<i>Cympolia barbata</i>	Jensen (1981)
<i>Aplysiopsis enteromorphae</i> (= <i>A. smithi</i> = <i>Hermacina smithi</i>)	Hermacidae	No	Greene (1970)	<i>Cladophora</i> , <i>Chaetomorpha</i>	Trowbridge (1993a)

<i>Aplystopsis zebra</i>	Hermaeidae	No	Clark et al. (1990)	<i>Cladophora fuliginosa</i> , <i>Chaetomorpha</i>	Jensen (1983)
<i>Hermaea bifida</i>	Hermaeidae	Yes	Kremer & Schmitz (1976)	<i>Griffithsia</i>	Kremer & Schmitz (1976)
<i>Hermaea cruciata</i>	Hermaeidae	No	Clark et al. (1990)	<i>Griffithsia</i>	Jensen (1983)
<i>Alderia modesta</i>	Limapontiidae (=Stiligeridae)	Yes	Clark et al. (1990)	<i>Vaucheria</i>	Evans (1953) and Hartog (1959) cited in Jensen (1980)
<i>Costasiella liliana</i>	Limapontiidae (=Stiligeridae)	Yes	Clark et al. (1981)	<i>Caulerpales (Avrainvillea,</i> <i>Caulerpa)</i>	Clark & Busacca (1978), Jensen (1981, 1983)
<i>Placida dendritica</i>	Limapontiidae (=Stiligeridae)	No	Hinde (1980) Clark et al. (1990)	Codiales Derbesiales	Brüel (1904), Fretter (1941), and Greene (1970a) cited in Jensen (1980)
<i>Placida kingstoni</i>	Limapontiidae (=Stiligeridae)	Yes	Clark et al. (1990)	Derbesiales, Cladophorales	Jensen (1980, 1981)
<i>Ercolania coerulea</i>	Limapontiidae (=Stiligeridae)	No	Clark et al. (1990)	Siphonocladales	Schmekel (1968) cited in Jensen (1980)
<i>Ercolonia fuscata</i>	Limapontiidae (=Stiligeridae)	No	Clark et al. (1990)	Cladophorales	Clark (1975) cited in Jensen (1980), Jensen (1983)
<i>Limapontia capitata</i>	Limapontiidae (=Stiligeridae)	No	Hinde & Smith (1974)	Cladophorales	Gascoigne (1956), and Jensen (1975) cited in Jensen (1980)
<i>Limapontia depressa</i>	Limapontiidae (=Stiligeridae)	Yes	Hinde & Smith (1974)	Cladophorales	Gascoigne (1956), and Hartog (1959) cited in Jensen (1980)

¹ Taxonomic classification of sacoglossans is taken from Jensen (1997a).

² Functional kleptoplasty is defined as "yes" if the animal has been shown to fix significantly more ¹⁴C in the light than in the dark or produces O₂ in the light.

³ Taxonomic classification of algae is taken from Womersley (1984). Note that the diets of the animals may be incomplete as some investigators have not attempted to feed the animal more than one alga.

Table 8 Rates of carbon fixation by *Codium* and *Elysia viridis* after 1 h at an illumination of 21 500 lm m⁻² (after Trench et al. 1973b, Table 1).

Temp. °C	Tissue	μmol C fixed mg	μmol C fixed mg
		chlorophyll h ⁻¹	chlorophyll h ⁻¹
		Light	Dark
18	<i>Codium</i>	11.97	0
	<i>Elysia</i>	7.89	0
11	<i>Codium</i>	6.15	0
	<i>Elysia</i>	3.35	0
12	<i>Codium</i>	0	0.14
	<i>Elysia</i>	0	0.13

Methods used in identifying kleptoplasty in Sacoglossa

Photosynthesis by kleptoplastids

The evidence for photosynthesis by kleptoplastids in sacoglossans has come from two classical methods—net oxygen production and/or fixation of ¹⁴C from labelled sodium hydrogen carbonate in the light by slugs isolated from their food algae (Taylor 1971, Trench et al. 1973a, Hinde & Smith 1974, 1975, Kremer & Schmitz 1976, Hinde 1980, Clark et al. 1981, Marín & Ros 1992). Trench et al. (1973b) used this method to show that *Elysia viridis* is able to fix carbon in the light when kept away from its algal food source (Table 8). Using the ¹⁴C method, it has been calculated that 36–40% of the carbon fixed by kleptoplasts in *Elysia viridis* is taken up by the slug and for *Tridachia crispata*, this figure is 50% (Trench 1975). The ¹⁴C method has also been used to show that kleptoplasts do not synthesize chlorophyll—as ¹⁴C was not detected in chlorophyll extracted from the slugs (Trench et al. 1973b).

Contribution of kleptoplasty to carbon requirements of slug

Few detailed studies have been carried out on this subject. Hinde & Smith (1975) concluded that photosynthesis by kleptoplasts is of considerable importance in the nutrition of *Elysia viridis*. The basis for this conclusion was that *Elysia viridis* deprived of both light and food lost weight approximately twice as fast as those deprived only of food. Exclusion of food resulted in a smaller loss of weight than exclusion of light. However, the authors admitted that behavioural changes may have played a role in this result—slugs kept in the dark with or without food became passive and appeared not to feed.

A more recent publication by Marín & Ros (1992) addresses the importance to the slugs of carbon obtained from kleptoplasts under ecologically relevant conditions. They calculated that for a population of *Elysia timida*, kleptoplasty contributes carbon equal to 8% of the algal stalks grazed by the slugs annually. This figure was obtained by determining the carbon fixation rate of the slugs throughout the year (using ¹⁴C methods), the carbon fixation rate of the alga, the alga's production rate and the slugs' grazing rate. This appears to be the only study that has quantified and compared grazing and photosynthetic carbon fixation by the slugs. Clearly, more work is required in this area.

Kleptoplast turnover rate

Gallop et al. (1980) used the fact that kleptoplasts do not synthesize chlorophyll to estimate chloroplast turnover time in *Elysia viridis*. The slugs were fed *Codium fragile* for 4–5 days. The *Codium* had been previously labelled with ^{14}C . The slugs were then fed on unlabelled *Codium* for a chase period of 4 days. The slugs were then divided into two groups—one group starved in the light, the other fed in the light. The loss of ^{14}C chlorophyll from the slugs was then measured over a 9-day period. This information was combined with measurements of acquisition rates of chloroplasts (obtained in a similar fashion) to calculate a chloroplast turnover rate of one-half to one-third of the slugs' chloroplast population per week.

^{14}C experiments were also used by Gallop et al. (1980) to obtain measures of the slugs' feeding preferences for different parts of the alga. They found that the slugs in laboratory feeding experiments acquired more chloroplasts from the tip of the alga than the base—interestingly, the chloroplasts at the tip have higher rates of photosynthesis. This may not reflect slug feeding patterns in the field, however, with few *Elysia viridis* individuals found on *Codium fragile* tips in the field (C.D.Trowbridge, pers. comm.).

Identifying the source of kleptoplastids

Chloroplast structure (TEM) The fine structure of kleptoplasts has been examined using transmission electron microscopy, enabling an examination of thylakoid structure and other identifying features of chloroplasts. The algal sources of the kleptoplasts in *Elysia atroviridis* (Kawaguti & Yamasu 1965) and in *Elysia furvacauda* (Brandley 1984) have been identified this way. However, fine structure alone is not generally sufficient to identify kleptoplast source to species.

Pigment analysis Photosynthetic pigments of kleptoplasts have been extracted and analyzed by thin layer chromatography (Trench 1975). As chlorophyll pigments are indicative of the algal group from which the plastids are derived, this can be a useful tool where the diet of the animal is unknown. The presence of the xanthophyll pigments siphonaxanthin and siphonein in extracts of *Tridachia crispata* has been used to help identify the siphonalean diet of this sacoglossan. Trench (1975) also carried out a spectrophotometric analysis of the chloroplast pigments of five sacoglossan species and was able to conclude that the pigments were very similar to those of *Codium fragile* and *Caulerpa racemosa*. This technique, like that above, does not always permit identification of kleptoplast source to species.

In a recent publication, Roller & Bianchi (1995) used HPLC analysis of chloroplast pigments in the slug *Tridachia crispata* to show that the slug contains fucoxanthin, attributed to the ingestion of epibenthic diatoms, as well as pigments identical to those of the host plant *Caulerpa sertularioides*.

Analysis using chloroplast DNA There do not appear to have been any studies published that use genetic markers to identify the source of kleptoplastids in sacoglossans. Satoh et al. (1992) found extremely heterogeneous restriction patterns in chloroplast DNA from four species of *Caulerpa*, suggesting that this approach may be useful in identifying the source of chloroplasts retained in slugs.

^{13}C signature of the slug There do not appear to have been any studies published that attempt to use the d^{13}C signature of the slug and potential food algal species in order to identify the source of kleptoplastids. This method may be useful in conjunction with those detailed above.

Effects of sacoglossans on algal population dynamics and distribution

A great deal of literature exists on the role of large generalist herbivores in community ecology, with the aim of synthesizing the impact of these grazers on algal community structure (e.g. Lubchenco & Gaines 1981, Underwood & Jernakoff 1981, Hawkins & Hartnoll 1983). In general, small specialist herbivores such as sacoglossans have tended to be excluded from such reviews, perhaps because little is known of the impacts of these grazers on algal populations and communities. Where specialist grazers have been considered, they are generally relatively large (e.g. limpets) such as in the review by Hawkins & Hartnoll (1983). These authors suggest that specialist herbivores may have a less marked effect on algal communities than generalists, but they may have a major effect on the population dynamics of their host algae. In arguing this point, Hawkins & Hartnoll (1983) use examples of limpet-kelp interactions from Black (1976). Specialist mesoherbivores such as sacoglossans in some cases have even been dismissed by the researchers working on them—for example, Hinde (1983) states that most sacoglossans are “small, usually rare and sparsely distributed on plants, causing little visible damage”.

At first glance, such a view may seem justified. Small, rare animals would seem unlikely to eat much and therefore unlikely to impact the algae they eat. However, work published in recent years on sacoglossans does not support this view (Marín & Ros 1992, Trowbridge 1992, 1993b,c, Clark 1994, Meinesz et al. 1996). These studies suggest that sacoglossans may affect the algae they eat in a number of ways, through:

- (a) Direct consumption of the alga—i.e. quantity consumed may be important;
- (b) Consuming/damaging structurally important parts of the alga (e.g. damaging the holdfast), i.e. quality consumed/damaged may be important;
- (c) Preferentially attacking stressed algal thalli, resulting in greater damage/stress;
- (d) Preferentially attacking reproductive parts of the algal thalli.

Quantity of algae consumed

In order for mesoherbivores to consume a quantity of algae important to the alga, the grazer's population density and the amount grazed per animal needs to be sufficiently high. Hinde (1983) remarked that sacoglossan population densities are generally low. However, recent studies show that sacoglossans are not always rare—for example, the slug *Alderia modesta* is common on *Vaucheria* mats in some parts of Oregon (Trowbridge 1993c), *Elysia timida* is common on the alga *Acetabularia acetabulum* in some bays in the Mediterranean (Marín & Ros 1992), *Elysia viridis*, *Ercolania nigra*, *Limapontia capitata* and *Limapontia depressa* may form dense seasonal populations on *Chaetomorpha linum* in Denmark (Theisen & Jensen 1991) and *Placida dendritica* is common in warm-temperate to boreal coastal waters throughout the world (Schmekel & Portmann 1982 cited in Trowbridge 1991a). Rather than being rare, sacoglossans may simply be patchily distributed (Trowbridge 1991a). Slugs may also be difficult to locate in the field owing to their cryptic coloration and behaviour, with some species thought to hide within the host algal fronds by day, feeding nocturnally (Weaver & Clark 1981). Slugs may be more important grazers in temperate regions than in the tropics, with slug population density increasing on a log scale with latitude (Clark & DeFreese 1987).

Additionally, there is some evidence to suggest that sacoglossans may be the major invertebrate grazers on some species of algae in the order Caulerpaales. For example, Burn

(1966) reported that opisthobranchs are often the only molluscs found on *Caulerpa* in Fiji. Paul & Fenical (1986) noted that earlier studies have shown that caulerpalean algae are of low preference in the diets of most macroherbivores, which led them to survey forty tropical species in the order Caulerpales for toxic substances. They found almost all of these species produce secondary metabolites which are toxic to, or deter feeding by herbivorous fish. Sacoglossans appear to be one of the few groups of grazers that are able to cope with the toxins produced by these algae, in some cases sequestering these chemicals for their own defence against predation (Paul & Van Alstyne 1988). Similar results have been reported from the Mediterranean, where the introduced alga *Caulerpa taxifolia* has been shown to contain caulerpenyne, which has been linked with avoidance of the alga by herbivorous animals (Lemée et al. 1996). Levels of caulerpenyne in *Caulerpa taxifolia* vary seasonally, with levels lowest in winter—the only season during which epiphytes are found on the alga (Lemée et al. 1993) and when sea urchins are able to graze the alga (Lemée et al. 1996). In diet studies, the sacoglossans *Oxynoe azuropunctata* and *Elysia subornata* were able to consume *Caulerpa taxifolia* without any apparent toxic effects (Meinesz et al. 1996).

Sacoglossans may also be the numerically dominant invertebrate associated with some non-caulerpalean algae, at least during certain times of the year, implying that they may be one of the more important grazers on these algae (Trowbridge 1992, 1993c). In such cases, sacoglossans may influence the alga's distribution (Trowbridge 1992). A study by Trowbridge (1992) reported that *Placida dendritica* was a major, often numerically dominant component of the herbivore fauna on the alga *Codium setchellii* in spring-summer, while in autumn-winter the dominant herbivore was the small snail *Lacuna marmorata*. On the central coast of Oregon, the alga's distribution is restricted primarily to shaded rock surfaces in low intertidal areas that are strongly influenced by sand scour and burial. In laboratory and field studies, Trowbridge (1992) found that grazing by the sacoglossans damaged the alga to a greater extent than that of the other herbivores. The sacoglossan larvae were also extremely efficient at locating the algae, so that the alga was unable to exist in low density refuges. The only real refuge for the algae was in areas of higher physical disturbance, where the sacoglossans were easily dislodged. This led her to conclude that the restricted distribution of this alga may reflect spatial variation in the effects of disturbance on sea slug recruitment and herbivory. These conclusions were confirmed in a later study (Trowbridge 1998b), in which it was shown that the abundance of the sacoglossan *Placida dendritica* was disproportionately higher on desiccation—prone thalli of *Codium setchellii*. Few studies of grazing on Chlorophyta address herbivory by amphipods and isopods. One of the few is that of Trowbridge (1992), which suggests these animals are not major consumers of *Codium* tissue, relative to sacoglossans, with the amphipods and isopods being generalist in their feeding behaviour in laboratory food choice experiments.

On some green algae, however, sacoglossans appear to be relatively unimportant herbivores. For example, Trowbridge (1993a) obtained very different results for another sacoglossan *Aplysiopsis enteromorphae* (= *A. smithi*), which is thought to eat at least four genera of algae (Table 2, p. 97). Although feeding by this slug on *Chaetomorpha linum* and *Cladophora columbiana* in the laboratory caused a large loss of algal mass, this was not the case in the field. The sacoglossan occurred on the algae in only sparse numbers, with the snail *Littorina scutulata* being the dominant mesoherbivore during much of the year. This snail accounted for more than 90% of *Chaetomorpha* mass loss, whereas herbivory by *Aplysiopsis* accounted for less than 5% of mass loss, even on a local scale. The width of the sacoglossan's dietary range and the rates of larval recruitment and adult local migration may influence how important an effect these herbivores have on their algal

hosts (Trowbridge 1993a). Additionally, *Placida dendritica* appears to feed in large groups, which may mean it has a greater impact on individual thalli (Trowbridge 1991a, 1993a).

The presence of epiphytes may influence the interactions between sacoglossans and their algal prey. Trowbridge (1993b) found evidence of an interaction between *Placida dendritica* and the red algal epiphyte on *Codium fragile*—*Ceramium codicola*. The slug consumes *Codium* and not the epiphyte, but the presence of *Ceramium* enhanced the herbivore's attack. The slugs displayed more frequent settlement and greater survival on *Codium* thalli with attached epiphytes than on *Codium* with epiphytes that had been experimentally clipped. Trowbridge (1993b) found that this association was most common where the slugs were small. This led her to conclude that the presence of the epiphyte may enhance settlement and/or post-settlement survival by ameliorating environmental conditions—for example, the epiphyte may provide baffle action and a cool moist microhabitat during emersion at low tide. Dislodgment and desiccation may be more important for smaller slugs.

Few studies to date have attempted to quantify algal consumption by sacoglossans or grazing relative to algal production. Trowbridge (1992, 1993a) and Meinesz et al. (1996) quantified grazing by the sacoglossans *Placida dendritica*, *Aplysiopsis enteromorphae* and two tropical species *Oxynoe azuropunctata* and *Elysia subornata*, respectively. Grazing by *Placida dendritica* was not significant over the time frame of the experiment (Trowbridge 1992). Trowbridge (1993a) found the rate of algal consumption by *Aplysiopsis enteromorphae* to be 3.8 mg ww algae mg slug⁻¹ day⁻¹. Meinesz et al. (1996) found that an individual *Oxynoe azuropunctata* (1 cm to 3 cm in length) may eat up to 100 mg ww day⁻¹ of the alga *Caulerpa taxifolia* and on the same alga, an individual *Elysia subornata* (4 cm to 6 cm long) may eat up to 400 mg ww algae⁻¹ day⁻¹. Meinesz et al. (1996) found the grazing rate to be temperature dependent (these sacoglossans are tropical in distribution), with maximum consumption at around 28–30°C. It is difficult however, to determine how important this herbivory may be to the alga as the authors do not report algal production figures.

Only one publication to date appears to examine sacoglossan herbivory in relation to algal production, that of Marín & Ros (1992). A re-analysis of their data shows that during much of the year, *Elysia timida* consumes 2–5% (Table 9) of the non-calcified stalks produced by *Acetabularia acetabulum*. During March and May, this consumption is much higher—at around 17–18% of non-calcified stalks produced (Table 9)—suggesting that

Table 9 Seasonal variations in grazing on *Acetabularia acetabulum* by *Elysia timida* in the Mediterranean. (A)=grazing as a % of stalk production, (B)=grazing as a % of non-calcified stalk production (after Marín & Ros, 1992: Table 1).

Month	No. stalks produced m ⁻²	No. non-calcified stalks produced m ⁻²	No. of stalks grazed m ⁻²	Grazing impact (A)	Grazing impact (B)
Oct	2 764	2 764	89	3.2	3.2
Nov	11 333	11 333	510	4.5	4.5
Dec	12 000	12 000	368	3.1	3.1
Jan	11 555	9 111	285	2.5	3.1
Feb	10 444	9 555	521	5.0	5.5
Mar	11 333	10 665	1 809	16.0	17.0
Apr	14 222	6 222	143	1.0	2.3
May	16 950	1 753	312	1.8	17.8
Jun	13 997	0	0	0	0

herbivory by the slug may be important to the alga at least during some months of the year (Marín & Ros 1992).

Quantity of algae grazed and kleptoplasty

It is not clear what role, if any, kleptoplasty may play in reducing the grazing impact of the sacoglossan on its host alga. Trench (1975) argued that the chloroplasts of green algae such as *Codium* are particularly resistant to stress and removal from the algal cell, arguing that it is a property of the alga which allows kleptoplasty to occur. Hay & Steinberg (1992) state “because energy from chloroplast symbiosis can supply some ascoglossans with all of their respiratory needs, these ascoglossans may do minimal damage to their host plant”. Hay & Steinberg (1992) suggest that the alga is more than just fodder for the sacoglossan, providing the slug with not only food but also habitat and a refuge from predation. This leads to the interesting (but perhaps untestable) question suggested by Hinde (1983) of whether kleptoplasty is as much a defence strategy of the alga as it is a feeding strategy of the slug.

Marín & Ros (1992) suggested that retention of functional chloroplasts by *Elysia timida* may reduce grazing pressure on the alga *Acetabularia acetabulum* by 8%, as carbon fixation by the slug population was equal to 8% of algal stalks grazed during October to June (the alga is calcified during July-September, so unavailable to the slugs and the slugs were not observed on the alga during this period).

Grazing that targets particular parts of the algal thallus

Recent work suggests that even where sacoglossans are present at low densities, their grazing may have ecologically important effects on their macroalgal host (Trowbridge 1993b). Trowbridge found that the sacoglossan *Placida dendritica* is present at low densities on the alga *Codium fragile* and does not consume a large amount of algal tissue. However, approximately 70% of thalli were attacked by the slugs. Algal biomass loss was enhanced through slug grazing damaging and weakening the algal thallus at critical axial points (Trowbridge 1993b). Most of the *Codium* axes removed by *Placida* were the larger, older fronds, leading Trowbridge (1993b) to mount a similar argument to that of Black (1976) in relation to limpet-kelp interactions: that the *Codium* may benefit from *Placida* grazing through the resulting reduction in hydrodynamic drag and thus enhanced survival. The study by Trowbridge (1993b) highlights the fact that the impact of herbivory on an alga is not just dependent on the amount consumed—indirect loss of algal biomass through grazing damage is equally important. Trowbridge (1992) also reports that *Placida dendritica* often re-attacks *Codium setchellii* thalli already damaged by slug grazing, resulting in extensive damage.

These results led Trowbridge (1993b) to suggest that sacoglossans may be major pruners of *Codium*—by grazing areas of structural importance to the alga. Although there is not yet evidence of secondary metabolites in *Codium*, such parts of other species of algae are often strongly chemically defended (Hay & Fenical 1988). Sacoglossans appear to have circumvented these defences to a greater extent than other algal grazers (Hay & Fenical 1988), implying that sacoglossans may play a more important pruning role than other algal grazers.

Sacoglossans may also preferentially consume algal reproductive structures—for example, *Elysia tuca* is thought to feed on the gametangia of *Halimeda incrassata* when all the other tissue of this alga is calcified (Clark & DeFreese 1987). In Caulerpaes such

as *Halimeda*, toxic secondary metabolites are generally found at highest concentrations in young growing tips and reproductive structures (Paul & Fenical 1986). As these compounds have been shown to be toxic to, or deter feeding by, macroherbivores (Paul & Fenical 1986), it is possible that sacoglossans are the dominant herbivores on the reproductive structures of algae in the order Caulerpales.

Studies of the impacts of sacoglossans on their food algae have been limited to slugs that feed on *Codium* spp. (Trowbridge 1992, 1993b), filamentous algae (Trowbridge 1993a) and calcified algae (Marín & Ros 1992). There is clearly a need for such studies on slugs that feed on the order's most common food—*Caulerpa* spp.

Conclusion

Sacoglossans are mesoherbivores, with a narrow dietary range, restricted to green algae in most cases. Shelled sacoglossans are restricted to one algal genus, *Caulerpa*, with non-shelled sacoglossans able to feed on a wider range of foods including other Chlorophyta, Phaeophyta, Rhodophyta, Chrysophyta, seagrasses and even molluscan egg masses. This view, however, is based on a small number of studies of feeding preference, conducted in the laboratory in short-term experiments, sometimes lasting only hours, and slug-algal associations observed in the field. We need to know more about the slugs' food choice in the field and over the longer term. Analysis of the isotopic signature of the slugs and their potential diets may help to provide this information.

Many sacoglossan species appear to be capable of functional kleptoplasty, with 20 of the world's 250–300 described species having been shown to do so. Despite some 30 years of research on kleptoplasty, its role in the feeding ecology of slugs is still not clear, with few detailed studies on this subject. A number of theories have developed explaining the role of kleptoplasty in sacoglossan feeding ecology:

- (a) it may be a strategy that allows the slugs to live on a seasonal diet—such as the calcified alga *Acetabularia acetabulum* in the Mediterranean.
- (b) it may allow the slugs to live on a diet with patchy distribution.
- (c) it may be a strategy that helps compensate for a diet that requires a high feeding effort.
- (d) it may have allowed sacoglossans to radiate out from the postulated ancestral diet, the Caulerpales.

The feeding ecology of only a very few kleptoplastic sacoglossans has been studied, none of which appears to include *Caulerpa* spp. in their diet. There is a clear need for more work on the importance of kleptoplasty to the full range of sacoglossan diets. A comparison of the incidence of kleptoplasty in sacoglossans feeding on *Caulerpa* and other green algae may help to throw light on the role (if any) of kleptoplasty in diet radiation among the Sacoglossa.

In some cases, sacoglossans may have substantial impacts on the algae they eat, causing large loss of algal biomass and influencing the alga's distribution. This appears to be the case where the slugs are abundant and feed in large groups, but can also occur where the slugs are not present in high numbers, but attack critical structural parts of the algal thallus. These studies on grazing by sacoglossans on *Codium* spp. suggest that these slugs may be major pruners of green algae. There is a need for such studies to be extended to *Caulerpa* spp., the most common food of the Sacoglossa, before any general statements can be made about the impact of sacoglossan grazing on their host/food.

Acknowledgments

This review was improved by comments from C.Trowbridge, K.Jensen, J.Raven and A.Brearley. The work was produced as part of the PhD programme for S.I.Williams at The University of Western Australia. We also thank P.Jernakoff for his inspiring suggestion!

References

- Black, R. 1976. The effects of grazing by the limpet, *Acmaea incessa* on the kelp *Egrecia laevigata* in the intertidal zone. *Ecology* **57**, 265–77.
- Brandley, B.K. 1981. Ultrastructure of the envelope of *Codium australicum* (Silva) chloroplasts in the alga and after acquisition by *Elysia maoria* (Powell). *New Phytologist* **89**, 679–86.
- Brandley, B.K. 1984. Aspects of the ecology and physiology of *Elysia* cf. *furvacauda* (Mollusca: Sacoglossa) *Bulletin of Marine Science* **34**(2), 207–19.
- Brawley, S.H. 1992. Mesoherbivores. In *Plant-animal interactions in the marine benthos*, Systematics Association Special Volume No. 46, D.M.John, S.J.Hawkins & J.H.Price (eds). Oxford: Clarendon Press, 235–63.
- Burn, R. 1966. The opisthobranchs of a Caulerpan microfauna from Fiji. *Proceedings of the Malacological Society of London* **37**, 45–65.
- Burn, R. 1972. A guide to the Ascoglossa or sap-sucking sea-slugs of Australia. *Australian Natural History* **17**, 174–8.
- Burn, R. 1998. Order Sacoglossa. In *Mollusca: the southern synthesis. Fauna of Australia. Vol. 5, Part B*, P.L.Beesley, G.J.B.Ross & A.Wells (eds). Melbourne: CSIRO Publishing, 961–74.
- Clark, K.B. 1975. Nudibranch life cycles in the northwest Atlantic and their relationship to the ecology of fouling communities. *Helgoländer Wissenschaftliche Meeresuntersuchungen* **27**, 28–69.
- Clark, K.B. 1992. Plant-like animals and animal-like plants: symbiotic coevolution of ascoglossan (= sacoglossan) molluscs, their algal prey and algal plastids. In *Algae and symbioses: plants, animals, fungi, viruses, interactions explored*, W.Reisser (ed.). Bristol, England: Biopress, 515–30.
- Clark, K.B. 1994. Ascoglossan (= Sacoglossa) molluscs in the Florida Keys: rare marine invertebrates at special risk. *Bulletin of Marine Science* **54**(3), 900–16.
- Clark, K.B. & Busacca, M. 1978. Feeding specificity and chloroplast retention in four tropical Ascoglossa, with a discussion of the extent of chloroplast symbiosis and the evolution of the order. *Journal of Molluscan Studies* **44**, 272–82.
- Clark, K.B., Busacca, M. & Stirts, H.M. 1979. Nutritional aspects of development of the ascoglossan *Elysia cauze*. In *Reproductive Ecology of Marine Invertebrates*, S.F.Stancyk (ed.). Columbia: University of South Carolina Press, 11–14.
- Clark, K.B. & DeFreese, D. 1987. Population ecology of Caribbean Ascoglossa (Mollusca: Opisthobranchia): a study of specialized algal herbivores. *American Malacological Bulletin* **5**(2), 259–80.
- Clark, K.B., Jensen, K.R. & Stirts, H.M. 1990. Survey for functional kleptoplasty among West Atlantic Ascoglossa (= Sacoglossa) (Mollusca: Opisthobranchia). *The Veliger* **33**(4), 339–45.
- Clark, K.B., Jensen, K.R., Stirts, H.M. & Fermin, C. 1981. Chloroplast symbiosis in a non-elysiid mollusc, *Costasiella lilianae* Marcus (Hermaeidae: Ascoglossa=Sacoglossa): effects of temperature, light intensity, and starvation on carbon fixation rate. *Biological Bulletin* **160**, 43–54.
- Clayton, M.N. & King, R.J. 1990. *Biology of marine plants*. Melbourne: Longman Cheshire.
- Croley, F.C. & Dawes, C.J. 1970. Ecology of the algae of a Florida key. I. A preliminary checklist, zonation and seasonality. *Bulletin of Marine Science* **20**, 165–85.
- Dawes, C.J. & Barilotti, D.C. 1969. Cytoplasmic organization and rhythmic streaming in growing blades of *Caulerpa prolifera*. *American Journal of Botany* **56**, 8–15.
- Dawes, C.J. & Goddard, R.H. 1978. Chemical composition of the wound plug and entire plants for species of the coenocytic green alga, *Caulerpa*. *Journal of Experimental Marine Biology and Ecology* **35**, 259–63.

- DeFreese, D.E. & Clark, K.B. 1991. Transepidermal uptake of dissolved free amino acids from seawater by three ascoglossan opisthobranchs. *Journal of Molluscan Studies* **57**, 65–74.
- DeNiro, M.J. & Epstein, S. 1978. Influence of diet on the distribution of carbon isotopes in animals. *Geochimica et Cosmochimica Acta* **42**, 495–506.
- DeNiro, M.J. & Epstein, S. 1981. Influence of diet on the distribution of nitrogen isotopes in animals. *Geochimica et Cosmochimica Acta* **45**, 341–51.
- Drew, E.A. & Abel, K.M. 1992. Studies on *Halimeda*, IV. An endogenous rhythm of chloroplast migration in the siphonous green alga *Halimeda distorta*. *Journal of Interdisciplinary Cycle Research* **23**(2), 128–35.
- Farquhar, G.D., Ehleringer, J.R. & Hubick, K.T. 1989. Carbon isotope discrimination and photosynthesis. *Annual Review of Plant Physiology and Plant Molecular Biology* **40**, 503–37.
- Gallop, A. 1974. Evidence for the presence of a “factor” in *Elysia viridis* which stimulates photosynthate release from its symbiotic chloroplasts. *New Phytologist* **73**, 1111–17.
- Gallop, A., Bartrop, J. & Smith, D.C. 1980. The biology of chloroplast acquisition by *Elysia viridis*. *Proceedings of the Royal Society of London, Series B* **207**, 335–49.
- Gascoigne, T. 1985. A provisional classification of families of the order Ascoglossa (Gastropoda: Nudibranchiata). *Journal of Molluscan Studies* **51**, 8–22.
- Gibson, G.D., Toews, D.P. & Bleakney, J.S. 1986. Oxygen production and consumption in the sacoglossan synonym ascoglossan *Elysia chlorotica*. *The Veliger* **28**(4), 397–400.
- Greene, R.W. 1970. Symbiosis in sacoglossan opisthobranchs: functional capacity of symbiotic chloroplasts. *Marine Biology* **7**, 138–42.
- Greene, R.W. & Muscatine, L. 1972. Symbiosis in sacoglossan opisthobranchs: photosynthetic products of animal-chloroplast associations. *Marine Biology* **14**, 253–9.
- Hawkins, S.J. & Hartnoll, R.G. 1983. Grazing of intertidal algae by marine invertebrates. *Oceanography and Marine Biology: an Annual Review* **21**, 195–282.
- Hay, M.E. & Fenical, W.F. 1988. Marine plant-herbivore interactions: the ecology of chemical defense. *Annual Review of Ecology and Systematics* **19**, 111–45.
- Hay, M.E. & Steinberg, P.D. 1992. The chemical ecology of plant-herbivore interactions in marine versus terrestrial communities. In *Herbivores: their interactions with secondary metabolites, Vol. 2, Ecological and evolutionary processes*, G.Rosenthal & M.R.Berenbaum (eds). San Diego: Academic Press, 371–413.
- Hinde, R. 1980. Chloroplast “symbiosis” in sacoglossan molluscs. In *Endocytobiology, Endosymbiosis and cell biology. Proceedings of the international colloquium on endosymbiosis and cell research*, W.Schwemmler & H.E.A.Schenk (eds). Tübingen, Germany: Walter de Gruyter, 729–36.
- Hinde, R. 1983. Retention of algal chloroplasts by molluscs. In *Algal symbiosis: a continuum of interaction strategies*, L.J.Goff (ed.). Cambridge: Cambridge University Press, 97–107.
- Hinde, R. & Smith, D.C. 1972. Persistence of functional chloroplasts in *Elysia viridis* (Opisthobranchia, Sacoglossa). *Nature New Biology* **239**, 30–31.
- Hinde, R. & Smith, D.C. 1974. “Chloroplast symbiosis” and the extent to which it occurs in Sacoglossa (Gastropoda: Mollusca). *Biological Journal of the Linnean Society* **6**, 349–56.
- Hinde, R. & Smith, D.C. 1975. The role of photosynthesis in the nutrition of the mollusc *Elysia viridis*. *Biological Journal of the Linnean Society* **7**, 161–71.
- Jacobs, W.P. 1994. *Caulerpa*. *Scientific American* **271**(6), 66–71.
- Jensen, K.R. 1980. A review of sacoglossan diets, with comparative notes on radular and buccal anatomy. *Malacological Review* **13**, 55–77.
- Jensen, K.R. 1981. Observations on feeding methods in some Florida ascoglossans. *Journal of Molluscan Studies* **47**, 190–99.
- Jensen, K.R. 1983. Factors affecting feeding selectivity in herbivorous Ascoglossa (Mollusca: Opisthobranchia). *Journal of Experimental Marine Biology and Ecology* **66**, 135–48.
- Jensen, K.R. 1989. Learning as a factor in diet selection by *Elysia viridis* (Montagu) (Opisthobranchia). *Journal of Molluscan Studies* **55**, 79–88.
- Jensen, K.R. 1990. Foraging behaviour of two Australian species of *Elysia* (Mollusca, Opisthobranchia). In *The marine flora and fauna of Albany, Western Australia. Proceedings of the third international marine biology workshop, Vol. 2*, F.E.Wells, D.I.Walker, H.Kirkman & R.Lethbridge (eds). Perth: Western Australian Museum, 541–51.
- Jensen, K.R. 1991. Comparison of alimentary systems in shelled and non-shelled Sacoglossa (Mollusca: Opisthobranchia). *Acta Zoologica* **72**(3), 143–50.

- Jensen, K.R. 1992. Review of the usage of the synonyms *Sacoglossa* Ihering, 1876 and *Ascoglossa* Bergh, 1876. *Proceedings of the Tenth International Malacological Congress (Tübingen 1989)*. Tübingen: on behalf of UNITAS Malacologica, 541–4.
- Jensen, K.R. 1993a. *Sacoglossa* (Mollusca: Opisthobranchia) from Rottnest island and central Western Australia. In *The marine flora and fauna of Rottnest Island, Western Australia, Proceedings of the fifth international marine biology workshop, Vol. 1*, F.E.Wells, D.I.Walker, H.Kirkman & R.Lethbridge (eds). Perth: Western Australian Museum, 207–53.
- Jensen, K.R. 1993b. *Sacoglossa* (Mollusca: Opisthobranchia)—specialist herbivores and partial predators: integrating ecological, physiological and morphological data. In *Marine Biology of the South China Sea, Proceedings of the first international conference on the marine biology of Hong Kong and the South China Sea*, B.Morton (ed.). Hong Kong: Hong Kong University Press, 437–58.
- Jensen, K.R. 1996. Phylogenetic systematics and classification of the *Sacoglossa* (Mollusca, Gastropoda, Opisthobranchia). *Philosophical Transactions of the Royal Society of London B*, **351**, 91–122.
- Jensen, K.R. 1997a. *Sacoglossernes Systematik, fylogeni og evolution (Mollusca, Opisthobranchia)*. *Systematics, phylogeny and evolution of the Sacoglossa (Mollusca, Opisthobranchia)*. Copenhagen: Vestjydsk Forlag.
- Jensen, K.R. 1997b. Evolution of the *Sacoglossa* (Mollusca, Opisthobranchia) and their ecological associations with their food plants. *Evolutionary Ecology* **11**, 301–35.
- Jensen, K.R. & Wells, F.E. 1990. *Sacoglossa* (= *Ascoglossa*) (Mollusca: Opisthobranchia) from southern Western Australia. In *The Marine Flora and Fauna of Albany, Western Australia, Proceedings of the third international marine biology workshop, Vol. 1*, F.E.Wells, D.I.Walker, H. Kirkman & R.Lethbridge (eds). Perth: Western Australian Museum, 297–331.
- Kawaguti, S. & Yamasu, T. 1965. Electron microscopy on the symbiosis between an elysiid gastropod and chloroplasts of a green alga. *Biological Journal of Okayama University* **11**, 57–65.
- Koop, H.U., Schmid, R., Heunert, H.H. & Mitlathaler, B. 1978. Chloroplast migration; a new circadian rhythm in *Acetabularia*. *Protoplasma* **97**, 301–10.
- Kremer, B.P. & Schmitz, K. 1976. Aspects of $^{14}\text{CO}_2$ fixation by endosymbiotic rhodoplasts in the marine opisthobranchiate *Hermea bifida*. *Marine Biology* **34**, 313–16.
- Lemée, R., Resando, D., Durand-Clément, M., Dubreuil, A., Meinesz, A., Guerriero, A. & Pietra, F. 1993. Preliminary survey of toxicity of the green alga *Caulerpa taxifolia* introduced into the Mediterranean. *Journal of Applied Phycology* **5**, 485–93.
- Lemée, R., Boudouresque, C.F., Gobert, J., Malestroit, P., Mari, X., Meinesz, A., Menager, V. & Ruitton, S. 1996. Feeding behaviour of *Paracentrotus lividus* in the presence of *Caulerpa taxifolia* introduced in the Mediterranean Sea. *Oceanologica Acta* **19**(3–4), 245–53.
- Lopez, E. 1979. Algal chloroplasts in the protoplasm of three species of benthic foraminifera: taxonomic affinity, viability and persistence. *Marine Biology* **53**, 201–11.
- Lubchenco, J. & Gaines, S.D. 1981. A unified approach to marine plant-herbivore interactions. I. Populations and communities. *Annual Review of Ecology and Systematics* **12**, 405–37.
- Maberly, S.C., Raven, J.A. & Johnston, A.M. 1992. Discrimination between ^{12}C and ^{13}C by marine plants. *Oecologia* **91**, 481–92.
- Macko, S.A., Lee, W.Y. & Parker, P.L. 1982. Nitrogen and carbon isotope fractionation by two species of marine amphipods: laboratory and field studies. *Journal of Experimental Marine Biology and Ecology* **63**, 145–9.
- Macko, S.A., Estep, M.L.F., Engel, M.H. & Hare, P.E. 1986. Kinetic fractionation of stable nitrogen isotopes during amino acid transamination. *Geochimica et Cosmochimica Acta* **50**, 2143–6.
- Marín, A. & Ros, J.D. 1989. The chloroplast-animal association in four Iberian sacoglossan opisthobranchs: *Elysia timida*, *Elysia translucens*, *Thuridilla hopei* and *Bosellia mimetica*. *Scientia Marina* **53**, 429–40.
- Marín, A. & Ros, J.D. 1992. Dynamics of a peculiar plant-herbivore relationship: the photosynthetic sacoglossan *Elysia timida* and the chlorophycean *Acetabularia acetabulum*. *Marine Biology* **112**, 677–82.
- Marín, A. & Ros, J.D. 1993. Ultrastructural and ecological aspects of the development of chloroplast retention in the sacoglossan *Elysia timida*. *Journal of Molluscan Studies* **59**, 95–104.
- McLean, N. 1976. Phagocytosis of chloroplasts in *Placida dendritica* (Gastropoda: Sacoglossa). *Journal of Experimental Zoology* **197**, 321–30.
- Meinesz, A., Melnyk, J., Blachier, J. & Charrier, S. 1996. Etude préliminaire, en aquarium, de deux ascoglosses tropicaux consommant *Caulerpa taxifolia*: une voie de recherche pour la lutte biologique.

- In *Second International Workshop on Caulerpa taxifolia*, M.A.Ribera, E.Ballasteros, C.F. Boudouresque, A.Gómez & V.Gravez (eds). Barcelona: Publicacions Universitat, pp. 157–61.
- Michener, R.H. & Schell, D.M. 1994. Stable isotope ratios as tracers in marine aquatic food webs. In *Stable isotopes in ecology and environmental science*, K.Lajtha & R.H.Michener (eds). Oxford: Blackwell Scientific Publications, 138–57.
- Minagawa, M. & Wada, E. 1984. Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between d^{15}N and animal age. *Geochimica et Cosmochimica Acta* **48**, 1135–40.
- Mujer, C.V., Andrews, D.L., Manhart, J.R., Pierce, S.K. & Rumpho, M.E. 1996. Chloroplast genes are expressed during intracellular symbiotic association of *Vaucheria litorea* plastids with the sea slug *Elysia chlorotica*. *Proceedings of the National Academy of Sciences of the United States of America* **93**, 12333–8.
- Muscatine, L. & Greene, R.W. 1973. Chloroplasts and algae as symbionts in molluscs. *International Review of Cytology* **36**, 137–69.
- Nicotri, M.E. 1980. Factors involved in herbivore food preference. *Journal of Experimental Marine Biology and Ecology* **42**, 13–26.
- Owens, N.J.P. 1987. Natural variations in ^{15}N in the marine environment. *Advances in Marine Biology* **24**, 389–451.
- Parsons, T.R. & Lee Chen, Y.-L. 1995. The comparative ecology of a subarctic and tropical estuarine ecosystem as measured with carbon and nitrogen isotopes. *Estuarine, Coastal & Shelf Science* **41**, 215–24.
- Paul, V.J. & Fenical, W. 1986. Chemical defense in tropical green algae, order Caulerpales. *Marine Ecology Progress Series* **34**, 157–69.
- Paul, V.J. & Van Alstyne, K.L. 1988. Use of ingested algal diterpenoids by *Elysia halimeda* Macnae (Opisthobranchia: Ascoglossa) as antipredator defenses. *Journal of Experimental Marine Biology and Ecology* **119**, 15–29.
- Peterson, C.H. & Renaud, P.E. 1989. Analysis of feeding preference experiments. *Oecologia* **80**, 82–6.
- Pierce, S.K., Biron, R.W. & Rumpho, M.E. 1996. Endosymbiotic chloroplasts in molluscan cells contain proteins synthesized after plastid capture. *Journal of Experimental Biology* **199**, 2323–30.
- Rau, G.H., Sweeney, R.E., Kaplan, I.R., Mearns, A.J. & Young, D.R. 1981. Differences in animal C, N and D abundance between a polluted and an unpolluted coastal site: likely indicators of sewage uptake by a marine food web. *Estuarine, Coastal & Shelf Science* **13**, 701–7.
- Rau, G.H., Hopkins, T.L. & Torres, J.J. 1991. $^{15}\text{N}/^{14}\text{N}$ and $^{13}\text{C}/^{12}\text{C}$ in Weddell Sea invertebrates: implications for feeding diversity. *Marine Ecology Progress Series* **77**, 1–6.
- Raven, J.A. 1996. Inorganic carbon assimilation by marine biota. *Journal of Experimental Marine Biology and Ecology* **203**, 39–47.
- Raven, J.A., Walker, D. I., Jensen, K.R., Handley, L.L., Scrimgeour, C.M. & McInroy, S.G. 1999. What fraction of the organic carbon in saccoglossans is obtained from photosynthesis by kleptoplastids? An investigation using the natural abundance of stable carbon isotopes. *Marine Ecology Progress Series*, in press.
- Risk, M.J., Sammarco, P.W. & Schwartz, H.P. 1994. Cross-continental shelf trends in d^{13}C in coral on the Great Barrier Reef. *Marine Ecology Progress Series* **106**, 121–30.
- Roller, R.A. & Bianchi, T.S. 1995. HPLC analysis of chloroplast pigments from the marine ascoglossan *Tridachia crispata* (Morch, 1863) (Mollusca: Opisthobranchia). *American Malacological Bulletin* **11**(2), 139–43.
- Satoh, M., Miyamura, S. & Hori, T. 1992. Inter- and intraspecific variations of chloroplast DNA of the siphonous green algal genus *Caulerpa* (Caulerpales, Chlorophyta). *Japan Journal of Phycology* **40**, 365–72.
- Silva, P.C. 1992. Geographic patterns of diversity in benthic marine algae. *Pacific Science* **46**, 429–37.
- Stephens, G.C. 1988. Epidermal amino acid transport in marine invertebrates. *Biochimica et Biophysica Acta* **947**, 113–38.
- Stephenson, R.L., Tan, F.C. & Mann, K.H. 1986. Use of stable carbon isotope ratios to compare plant material and potential consumers in a seagrass bed and a kelp bed in Nova Scotia, Canada. *Marine Ecology Progress Series* **30**, 1–7.
- Stirts, H.M. & Clark, K.B. 1980. Effects of temperature on products of symbiotic chloroplasts in *Elysia tuca* Marcus (Opisthobranchia: Ascoglossa). *Journal of Experimental Marine Biology and Ecology* **43**, 39–47.
- Stoecker, D.K., Michaels, A.E. & Davis, L.H. 1987. Large proportion of marine planktonic ciliates found to contain functional chloroplasts. *Nature* **326**, 790–92.

- Stoecker, D.K., Silver, M.W., Michaels, A.E. & Davis, L.H. 1988–1989. Enslavement of algal chloroplasts by four *Strombidium* spp. (Ciliophora, Oligotrichida). *Marine Microbial Food Webs* **3**, 79–100.
- Taylor, D.L. 1968. Chloroplasts as symbiotic organelles in the digestive gland of *Elysia viridis* (Gastropoda: Opisthobranchia). *Journal of the Marine Biological Association of the United Kingdom* **48**, 1–15.
- Taylor, D.L. 1971. Photosynthesis of symbiotic chloroplasts in *Tridachia crispata* (Bérgh). *Comparative Biochemistry and Physiology* **38A**, 233–6.
- Theisen, B.F. & Jensen, K.R. 1991. Genetic variation in six species of sacoglossan opisthobranchs. *Journal of Molluscan Studies* **57**, 267–75.
- Tieszen, L.L., Boutton, T.W., Tesdahl, K.G. & Slade, N.A. 1983. Fractionation and turnover of stable carbon isotopes in animal tissues: implications for $d^{13}C$ analysis of diet. *Oecologia* **57**, 32–7.
- Trench, R.K. 1969. Chloroplasts as endosymbiotic organelles in *Tridachia crispata* (Bergh), Sacoglossa, Opisthobranchia. *Nature* **222**, 1071–2.
- Trench, R.K. 1973. Further studies on the mucopolysaccharide secreted by the pedal gland of the marine slug *Tridachia crispata* (Opisthobranchia, Sacoglossa). *Bulletin of Marine Science* **23**, 299–312.
- Trench, R.K. 1975. Of “leaves that crawl”: functional chloroplasts in animal cells. *Symposia of the Society of Experimental Biology* **29**, 229–65.
- Trench, R.K., Boyle, E. & Smith, D.C. 1973a. The association between chloroplasts of *Codium fragile* and the mollusc *Elysia viridis*, I. Characteristics of isolated *Codium* chloroplasts. *Proceedings of the Royal Society of London, Series A* **184**, 51–61.
- Trench, R.K., Boyle, E. & Smith, D.C. 1973b. The association between chloroplasts of *Codium fragile* and the mollusc *Elysia viridis*, II. Chloroplast ultrastructure and photosynthetic carbon fixation in *E. viridis*. *Proceedings of the Royal Society of London, Series A* **184**, 63–81.
- Trench, R.K., Greene, R.W. & Bystrom, B.G. 1969. Chloroplasts as functional organelles in animal tissues. *Journal of Cell Biology* **42**, 404–17.
- Trowbridge, C.D. 1991a. Group membership facilitates feeding of the herbivorous sea slug *Placida dendritica*. *Ecology* **72**(6), 2193–203.
- Trowbridge, C.D. 1991b. Diet specialization limits herbivorous sea slug’s capacity to switch among food species. *Ecology* **72**(5), 1880–88.
- Trowbridge, C.D. 1992. Mesoherbivory: the ascoglossan sea slug *Placida dendritica* may contribute to the restricted distribution of its algal host. *Marine Ecology Progress Series* **83**, 207–20.
- Trowbridge, C.D. 1993a. Feeding ecology of the ascoglossan opisthobranch *Aplysiopsis enteromorphae* (Cockerell & Eliot): patterns of distribution and impact on tidepool-dwelling green algae. *Journal of Experimental Marine Biology and Ecology* **169**, 233–57.
- Trowbridge, C.D. 1993b. Interactions between an ascoglossan sea slug and its green algal host: branch loss and role of epiphytes. *Marine Ecology Progress Series* **101**, 263–72.
- Trowbridge, C.D. 1993c. Local and regional abundance patterns of the ascoglossan (= sacoglossan) opisthobranch *Alderia modesta* (Lovén, 1844) in the northeastern Pacific. *The Veliger* **36**(4), 303–10.
- Trowbridge, C.D. 1995. Establishment of the green alga *Codium fragile* ssp. *tomentosoides* on New Zealand rocky shores: current distribution and invertebrate grazers. *Journal of Ecology* **83**, 949–65.
- Trowbridge, C.D. 1998a. Ecology of the green macroalga *Codium fragile* (Suringar) Hariot 1889: invasive and non-invasive subspecies. *Oceanography and Marine Biology: an Annual Review* **36**, 1–64.
- Trowbridge, C.D. 1998b. Stenophagous, herbivorous sea slugs attack desiccation-prone, green algal hosts (*Codium* spp.): indirect evidence of prey-stress models (PSMs)? *Journal of Experimental Marine Biology and Ecology* **230**, 31–53.
- Underwood, A.J. & Jernakoff, P. 1981. Effects of interactions between algae and grazing gastropods on the structure of a low-shore intertidal algal community. *Oecologia* **48**, 221–33.
- Wada, E., Terazaki, M., Kabaya, Y. & Nemoto, T. 1987. ^{15}N and ^{13}C abundances in the Antarctic Ocean with emphasis on the biogeochemical structure of the food web. *Deep-Sea Research* **34**, 829–41.
- Waugh, G.R. & Clark, K.B. 1986. Seasonal and geographic variation in chlorophyll level of *Elysia tuca* (Ascoglossa: Opisthobranchia). *Marine Biology* **92**, 483–7.
- Weaver, S. & Clark, K.B. 1981. Light intensity and color preferences of five ascoglossan (=sacoglossan) molluscs (Gastropoda: Opisthobranchia): a comparison of chloroplast-symbiotic and aposymbiotic species. *Marine Behaviour and Physiology* **7**, 297–306.

- Wells, F.E. & Bryce, C.W. 1993. *Sea slugs of Western Australia*. Perth: Western Australian Museum.
- Williams, M.L. & Cobb, A.H. 1989. Isolation of functional chloroplasts from the sacoglossan mollusc *Elysia viridis* Montague. *New Phytologist* **113**, 153–60.
- Williams, M.L. & Cobb, A.H. 1992. Chloroplasts in animals: photosynthesis and assimilate distribution in chloroplast 'symbioses'. In *Carbon partitioning within and between organisms*, C.J.Pollock, J.F.Farrar & A.J.Gordon (eds). Cambridge: BIOS Scientific Publishers, 27–51.
- Womersley, H.B.S. 1984. *The marine benthic flora of southern Australia, Part 1*. Government Printer, South Australia.
- Yamamuro, M., Kayanne, H. & Minigawa, M. 1995. Carbon and nitrogen stable isotopes of primary producers in coral reef ecosystems. *Limnology and Oceanography* **40**(3), 617–21.
- Yonge, C.M. & Thompson, T.E. 1976. *Living marine molluscs*. London: Collins.

POPULATION STRUCTURING, GENE DISPERSAL AND REPRODUCTION IN THE *ACTINIA EQUINA* SPECIES GROUP

M.C.PERRIN¹, J.P.THORPE¹, A.M.SOLÉ-CAVA^{1,2}

¹ *School of Biological Sciences, University of Liverpool, Port Erin Marine
Laboratory, Port Erin, Isle of Man, UK*

² *Departamento de Genética, Instituto de Biologia, Universidade Federal do Rio de
Janeiro, Bloco A—CCS—Ilha do Fundao, 21941-Rio de Janeiro-RJ, Brazil*

Abstract Sea anemones of the genus *Actinia* are common on many shores worldwide and hence have received much attention from ecologists and many other workers. The most extensively studied species, *A. equina*, is abundant on many rocky shores around Britain and elsewhere in Europe. It has long been known to be phenotypically highly variable with many colour morphs and great variation, for example, in size and mode of reproduction. More recently molecular and other studies have revealed unexpected levels of population structuring with genetic divergence and, in some cases, evidence for reproductive isolation between morphs. This has resulted in taxonomic problems, exacerbated by our lack of detailed understanding of processes of reproduction and recruitment in *Actinia* species in Europe. Work on population genetics, systematics and speciation in *A. equina* and other *Actinia* species is discussed and attention is drawn to areas in which further work is needed.

Introduction

Sea anemones (Phylum Cnidaria, Class Anthozoa, Subclass Hexacorallia, Order Actiniaria) are common organisms in many benthic marine communities (Sebens 1986, Longhurst & Pauly 1987). Because of their ubiquity, ecological importance and a variety of reproductive modes, various sea anemones have, in the past few years, attracted much attention from research workers in several fields. It has become clear that in several species of sea anemone the genetic structuring of populations is more complex than previously suspected, leading to problems in understanding species boundaries and modes of speciation and, of course, consequent taxonomic and systematic difficulties. The problems are illustrated particularly well by species of the genus *Actinia* Linnaeus 1767, especially the abundant and widely distributed European *A. equina* (*sensu* Gosse 1860). The aims of this paper are to review the literature on the taxonomy, population genetics and breeding systems of the genus, particularly *A. equina*, and to use the available information as a starting point to indicate possible future studies.

Sea anemones are opportunistic predators (Sebens 1981, Zamer 1986, Kruger & Griffiths 1996) or filter feeders (Rubenstein & Koehl 1977) and are themselves eaten by a few invertebrate and fish species (Ottaway 1977, Hall et al. 1982, 1984, Ates 1989). Sea anemones also interact both interspecifically and intraspecifically via aggression (Bonnin 1964, Bigger 1980, Ayre 1982, Sebens 1984) and commensal or mutualistic symbiosis

(Mariscal 1970, Ross 1983). In general, sea anemones show variety in form (Stephenson 1935, Hand 1955a,b, Schmidt 1971, 1972, Manuel 1988), reproduction (Chia 1976, Fautin 1991, Shick 1991) and behaviour (Herndl 1984, Brace & Reynolds 1989), making them useful model species for the investigation of theories of speciation (Quicke & Brace 1984, Shaw et al. 1987, Solé-Cava & Thorpe 1992), larval dispersal and the genetic structuring of populations (Hunt & Ayre 1989, Ayre et al. 1991, Russo & Solé-Cava 1991, Solé-Cava et al. 1994a, Monteiro et al. 1997) and evolutionary strategies (Ayre 1982, Shaw 1989).

The genus *Actinia* has been the focus of a significant number of wide ranging biological studies. Physiological investigations have included those of reproduction (e.g. Polteva 1963, Schaefer 1981), growth (e.g. Abeloos 1955, Ottaway 1980), nutrition (Kruger & Griffiths 1996) and environmental tolerances (e.g. Ottaway 1973, Griffiths 1977a,b), together with fields as diverse as allorecognition (e.g. Bigger 1980, Lubbock 1980) and strength of attachment to substrata (Young et al. 1988). Behavioural investigations of species in this group have included examinations of feeding (e.g. Herndl 1984), movement and spacing (e.g. Parker 1917, Ottaway & Thomas 1971, Ottaway 1978, 1979a, Brace & Quicke 1985, 1986a,b, Ayre 1987), and aggression (e.g. Bonnin 1964, Brace et al. 1979, Ayre 1982, Brace & Reynolds 1989). Ecological studies have been concerned essentially with reproductive ecology (e.g. Chia & Rostron 1970, Carter & Thorp 1979, Gashout & Ormond 1979, Carter & Thorpe 1981, Lubbock & Allbut 1981, Orr et al. 1982, Ayre 1984a,b, Carter & Miles 1989) and population dynamics (e.g. Ottaway 1979b, Rees 1984, Ayre 1985, Brace & Quicke 1986a,b). The taxonomy of the group has received continuing interest through both traditional morphological investigations (e.g. Carlgren 1949, Schmidt 1971, 1972, Chintiroglou & Sirmsiridou 1997, Allcock et al. 1998) and more recently through the application of biochemical genetic techniques (Carter & Thorpe 1981, Quicke et al. 1983, Quicke & Brace 1983, Quicke et al. 1985, Haylor et al. 1984, Solé-Cava et al. 1994b, Solé-Cava & Thorpe 1992, Russo et al. 1994, Monteiro et al. 1997, 1998). The genetic structuring of *Actinia* populations on small and large scales has also received some attention (Ayre 1983a, 1984a, Quicke & Brace 1983, Brace & Quicke 1985, Ayre et al. 1991, Russo et al. 1994, Monteiro et al. 1997).

In addition to their ecological importance, there are other obvious reasons for the apparent scientific popularity of *Actinia*. Individuals of this genus are small, they are exclusively occupants of hard substrata in the intertidal and shallow subtidal and commonly occur at high densities (Ottaway 1979a, 1980, Brace & Quicke 1986b). They are easily collected owing to their often conspicuous and almost sedentary nature (Rees 1984, Brace & Quicke 1986b) and in the laboratory they are simple to maintain, requiring far less husbandry than most marine invertebrates (Brenowitz 1972).

Systematics of *Actinia*

The genus *Actinia* is represented globally by about nine nominate species. Although some of these are poorly described and may be synonyms, other species are considered to be very polymorphic and may encompass groups of distinct species. Traditionally, discrimination between species in this genus is based on external morphological characteristics, such as the number of tentacles, the size and the colour of the column and foot, nematocyst type and distribution, and the type, colour, size and number of acrorhagi (special organs of defence that have abundant nematocysts and that are found on the top of the column, close to the tentacles). The species currently recognized are described below.

Only the last three are known to occur in the British Isles, although three others are described from the shores of continental Europe.

Actinia bermudensis McMurrich 1889

A. bermudensis is a tropical sea anemone of the west Atlantic and Caribbean, recorded from the shores of Florida southwards to southern Brazil. It may sexually reproduce a planktonic larva (Jennison 1983), but it is also documented as reproducing asexually through the production of brooded young (Russo et al. 1994, Monteiro et al. 1998). As a species it shows phenotypic variability with red, brown and yellow column morphs having been described (Russo et al. 1994). Using enzyme electrophoresis, Russo et al. (1994) report that at one location, Florianopolis (Brazil), populations of red and brown morphs were genetically different enough to suggest that the two groups were not the same species. Electrophoretic comparison of enzymes has shown *A. bermudensis* from Brazil to be genetically distinct (i.e. a separate species) from *Actinia* from Britain (*A. equina*, *A. prasina* and *A. fragacea*) (Solé-Cava et al. 1994b).

Actinia cari Delle Chiaje 1825

This is a Mediterranean species, which, like other *Actinia*, has a history of taxonomic revision, being seen as a separate species by most workers, often under a different species name (Risso 1826, Gravenhorst 1831, Andres 1884, Carlgren 1949). Other biologists have viewed the form merely as a variety of *A. equina* (Pax 1907). *A. cari* typically has a greenish brown column, on which there are 28 unevenly distributed brownish blue to brown black rings which are often open or can blend. The pedal disc of this species is said to be 5.5 cm in diameter and brown to greenish brown in colour. *A. cari* shows variability in the colour and form of the rings, leading Andres (1884) to detail several varieties. The sexes are separate in this species, the female is oviparous with no record of individuals brooding young internally (Schmidt 1972).

Actinia sali Monteiro et al. 1997

A. sali was described by Monteiro et al. (1997) from specimens collected on the Cape Verde Island of Sal (off the west coast of Africa). It is apparently morphologically indistinguishable from red footed red column morphs of *A. equina* from elsewhere, but it is genetically very divergent and may show small nematocyst differences (see Monteiro et al. 1997). It is known to brood small anemones in the enteron and these are presumably produced asexually. Distribution is unknown other than that it occurs on Sal, but presumably it may occur also on other islands in the Cape Verde group and possibly further afield.

Actinia schmidti Monteiro et al. 1997

This species was recently described by Monteiro et al. (1997) following molecular work on samples collected from the coast of the Mediterranean Sea near Marseille. It is a large

species (mean pedal disc diameter 3.7 cm), with red column, tentacles and pedal disc, blue acrorhagi and a blue rim at the edge of the pedal disc (limbus). In this species there is a clear nematocyst difference from most other *Actinia* in that the microbasal B-mastigophores of the mesenteric filaments are smaller than the basitrichs of the actinopharynx (see Monteiro et al. 1997; also Chintiroglou & Simsiridou 1997). The species is unusual because as far as is known it never broods young in the enteron and hence may not reproduce asexually (cf. *A. fragacea*). *A. schmidtii* appears to be indistinguishable from, and is probably conspecific with, the *A. equina mediterranea* I of Schmidt (1971, 1972). If so, its distribution probably includes most of the Mediterranean and the Atlantic coast as far north as northern Portugal.

Actinia striata Rizzi 1907

This is another Mediterranean species and has a red-brown column on which there are superimposed numerous continuous and broken dark brown-red vertical stripes (Schmidt 1972). The pedal disc of this species is approximately 6 cm and opaque red-brown with visible mesenterial insertions. The sexes are separate and reproduction is by viviparity. Schmidt (1972) notes that most of these forms and species of Mediterranean *Actinia* show diagnostic differences in their cnidae (nematocyst complements) and have differing littoral and large-scale distributions.

Actinia tenebrosa Farquhar 1898

A. tenebrosa is a very common anemone on New Zealand and Australian shores (Ottaway 1979b, Ayre 1983b). This species is dark red-brown in column colour (Dakin 1952) with no apparent documented evidence for phenotypic variation. Enzyme electrophoretic studies of *A. tenebrosa* report high levels of genetic variation within and between some populations (Ayre 1984a, Ayre et al. 1991), but have offered no evidence for cryptic speciation. A genetic comparison of Australian *A. tenebrosa* populations with *A. equina* populations from South African shores, has confirmed that they are distinct species (Ayre 1984a).

Actinia fragacea Tugwell 1856

The “strawberry” anemone, so called because of its regular yellow or green spotting on a red column was, until recently, regarded as being a morph of *A. equina* (e.g. Gosse 1860, Schmidt 1971). Stephenson (1935) agreed with Gosse in grouping all *Actinia* occurring in Britain under the name *A. equina*. He mentioned that he considered the “strawberry” morph to be a possible separate species, but he cited it merely as *A. equina* var. *fragacea*.

Although, because of its larger size and the lack of viviparity, var. *fragacea* was recognized to be conspicuously different from other varieties of *A. equina*, its systematic position remained unchallenged until 1981, when Carter & Thorpe demonstrated, through the use of allozyme electrophoresis, that sympatric samples of the strawberry and the beadlet anemone (from Wembury, south Devon, UK), were consistently genetically different and were, therefore, reproductively isolated. Genetic identity (Nei 1972) between *A. fragacea* and *A. equina* was estimated as 0.726, a value usually associated to interspecific comparisons

(see Thorpe 1979, 1982) and therefore further supporting the hypothesis of the distinctness of the two species. This was the first use of molecular systematics in the genus *Actinia*, and it started a series of discoveries on the fine genetic differentiation between many of the so-called varieties of *A. equina*. Perrin (1993) re-affirmed the specific status of *A. fragacea* through genetic comparisons with a number of *Actinia* morphs and produced identity values of 0.50, 0.85 and 0.87 between *A. fragacea* and the *A. equina* morphs, a range comparable with the value of 0.726 calculated by Carter & Thorpe (1981), although obtained over a slightly different mix of loci.

A. fragacea is probably nowhere abundant and its range is apparently restricted to certain rocky shores in southwest England (Devon and Cornwall) and northern France (Brittany Peninsula) (Manuel 1988).

Actinia prasina Gosse 1860

Gosse (1860) considered the “green colour morph” of the beadlet anemone to be conspecific with *A. equina*, a trend that was followed later by other sea anemone systematists (Stephenson 1935, Manuel 1981). However, Haylor et al. (1984) found significant differences between the gene frequencies of the green morph and sympatric individuals of the red morph of *A. equina*, at four out of 17 loci examined (*Est**, *Sod-2**, *Pgm**, *Odh**). This, together with other studies showing differences in internal morphology (Schmidt 1971), behaviour (Brace et al. 1979) and predation (Hall et al. 1982, 1984) led the authors to suggest that, for the Isle of Man populations at least, the green morph should be afforded specific status, suggesting the name *A. prasina* Gosse (1860). Subsequent work by Solé-Cava & Thorpe (1987) confirmed the differentiation between *A. prasina* and the red morph of *A. equina*.

Actinia equina (Linnaeus 1758)

This is the most studied species, the beadlet anemone. It is thought to be distributed from the coasts of north Russia (Kola Peninsula) to those of South Africa (Stephenson 1935, Branch & Branch 1981, Manuel 1988). It is very common on shores around the British Isles and western Europe and extends into the Mediterranean. *A. equina* is typically intertidal, occurring as high on the shore as mean high water neaps, although it may be found subtidally down to 20 m below sea level (Manuel 1988). In common with many sea anemone species, *A. equina* is highly variable in both colour and form throughout its geographical range from Europe (Schmidt 1972, Manuel 1988) to South Africa (C.Russo, pers. comm. 1998). This variability has led to much taxonomic debate. On shores in the British Isles the existence of various green, orange, brown, red and striped or spotted column forms has long been recognized, with early natural historians considering certain of these morphs to be separate species (Templeton 1836, Johnston 1847, Dalyell 1848, Cocks 1850, Tugwell 1856, Milne-Edwards 1857). Gosse (1860) considered all colour forms to be *A. equina*, but did detail and name 11 colour varieties. Stephenson (1935) considered only the “strawberry” morph (his var. *fragacea*) to be a possible separate species. All other forms, were considered by Stephenson to be *A. equina* var. *mesembryanthemum*. Generally the various forms of *A. “equina”* examined from Britain have not shown reliable nematocyst differences, but recent work indicates that there may be some useful nematocyst differences (Allcock et al. 1998).

A. equina also shows a large degree of polymorphism on the mainland shores of Europe and shores of North Africa. Taxonomic studies of these forms (Schmidt 1971, 1972) have involved only the more conventional morphological comparisons of cnidae, internal

structure, reproductive physiology and general body form. Schmidt described several different subspecies and varieties of *A. equina*.

1. *Actinia equina equina*, is considered by Schmidt to be identical to the type of the species *A. equina* of Linnaeus (1758). Within *A. equina equina* he recognizes a “brown-red” column form I, a “green” column form II and a “crimson to purple red” column form III, all of which have differing mesenterial arrangements. These forms are all viviparous and are described from the coastline of Britain and the northwest mainland of Europe.
2. *Actinia equina atlantica*, which can be found from Arcachon, France, to northwest Spain and in the Azores, exhibits two distinct forms: *A. equina atlantica* I has a red column, is the larger of the two forms (Schmidt does not detail size) and is oviparous. *A. equina atlantica* II has a red or green column and is viviparous. Schmidt (1971) notes that *A. equina atlantica* form I is found lower on the shore than form II.
3. *Actinia equina mediterranea* also has two forms: form I is relatively large (pedal disc diameter 7.5 cm), dioecious and oviparous, with a red column and a red pedal disc. Its distribution is limited essentially to the Mediterranean, but Schmidt reports finding this form also in northern Portugal. *A. equina mediterranea* form II is smaller than form I (pedal disc size 3 cm), is dioecious and oviparous, has a brown-red column with a greenish “shimmer” and a light red pedal disc. Outside of the Mediterranean Schmidt found this form on the northern coastline of Spain and in the Canary Islands. As noted above, it is likely that Schmidt’s *A. equina mediterranea* form I is conspecific with the species *A. schmidti*, recently described by Monteiro et al. (1997).

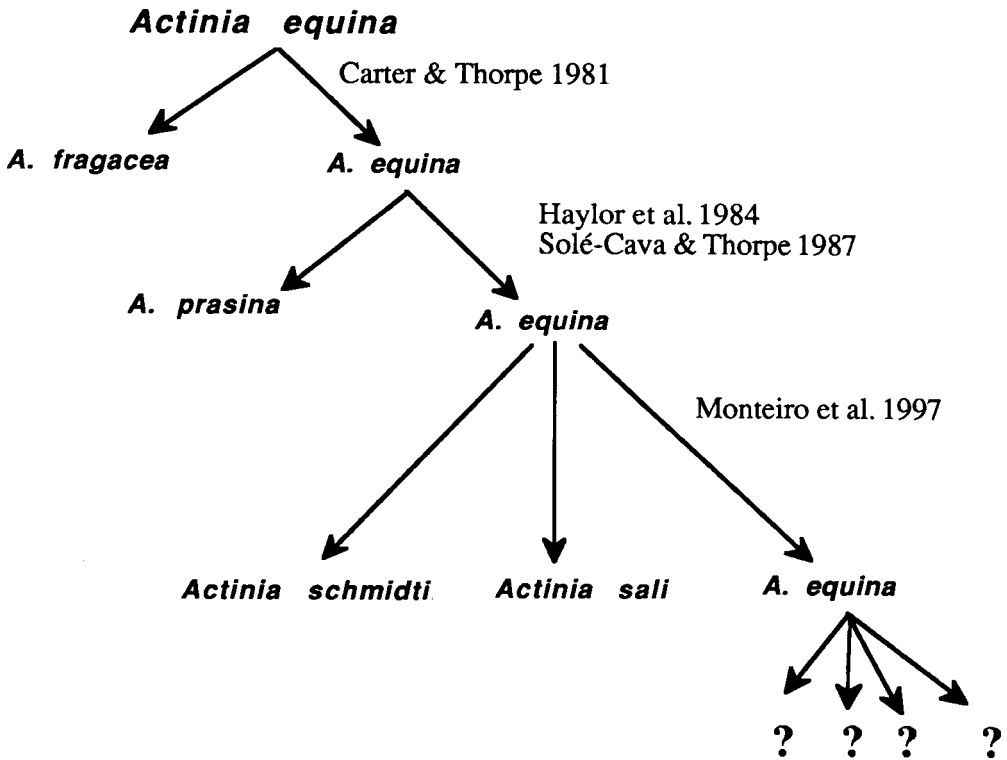


Figure 1 Diagram to illustrate the main taxonomic “splits” following genetic studies of population structure in *Actinia “equina”*.

To date there is only one published study examining the genetic relatedness of populations of *A. equina* across its broader range. This is the work of Monteiro et al. (1997), who compared genetic divergence between samples of red *Actinia* from the Isle of Man, the Mediterranean and the Cape Verde Islands. These all showed large-scale genetic differences and consequently the last two populations were considered to be separate species (*A. schmidtii* and *A. sali*; see above). This work combined with reports of morphological variability and the discovery of genetically different colour forms or cryptic speciation at some localities in Britain (e.g. Carter & Thorpe 1981, Quicke & Brace 1983, Quicke et al. 1983, 1985, Haylor et al. 1984, Solé-Cava & Thorpe 1987, 1992, Solé-Cava et al. 1994b) lead to doubts as to whether *A. equina* is likely to constitute a single species across its entire range (Fig. 1). The extensive cryptic speciation within *A. equina* (and also possibly in *A. bermudensis*, Russo et al. 1994) suggests that the many “colour morphs” may conceal further cryptic species.

Population genetics of *Actinia* in the British Isles

The application of enzyme electrophoresis to the study of sea anemones has had a significant impact on the field of taxonomy and systematics (McCommas & Lester 1980, Carter & Thorpe 1981, Bucklin & Hedgecock 1982, Haylor et al. 1984, Quicke & Brace 1983, Solé-Cava et al. 1985, Smith & Potts 1987, Solé-Cava & Thorpe 1992, McFadden et al. 1997, Monteiro et al. 1997). It has also been important in studies of factors influencing levels of genetic polymorphism (Hoffman 1983, Solé-Cava & Thorpe 1989, 1991, Zamer & Hoffman 1989), in investigations of population structure (Black & Johnson 1979, Ayre 1983a, 1984a, Hoffman 1987, Hunt & Ayre 1989, Ayre et al. 1991, Russo et al. 1994) and in the study of breeding systems (Ottaway & Kirby 1975, Black & Johnson 1979, Carter & Thorp 1979, Orr et al. 1982, Bucklin et al. 1984, Shaw et al. 1987, Monteiro et al., 1998).

Column and foot colour

Evidence for a relationship between the phenotypic diversity of *A. equina* and genotype was first produced by Quicke & Brace (1983). In the course of examining the phenotypic and genotypic spacing of a group of individuals at one site (Burniston, North Yorkshire) they reported associations between pedal disc (foot) colour and allele frequency at two loci. This association was used to describe two distinct morphs within the red-brown column coloured individuals of the species (Quicke et al. 1983). One of the morphs described had a pink or red pedal disc and was considered to differ in enzyme genotype from the other morph group which contained individuals with green (H), grey (G) or radially striped (L) pedal discs. Linkage between alleles at two enzyme loci was also suggested.

Quicke et al. (1983) further reported some potentially important ecological differences between morphs. Transect data showed that at two British shores (Burniston, North Yorkshire and Trevone, Cornwall), anemones with red or pink pedal discs were more common on upper mid-shore areas while anemones with green or grey pedal discs were more abundant on the low shore. Furthermore, data collected from one site showed that anemones with red or pink pedal discs were more common on vertical rock surfaces and were attached more strongly to the substratum than the other morph which was found more commonly on horizontal surfaces and was generally weakly attached. The authors put forward the

theory of two co-adapted gene complexes maintained by selection and involving the two enzyme loci and pedal disc colour.

Further transect surveys on two shores (Trevone, Cornwall and Burniston, North Yorkshire), combined with electrophoretic investigations of genotypes, suggested distributional differences for three groups of *Actinia* morphs (Quicke et al. 1985). Individuals with red or pink pedal discs were most common on the upper to midshore. These individuals were termed upper (U) shore morphs and differed genetically from the mid-shore (M) morph which had red or pink pedal discs and was relatively more abundant at the lower mid-shore level. The low (L) shore morph was also described as being genetically distinct and had a green, grey or lined pedal disc. It was suggested that the genetic differences between the upper and lower shore morphs and the mid-shore “hybrid” are maintained by selective forces varying with shore level and acting on linked loci.

Donoghue et al. (1985), studying anemones from Burniston, North Yorkshire, found significant differences in genotype frequencies between morphs which they termed red (Rd) and pink (P) pedal disc morphs. They also reported differences in the form of the acrorhagi between *Actinia* possessing different coloured pedal discs. Their examinations of acrorhagial form considered four parameters (type, size, colour, and number) in six pedal disc colour groups termed: dark red (DRd); light red (LRd); pink (P); grey (G); green (H); and grey or green with red or orange radiating lines (L). Comparisons of acrorhagial type between groups revealed differences between DRd pedal disc individuals and all other morphs, with the first possessing a higher proportion of “compound” acrorhagi than the other groups. Significant differences in size of acrorhagi were found between some groups. DRd pedal disc anemones had significantly larger acrorhagi than the other morphs. The colour of the acrorhagi was considered to separate the anemones into three groups: DRd, LRd and P, and G, H and L. Anemones with DRd pedal discs had on average significantly more acrorhagi than individuals of any of the other pedal disc colour groups. Thus Quicke, Brace and their colleagues (e.g. Quicke et al. 1983, 1985, Quicke & Brace 1983, 1984, Donoghue et al. 1985) working with *Actinia* they described as having red or brown columns, distinguished various groups of column and pedal disc colour morphs.

More recently our own and other work (Lynch 1996) at Port Erin has also provided evidence of three apparent gene pools in *A. equina*. Results to date suggest that both the morphology and genotypes at key loci of the anemones constituting these gene pools are similar from shore to shore. Thus, there is some evidence of morphs, characterized by particular combinations of genotype and phenotype, being consistent over a geographical range. Although interpretations of the genetic differences do not entirely concur, the morphs concerned appear partially similar to those differentiated originally by Quicke, Brace and co-workers (see e.g. Quicke et al. 1983, Quicke & Brace 1984). However, we doubt whether the three “morphs” are maintained solely by selection. This work is currently continuing.

Origins of the brooded offspring in Actinia

Several early studies of *A. equina* document viviparity and brooding in this species (Dalyell 1848, Gosse 1860, Gravier 1916). The brooded young of *A. equina* were considered of sexual origin primarily because of the presence of separate adult male and female individuals in the population (Stephenson 1929). Young anemones at several developmental stages are found in the enteron (gastric cavity) of the parent individual. The youngest form is the pre-planula larva which is merely a bundle of ciliated cells and is often seen in the tentacles of adults (Carter & Funnell 1980). It is assumed that these larvae then become planulae which are

approximately 300×200 µm (Chia & Rostron 1970). In metamorphosis of the planulae the development of tentacle buds is seen first followed by the development of a pedal disc. Tentaculate young may be brooded up to 10 mm in pedal disc diameter (Rees 1984), a size well above that of the smallest free living brooding adults (M.R.Brown & J.P.Thorpe, in prep.). The colour of brooded young has generally been observed to be the same as that of the parent (e.g. Cain 1974, Carter & Thorp 1979, Gashout & Ormond 1979).

Given the early hypothesis of sexual reproduction, it seemed peculiar that *A. equina*, which shows such a large degree of colour polymorphism (Gosse 1860, Stephenson 1935), should show such consistency in overall brood phenotype. Cain (1974) recognized this discrepancy and offered four possible explanations for individuals brooding coloured offspring of the same colour as the parent.

1. Each colour variety may in fact be a separate species.
2. Planula larvae may return from the plankton to enter only the adults of their own colour.
3. The colour of juveniles is in some way controlled by the fostering adult.
4. Juveniles may be produced by asexual or parthenogenetic means.

The second of these suggestions formed the basis of a theory that was initially proposed by Gravier (1916). Chia & Rostron (1970) were also in support of this “re-entry” theory. Their support for this idea followed the failure to find pre-planula larval forms in the enterons of adult *Actinia*. They explained this absence as being due to larval release into the plankton after only short periods of incubation. In order to test the “re-entry” theory attempts have been made by several groups of workers to induce adult *Actinia* to accept juveniles into the enteron; these have all failed (Chia & Rostron 1970, Carter & Thorp 1979, Gashout & Ormond 1979).

Using enzyme electrophoresis Carter & Thorp (1979) discovered that brooded young were invariably of the same esterase genotype as their parent individual. This was in line with discoveries that the Australasian congener, *A. tenebrosa* also brooded offspring genetically identical to the parent (Ottaway & Kirby 1975, Black & Johnson 1979). Carter & Thorp (1979) suggested a modification of the larval re-entry theory. They proposed that given the ability of *Actinia* to recognize self and non-self, like genotype larvae could be selected from the plankton and subsequently be accepted into the enteron. Following this, they proposed that vegetative proliferation (cloning) of such juveniles leads to increased brood size.

At about the same time, Gashout & Ormond (1979) were developing the idea that brooded young might be of parthenogenetic origin (hypothesis 4 of Cain 1974). One obvious failing of this hypothesis was the inability to explain why all *A. equina* populations studied were dioic, with both sexes brooding young in their enteron (Chia & Rostron 1970, Rostron & Rostron 1978, Carter & Thorp 1979, Carter & Miles 1989). The same studies also reveal that *Actinia* populations contain a large proportion of non-sexual individuals (i.e. individuals that possess no gonads) which also commonly brood. (These observations would clearly preclude self-fertilization in the species). By way of explaining these patterns of brooding Gashout & Ormond, (1979) suggested phasic hermaphroditism. This in itself was not a new suggestion for the species (Carter & Thorp 1979) and its existence has been implied for another actinian, *Epiactis prolifera*, by Dunn (1975). Interestingly, Gashout & Ormond (1979) rejected the possibility of somatic embryogenesis for the production of brooded young because attempts to induce tissue fragments to metamorphose into juveniles had been unsuccessful. Somatic embryogenesis as the mode of juvenile production was, however, supported by Orr et al. (1982). Using enzyme electrophoresis to analyze samples from the Isle of Man, those authors showed that broods shared the same genotype as their parents across all of the five polymorphic loci investigated. Parents heterozygous for any of these loci brooded similarly heterozygous

young. If the young had been produced by self-fertilization or inbreeding a degree of segregation would be expected in their genotypes. To date there is only the indirect evidence of apparently functional gonads (Larkman 1980, Larkman & Carter 1980, 1982, 1984, Carter & Miles 1989) and the detection of substantial amounts of genetic variation in populations (Solé-Cava & Thorpe 1992, Perrin 1993) to support the existence of any sexual reproduction in *Actinia equina*. A mixed mode reproductive strategy cannot be ruled out in this species (see below for further discussion of possible sexual reproduction).

Under the preconception that the brooded young of *Actinia* were sexually derived, studies concerning the reproductive ecology of *A. equina* have documented levels of brooding and sexual condition in an attempt to relate these two reproductive parameters (see e.g. Rostron & Rostron 1978, Gashout & Ormond 1979). Available data indicate that the brooding of juveniles in the enteron is a year round phenomenon, although peaks in brooding and gametogenic cycles have been identified at differing times of the year for differing populations. The first study of its kind by Chia & Rostron (1970) reported higher levels of brooding (as percentage of individuals brooding) during winter months in two populations on the English east coast. Gonads in individuals from these populations were seen to regress during November, December and January. Additional data from one of these locations (Broadstairs, Kent) provided by Rostron & Rostron (1978) suggests that gonads may also regress towards the end of the summer months, re-developing again through September and October. A study of a population in the south of England revealed brooding peaks (as mean number of brooding adults) in two successive August samples, but otherwise there was no detectable seasonality in brooding (Carter & Thorp 1979). In a North Yorkshire *Actinia* population, Gashout & Ormond (1979) found main brooding peaks (as percentage of individuals brooding and mean brood size) in May, June and July over the period 1977–78. The percentage of individuals bearing gonads appeared to peak around two periods, March to April and September to October. Rees (1984) reported the highest levels of brooding in early summer months for populations at Burniston, North Yorkshire and Rhossili, southwest Wales.

A critical evaluation of gametogenesis is provided by Carter & Miles (1989). Results from this study suggest that oogenesis and spermatogenesis are synchronized, occurring over the months of February to May before subsequent shedding of gametes during the summer. A pattern of spawning in the warmer months of the year appears to be a common feature in littoral species of sea anemone (Dunn 1975, Jennison 1978, Ottaway 1979b, Bucklin 1980, Schaefer 1981, Shaw et al. 1987).

Very few studies of *A. equina* have attempted to relate fecundity or gametogenic cycles to changes in environmental conditions, although the study of the Broadstairs population (Chia & Rostron 1970, Rostron & Rostron 1978) does highlight an inverse relationship between sea temperature and levels of brooding. It may also be of note that the higher proportions of individuals bearing gonads in spring and autumn is coincident with plankton blooms in the area (Colebrook & Robinson 1965), suggesting that food availability may influence breeding. Other environmental conditions that may effect levels of brooding in *A. equina*, include tidal height and exposure which have been shown to be negatively correlated with brood size and with frequency of brooding for populations studied in the Isle of Man (M.R.Brown & J.P.Thorpe, in prep.). This study also found marked differences in both frequency of brooding and mean brood size between *A. prasina* and several morphs of *A. equina* (with both being highest in *A. prasina*), but there was no apparent relationship between either of these parameters and estimates of population density or nearest neighbour distance for the brooding adult.

Biologists studying the reproductive ecology of *A. equina* have been almost entirely preoccupied by the investigations of natural populations, with little attention having been directed towards laboratory-based mating experiments. One inherent problem with such experiments is that sex in *A. equina* can only be assessed by histological examination of the gonads. In the course of laboratory-based investigations of gametogenic cycles, anemone isolation, and pairing experiments Carter & Miles (1989) successfully used a biopsy technique to remove gonad material for histological inspection and were able to identify the sex of experimental animals. Sex determination mechanisms are unknown in *A. equina*, but are thought to be genetic in *A. tenebrosa* (Ayre 1988). Carter & Miles (1989) found that males kept in isolation or paired with females released sperm during spring and summer months. In addition, isolated males, females and non-sexual individuals were observed to produce and brood young. Results from this study suggest that sex is stable in the species. Observations of females producing broods shortly after contact with males that had released sperm, in conjunction with the finding that larger broods tended to be carried by females, led the authors to suggest that females may brood sexually derived young over the summer months. They do acknowledge, however, that, as a result of observation of non-sexual individuals producing young, some brooded offspring must be produced asexually. Subsequently, Perrin (1993) examined brooded offspring from several morphs at different times of the year and concluded that all of the large number of offspring he examined were reproduced asexually.

Cloned offspring are also known to be similarly reared in the enteron in the Australian *A. tenebrosa* (Ottaway & Kirby 1975, Black & Johnson 1979) and in Brazilian populations of *A. bermudensis* (Russo et al. 1994, Monteiro et al., in press), but apparently do not occur in *A. fragacea* (Carter & Thorpe 1981, Larkman 1983, 1984a,b) or in *A. schmidtii* (Monteiro et al. 1997). They also apparently occur (Perrin 1993) in the related species *Bunodactis verrucosa*. In some European populations of *Actinia equina* it appears that some females may reproduce asexually also through the parthenogenetic development of unfertilized eggs (Schaefer 1981).

In *Actinia* the relative advantages of asexual reproduction are difficult to assess because, for such a well studied species, remarkably little is known of its sexual reproduction. As yet no species of *Actinia* has been found to brood sexually reproduced offspring. It is clear that sexual reproduction must occur in *A. equina*, because at any time of the year (but particularly in summer, Carter & Miles 1989) and in any population some individuals can be seen (in histological sections) to have male or female gonads in the mesenteries, although in many individuals (often most) gonads are apparently absent (see Carter & Thorpe 1981, Carter & Miles 1989). Possible advantages of internal brooding of asexually reproduced juveniles are the maintenance and amplification of co-adapted genotypes (see, e.g. Hughes 1989) and for the brooded young better conditions with the elimination of competition from other invertebrates for space or other resources. The asexually reproduced young are released at an advanced stage of development and growth, ready to settle onto the substratum. Ottaway (1979b) has shown that in *A. tenebrosa* the size of the brooded offspring at release significantly affects the chance of survival. When compared with the microscopic anemones which could be produced following the settlement of a putative larva the far greater initial size must give the brooded cloned offspring a huge survival advantage in the very stressful intertidal environments that the species occupies. Hence, asexual reproduction may be particularly advantageous in *Actinia*, thus possibly explaining the widespread incidence of internal brooding within the genus.

Further evidence that sexual reproduction does occur is that populations generally show high levels of genetic variability and allele frequencies approximate to Hardy-Weinberg

expectations (e.g. Solé-Cava & Thorpe 1992). The few studies of the timing of asexual reproduction have led to contradictory conclusions (see above), but the more recent data from the major study of Carter & Miles (1989) show evidence of seasonality in both brooding and in the production of gonads. The monitoring of recruitment on the shore appears unlikely to shed much light on the problems of understanding reproductive activity because currently available data (authors' unpublished results) suggest that longevity is very high (possibly centuries) and both recruitment and natural mortality are minimal (in some populations both recruitment and loss of "adult" sized anemones are possibly under 1% a year).

Dispersal and gene flow

Adult *Actinia* are essentially non-dispersive and, as it is difficult to envisage cross-fertilization occurring over other than very short distances, there is likely to be little gene flow between shores unless larval dispersal occurs. The generally high levels of genetic divergence between allopatric populations of most morphs of *Actinia*, even when sampled over only short geographical distances, indicate that genetic differentiation in *Actinia* takes place on a very small geographical scale (Solé-Cava & Thorpe 1992) and, thus, the likelihood of larval dispersal is, at best, very low.

The reason that dispersal is low could be simply that *Actinia* may not produce a dispersive larva. The brooded offspring in the enteron usually can be seen to be present in various stages of development from small balls of cells, to tiny "embryo" anemones with tentacle buds, to various sizes of juvenile anemones commonly up to about 6mm high. Various ciliated balls of cells found in the enteron approximate planulae; some look convincingly like the planula larvae of other anemone species and were assumed by Chia & Rostron (1970) to be sexually produced. Whether any of these are sexually reproduced larvae, which may be subsequently released and disperse, or whether they are all merely developmental stages in the asexually produced brooded offspring is not clear. In any case, the "planula larvae" found in the enteron do not seem to be capable of much dispersal, since rearing experiments (Chia & Rostron 1970, Perrin 1993) indicate that outside the enteron they are incapable of metamorphosis or of long-term survival.

Problems of the definition of species in *Actinia*

Before discussing the process of speciation or the existence of cryptic species in sea anemones, it is pertinent to outline what is meant by the term species. By definition some current concepts may not be applicable to *Actinia* and other similar species of sea anemone. Population geneticists and ecologists have generally embraced what is known as the biological concept of species (e.g. Lewontin 1974, Endler 1977, Nei 1987). There are currently several widely accepted forms of biological concept, the first of which is commonly termed simply "The Biological Species Concept", but is more accurately known as the isolation species concept (Paterson 1985). Under the isolation species concept, Mayr (1963) described species as "groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups". This is the most widely used concept in evolutionary literature. The recognition species concept (Paterson 1981, 1982, 1985), however, views the isolating mechanisms of the isolation

species concept as mechanisms facilitating reproduction among members of a given population. This concept defines the species as “the most inclusive population of individual biparental organisms which share a common fertilization system” (Paterson 1985). Neither the recognition nor the isolation species concept is considered applicable to asexually reproducing organisms or syngameons (units of interbreeding in a hybridizing group of species).

According to the evolutionary species concept, a species is a population or group of populations that shares a common evolutionary fate through time. This concept is applicable to both living and extinct groups and to sexual and non-sexual organisms and is, for practical purposes, the species definition used by most practising taxonomists and palaeontologists. Independent species status is usually attributed on the basis of patterns of phenotypic cohesion within, and discontinuity between, groups of organisms. The failures of this concept are that it does not set out clearly which phenotypic traits are important in defining species, and that it is vague in its judgment of just how common a “common evolutionary fate” should be. In addition, this concept works with the end product of cohesion but does not address the evolutionary mechanisms that result in cohesion.

Templeton (1989), in an attempt to define a species concept that can be applied to all organisms, has defined the cohesion species concept. Through this concept he defines a species as “the most inclusive population of individuals having the potential for phenotypic cohesion through intrinsic cohesion mechanisms”. The cohesive mechanisms to which he alludes can be classified as genetic exchangeability: “the factors that define the limits of spread of new genetic variants through gene flow”, and demographic exchangeability: “the factors that define the fundamental niche and the limits of new genetic variants through genetic drift and natural selection”. The inclusion of considerations of demographic exchangeability makes this concept applicable to asexual organisms. The factors Templeton identifies under his two cohesion mechanisms are too numerous to discuss here, but the summary table in his paper (Templeton 1989) presents an overview.

Ascribing specific status to colour morphs of *A. equina* using current species concepts may be a difficult task for a number of reasons. Any investigation of the genetics of *A. equina* colour morphs will rely to an extent on the pooling of similar colour morphs. Where concerted efforts are made to collect and use near identical or identical morphs it is likely that rarer morphs will be neglected. Thus, while an understanding of the genetic relationship between more common forms may be arrived at, this may be at the expense of understanding the genetics of the group as a whole. Even in instances where near identical morphs are used in investigations the possibility remains that cryptic species may exist within such well defined groups.

Species concepts that are based to any degree on phenotypic cohesion may falter when used to describe species of *Actinia* because of, first, the high phenotypic variability of *Actinia* within shores and, secondly, the similarity of colour morphs from different shores which can show high levels of genetic divergence (Solé-Cava & Thorpe 1992) that in instances would imply separate specific status.

A. equina may be considered reproductively “awkward”. This species can reproduce clonally (Carter & Thorp 1979, Orr et al. 1982, Perrin 1993), is dioecious, and is presumed to be able to reproduce sexually (Carter & Miles 1989). *A. equina* may be considered (see below) to challenge the isolation and recognition species concepts through engaging in both “too little” and “too much” sex (see Templeton 1989).

As detailed above there is, as yet, no direct evidence for successful sexual reproduction in *A. equina*. If non-sexual *Actinia* never develop gonads and produce brooded young which are also non-sexual for the whole of their lives, then it is possible to envisage clonal races of *Actinia* that take their own evolutionary path with specialization occurring via mutation and selection. Some populations of the sea anemone *Haliplanella luciae* are thought to be obligately clonal (Shick & Lamb 1977), although this species appears to possess functional gonads. The application of isolation or recognition species concepts to obligately clonal races of anemones is not possible, although these races do constitute separate species under definitions of the evolutionary and Templeton's cohesion species concepts (Templeton 1989).

The possible existence of hybrids (the middle shore morph of Quicke et al. 1985) within *Actinia* on British shores could also present problems for the future definition of species in the group. If the putative middle shore morph is indeed a hybrid of the upper and lower shore morphs (Quicke et al. 1985), it is pertinent to ask whether hybridization between the two ancestral forms is current (as proposed by Quicke et al. 1985) or whether this morph is the result of past hybridization events.

With the increased understanding of the genetics and reproduction of *A. equina*, the use of the conventional biological species concepts to define species in the group may not be viable. As highlighted above, any concept relying on phenotypic cohesion as a means of defining species in *Actinia* will face the problems of cryptic speciation or allopatric speciation of like colour morphs. Of the concepts defined above, the cohesion species concept outlined by Templeton (1989) may present the most useful approach to describing species in the group. The strength of this concept in defining species in *Actinia*, given the concerns over 'too much' and 'too little' sex in the group, lies with the relative importance that this concept places on demographic rather than genetic exchangeability for asexual taxa and syngameons.

Our understanding of the genetics of *A. equina*, at both the individual and population level, remains in its infancy. Added to this are the gaps in our knowledge surrounding reproduction in the group. Despite the obvious and potential flaws exposed for the reproductive and isolation species concepts, at present these serve to crudely describe species in what is taxonomically a generally poorly understood genus.

Possible mechanisms of speciation in *Actinia*

The increasing number of studies reporting genetic differentiation within sea anemone species suggest that cryptic species may be common within the group (McCommas & Lester 1980, Carter & Thorpe 1981, Bucklin & Hedgecock 1982, Haylor et al. 1984, Solé-Cava et al. 1985, Shaw et al. 1987, Solé-Cava & Thorpe 1987, 1992, Shaw 1988, Perrin 1993, McFadden et al. 1997, Monteiro et al. 1997). Considerations of the life history and life styles of *A. equina* suggest a number of possibilities for mechanisms of speciation.

Allopatric species may have arisen in *A. equina* through "founder effect speciation". Here, geographically isolated populations are thought to be established by a very small number of founder individuals, and subsequently grow through the localized recruitment of clonally produced young. This "genotype amplification effect" (Ayre 1984a, Bucklin 1985), combined with limited dispersal between populations, may consequently lead to divergence and speciation. Stochastic events, e.g. storm disruption of boulder fields (Ottaway

1979a) or climatic extremes (Crisp 1964), may cause bottlenecks in small populations of *Actinia*, enhancing rates of divergence.

The high genetic variability of *A. equina*, and of sea anemones in general, may facilitate speciation in these groups (Solé-Cava & Thorpe 1992). There is evidence to suggest a positive relationship between the heterozygosity of loci and their rates of divergence (Skibinski & Ward 1981, Ward & Skibinski 1985) and consequently species with high genetic variability, such as sea anemones (Solé-Cava & Thorpe 1991, Perrin 1993), may evolve more rapidly than less polymorphic species.

Hybridization in nature is a widely recognized and investigated phenomenon among plants (Stebbins 1950) and occurs in some animals such as marine molluscs (e.g. Skibinski et al. 1978), *Drosophila* (e.g. Bock 1980), fish (e.g. Brassington & Ferguson 1976, Child & Solomon 1977), and mammals (e.g. Hutchison et al. 1974, Serov et al. 1978). The application of enzyme electrophoresis to the investigation of animal and plant populations has made identifying hybrid individuals easier than reliance on purely morphological criteria (e.g. Littlejohn et al. 1971, Moran et al. 1980). Where different alleles are present at a locus in each parent the hybrid will exhibit a “heterozygote” type banding pattern. Results from the use of electrophoresis in the study of sea anemones suggest that past hybridization may have been an important speciating mechanism in this group (Quicke et al. 1985, Shaw et al. 1987, Perrin 1993). The existence of a hybrid form of *Actinia* on British shores seems likely with evidence to suggest that the ancestral and hybrid forms may currently coexist (Quicke et al. 1985, Perrin 1993), but in our opinion the hybridization, if it has occurred, has done so at some time during the past evolutionary history of the species. Quicke et al. (1985) considered that the differences between upper and lower shore morphs and the putative mid-shore hybrids resulted from, and were maintained by, selection acting on linked gene loci. The possibility that limited amounts of gene flow may be mediated through backcrossing with ancestral morphs (introgression) should also be considered, although the suggestion that differences in morphology and in alleles at various enzyme loci (“co-adapted gene complexes”) between lower and upper shore morphs and in the mid-shore “hybrids” are maintained by selection seems intuitively improbable. More geographically wide-ranging studies should determine whether there is a distinct hybrid zone in this group or whether the hybrid form exists out of the range of one or both of its ancestors.

Shaw et al. (1987) suggest that the actinian *Sagartia ornata* is of hybrid origin. They identify *S. troglodytes* (formerly *S. troglodytes* var. *decorata*) as being one ancestral “parent” to *S. ornata*, and report finding both species in sympatry at certain locations. Shaw et al. (1987), however, failed to identify the other ancestor in the populations they examined, leading them to suggest that it may be a geographically distant or a now extinct species. Furthermore, the authors report that *S. ornata* is polyploid. An alternative explanation to hybridization leading to fixed and near fixed heterozygosity (in the absence of two parental forms) is that autopoloidy in *S. troglodytes* gave rise to the tetraploid *S. ornata*. The fixed heterozygotes seen in this species would therefore be the result of divergence of alleles in the two genomes.

Evidence for historical duplication of genetic material in the Actiniidae is seen in the existence of duplicate loci in most species of actiniid sea anemones investigated by enzyme electrophoresis (e.g. McCommas & Lester 1980, Carter & Thorpe 1981, Bucklin & Hedgecock 1982, Bucklin et al. 1984, Ayre et al. 1991, Solé-Cava & Thorpe 1992, Russo et al. 1994). These studies in particular report the existence of two loci for both PGI and MDH in the species studied. Whether the existence of these multiple loci has resulted from duplication of restricted portions of the genome or from polyploidy remains unclear.

Actinia equina as a model species

The “strawberry-coral” model of Williams (1975) predicts that in organisms which possess the ability to reproduce both asexually and sexually, asexual reproduction acts to preserve locally adapted multi-locus genotypes, whereas the maintenance of sex is used to produce widely dispersed, genotypically diverse colonists. Furthermore, the model predicts intense competition among genotypically distinct colonists and that the area occupied by a clone will show an inverse relationship with habitat heterogeneity. Intertidal sea anemone species have become increasingly important as test organisms for this theory (e.g. Ayre 1982, 1983a, 1984a,b, 1985, Fujii 1987, Shaw 1988, Ayre et al. 1991). In particular, studies involving *Actinia tenebrosa* have shown this species to be highly conformative to the predictions of the model (Ottaway 1979b, Ayre 1982, 1983a, 1984b, Ayre et al. 1991). In common with this congener, *A. equina* is believed to employ both asexual (Carter & Thorp 1979, Orr et al. 1982, Perrin 1993) and sexual reproductive modes (Carter & Miles 1989). Competition for space via aggression is also demonstrated by *A. equina* (Brace & Pavey 1978, Brace et al. 1979, Rees 1984). Like *A. tenebrosa*, *A. equina* is found distributed through a range of microhabitats (Ayre 1983a, Haylor et al. 1984, Manuel 1988) some of which, e.g. boulder fields, are markedly heterogeneous. Despite these attributes, explicit attempts to relate the life history and population genetics of *A. equina* to the strawberry-coral model have not been made. Significant genetic differences between neighbouring populations of like morphs (Solé-Cava & Thorpe 1992) may indicate that larval dispersal and consequently panmixis are limited in this species. However, in the absence of any detailed genetic investigation of disparate populations of *A. equina*, the extent of gene flow and the role that sex plays in this process remain poorly understood. Localized clonal grouping, predicted by the strawberry-coral model, has been found for *A. tenebrosa* (Ayre 1983a, 1984a), but as yet has not been identified in *A. equina* (e.g. Quicke & Brace 1983).

Aspects of the behaviour as well as the various gene pools of *A. equina* on shores in the British Isles may create problems in investigations designed to apply this model to the species. The existence of cryptic species within *A. “equina”* (Haylor et al. 1984, Quicke et al. 1985, Solé-Cava & Thorpe 1992, Perrin 1993) presents the most obvious difficulty. Investigative and manipulative studies of *A. tenebrosa* have been facilitated by the absence of taxonomic problems within the species and the subsequent fact that this species forms monospecific stands (e.g. Ayre 1985). In comparison, a large number of *A. equina* aggregations are likely to be composed of more than one genetically distinct morph or species.

Ayre (1985) used reciprocal transplant experiments to confirm that clones of *A. tenebrosa* were locally adapted. In these experiments asexual fecundity and survival were used as indicators of relative fitness in transplanted and native colonies. Any similar investigations using *A. equina* must recognize the existence of genetic differentiation in the group in order to avoid highlighting possible species specific differences. This is particularly important given that life history characteristics (e.g. asexual fecundity) may vary between putative species irrespective of their location in the environment (see M.R.Brown & J.P.Thorpe in prep.).

Perrin (1993) provided estimates for genetic variability in *Actinia* colour morphs indicating markedly differing levels of heterozygosity between various morph groups. The genus *Actinia* on British shores would seem to present itself as an ideal group with which to examine the “niche-width” hypothesis (Van Valen 1965). This theory holds that there is a positive correlation between niche-breadth and the level of genetic diversity within an organism. This phenomenon has been reported to occur in a wide variety of organisms

(e.g. Beardmore 1961, Mackay 1980, Lavie & Nevo 1981, 1986, Lacy 1982, Noy et al. 1987), although its existence in some species is disputed (Schopf & Gooch 1971, Somero & Soule 1974, Solé-Cava & Thorpe 1991). If the niche-width hypothesis holds true the most genetically variable *Actinia* groups may be expected to have broader ecological niches. This may manifest itself as a wider vertical distribution or occupation of a greater variety of microhabitats. Alternatively, as found by Noy et al. (1987) for littorinid species, it may be that more heterozygous groups are found at higher shore levels where environmental fluctuations are greatest. A vertical distribution study conducted at Perwick Bay, Isle of Man (Perrin 1993) provided no clear evidence for a broader niche in relation to tidal height for any morph. In a study of three vertical transects (Quicke et al. 1985) only a red or pink pedal disc morph was found over the entire range of each transect, but the pooling of red and pink individuals in this and other studies is likely to be an oversimplification in sampling strategy, given that individuals of these groups show genetic differentiation at some locations (Quicke et al. 1985, Perrin 1993).

Suggestions for future work

At present there is limited information available as to the long-term stability of colour in individuals of *Actinia* (Gosse 1860, Elmhirst & Sharpe 1920). Such information, although elementary, would enable particular morphs or colour morph groups to be identified with greater confidence. Investigations should include both the field monitoring of different colour morphs and laboratory-based examination of colour stability under different environmental regimes.

The scope for further biochemical genetic investigation of *A. equina* populations in the British Isles remains great. To date populations from relatively few locations have been investigated and in general studies have used only small sample sizes. Within further studies of this nature the putative *Actinia* morphs of Quicke et al. (1985) and of Donoghue et al. (1985) need to be re-examined. The use of molecular genetic methodology could be helpful to approach some basic problems. The techniques of DNA fingerprinting and the random amplified polymorphic DNA (RAPD) analysis, for example could be used for the investigation of genetic identity, which would provide additional data about the origin of brooded individuals and an accurate recognition of clonal genotypes (Turner et al. 1990, Carvalho et al. 1991, Coffroth et al. 1992), and hybrid speciation (Hadrys et al. 1992). Single locus and multi loci polymerase chain reaction analysis would be an important tool to estimate levels of gene flow between populations (Bruford et al. 1992, Karl & Avise 1993), and DNA sequencing of nuclear or mitochondrial genes would help to formulate hypotheses about the phylogenetic relationships between the different species of the genus.

Of equal priority is the need for cytological studies of colour morphs of *A. equina*. Estimates of chromosome number, banding patterns and nucleolar organizing regions may shed light on whether the “fixed heterozygote” patterns observed in the group result from polyploidy and, thus, whether these should be interpreted as products of one, or more than one, locus.

If further investigation confirms the existence of “upper” and “lower” shore morphs in *A. equina* and these forms are shown to have differing ecologies (e.g. distributional and behavioural), then additional attempts to find morphologically distinguishing characteristics should be made. Characteristics that allow the separation of these forms in the field would

be of greatest value to ecologists and may be found in further, more objective and critical attention to differences in column and pedal disc pigmentation and acrorhagial form (Donoghue et al. 1985).

The question of how many species exist within *A. equina* on British shores remains to be answered. The existing body of evidence points to *A. equina* being a species complex. While continued efforts are being made to fully understand the genetics of the “species”, it would seem sensible that researchers whose studies involve *A. equina* should document to as fine a level as is practicable, the colour variation in individuals they encounter.

Acknowledgements

The authors thank Dr M.A.Carter, whose longstanding interest in *Actinia* has lead directly or indirectly to much of the work presented here. M.C.Perrin was supported by a research studentship from NERC. A.M.Solé-Cava was supported by a grant from CNPq (Brazilian Government).

References

- Abeloos, M. 1955. Sur le regeneration de l'*Actinia equina*. *Comptes Rendus de l'Academic des Sciences à Paris* **240**, 2261–3.
- Allcock, A.L., Watts, P.C. & Thorpe, J.P. 1998. Divergence of nematocysts in two colour morphs of the intertidal beadlet anemone *Actinia equina*. *Journal of the Marine Biological Association of the United Kingdom* **78**, 821–8.
- Andres, A. 1884. L'attinie. *Fauna und Flora des Golfes von Neapel*. Berlin **9**, 1–459.
- Ates, R.M.L. 1989. Fishes that eat sea anemones, a review. *Journal of Natural History* **23**, 71–9.
- Ayre, D.J. 1982. Inter-genotype aggression in the solitary sea anemone *Actinia tenebrosa*. *Marine Biology* **68**, 199–205.
- Ayre, D.J. 1983a. The effects of asexual reproduction and inter-genotype aggression on the genotypic structure of populations of the sea anemone *Actinia tenebrosa*. *Oecologia* **57**, 158–65.
- Ayre, D.J. 1983b. The distribution of the sea anemone *Actinia tenebrosa* Farquhar in south-western Australia. *Western Australian Naturalist* **15**, 136–40.
- Ayre, D.J. 1984a. The effects of sexual and asexual reproduction on geographic variation in the sea anemone *Actinia tenebrosa*. *Oecologia* **62**, 222–9.
- Ayre, D.J. 1984b. The effects of environment and density on the life-history characteristics of the sea anemone *Actinia tenebrosa*. *Australian Journal of Marine and Freshwater Research* **35**, 735–46.
- Ayre, D.J. 1985. Localized adaptation of clones of the sea anemone *Actinia tenebrosa*. *Evolution* **39**, 1250–60.
- Ayre, D.J. 1987. The formation of clonal territories in experimental populations of the sea anemone *Actinia tenebrosa*. *Biological Bulletin* **172**, 178–86.
- Ayre, D.J. 1988. Evidence for genetic determination of sex in *Actinia tenebrosa*. *Journal of Experimental Marine Biology and Ecology* **116**, 23–34.
- Ayre, D.J., Read, J. & Wishart, J. 1991. Genetic subdivision within the eastern Australian population of the sea anemone *Actinia tenebrosa*. *Marine Biology* **109**, 379–90.
- Beardmore, J.A. 1961. Diurnal temperature fluctuation and genetic variance in *Drosophila* populations. *Nature* **189**, 162–3.
- Bigger, C.H. 1980. Interspecific and intraspecific acrorhagial aggressive behaviour among sea anemones: a recognition of self and non-self. *Biological Bulletin* **159**, 117–34.
- Black, R. & Johnson, M.S. 1979. Asexual viviparity and population genetics of *Actinia tenebrosa*. *Marine Biology* **53**, 27–31.
- Bock, I.R. 1980. Interspecific hybridisation in the genus *Drosophila*. *Evolutionary Biology* **18**, 41–70.

- Bonnin, J.-P. 1964. Recherches sur la 'réaction d'agression' et sur le fonctionnement des acrorrhages d'*Actinia equina* L. *Bulletin Biologique de la France et de la Belgique, Paris* **98**, 225–50.
- Brace, R.C. & Pavey, J. 1978. Size-dependent dominance hierarchy in the sea anemone *Actinia equina*. *Nature* **273**, 752–3.
- Brace, R.C., Pavey, J. & Quicke, D.L.J. 1979. Intraspecific aggression in the colour morphs of the sea anemone *Actinia equina*: the 'convention' governing dominance ranking. *Animal Behaviour* **27**, 553–61.
- Brace, R.C. & Quicke, D.L.J. 1985. Further analysis of individual spacing within aggregations of the anemone *Actinia equina*. *Journal of the Marine Biological Association of the United Kingdom* **65**, 35–53.
- Brace, R.C. & Quicke, D.L.J. 1986a. Dynamics of colonisation by the beadlet anemone, *Actinia equina*. *Journal of the Marine Biological Association of the United Kingdom* **66**, 21–47.
- Brace, R.C. & Quicke, D.L.J. 1986b. Seasonal changes in dispersion within an aggregation of the anemone, *Actinia equina*, with a reappraisal of the role of intraspecific aggression. *Journal of the Marine Biological Association of the United Kingdom* **66**, 49–70.
- Brace, R.C. & Reynolds, H.A. 1989. Relative intraspecific aggressiveness of pedal disc colour phenotypes of the beadlet anemone, *Actinia equina*. *Journal of the Marine Biological Association of the United Kingdom* **69**, 273–8.
- Branch, G. & Branch, M. 1981. *The living shores of Southern Africa*. Capetown: Struik.
- Brassington, R.A. & Ferguson, A. 1976. Electrophoretic identification of roach (*Rutilus rutilus* L.), rudd (*Scardinius erythrophthalmus* L.), bream (*Abramis brama* L.) and their natural hybrids. *Journal of Fish Biology* **9**, 471–7.
- Brenowitz, A.H. 1972. A review of coelenterate laboratory culture. In *Culture of marine invertebrate animals*, W.L. Smith & M.H. Chanley (eds). New York: Plenum Press, 137–54.
- Bruford, M.W., Hanotte, O., Brookfield, J.F.Y. & Burke, T. 1992. Single locus and multilocus DNA fingerprinting. In *Molecular genetic analysis of populations*, A.R. Hoeltzel (ed.). Oxford: Oxford University Press, 225–70.
- Bucklin, A. 1980. *The reproduction and population biology of Metridium (Coelenterata, Actiniaria)*. Unpubl. thesis, Berkeley, University of California.
- Bucklin, A. 1985. Biochemical genetic variation, growth and regeneration of the sea anemone *Metridium senile* of British shores. *Journal of the Marine Biological Association of the United Kingdom* **65**, 141–57.
- Bucklin, A. & Hedgecock, D. 1982. Biochemical genetic evidence for a third species of *Metridium* (Coelenterata, Actiniaria). *Marine Biology* **66**, 1–7.
- Bucklin, A., Hedgecock, D. & Hand, C. 1984. Genetic evidence of self-fertilization in the sea anemone *Epiactis prolifera*. *Marine Biology* **88**, 175–82.
- Cain, A.J. 1974. Breeding system of a sessile animal. *Nature* **247**, 289–90.
- Carlgren, O. 1949. A survey of the Ptychodactaria, Corallimorpharia and Actiniaria. *Kungliga Svenska Vetenskapsakademiens Handlingar: Uppsala and Stockholm. Fjarde Ser.* **1**, 1–121.
- Carter, M.A. & Funnell, N. 1980. Reproduction and brooding in *Actinia*. In *Developmental and cellular biology of coelenterates*, P. Tardent & R. Tardent (eds). Amsterdam: North-Holland, 17–22.
- Carter, M.A. & Miles, J. 1989. Gametogenic cycles and reproduction in the beadlet anemone *Actinia equina* (Cnidaria: Anthozoa). *Biological Journal of the Linnean Society* **36**, 129–55.
- Carter, M.A. & Thorp, C.H. 1979. The reproduction of *Actinia equina* L. var. *mesembryanthemum*. *Journal of the Marine Biological Association of the United Kingdom* **59**, 989–1001.
- Carter, M.A. & Thorpe, J.P. 1981. Reproductive, genetic and ecological evidence that *Actinia equina* var. *mesembryanthemum* and var. *fragacea* are not conspecific. *Journal of the Marine Biological Association of the United Kingdom* **61**, 71–93.
- Carvalho, G.R., Maclean, N., Wratten, S.D., Carter, R.E. & Thurston, J.P. 1991. Differentiation of aphid clones using DNA fingerprints from individual aphids. *Proceedings of the Royal Society, London* **B243**, 109–114.
- Chia, F.-S. 1976. Sea anemone reproduction: patterns and adaptive radiations. In *Coelenterate ecology and behavior*, G.O. Mackie (ed.). New York: Plenum Press, 261–70.
- Chia, F.S. & Rostron, M.A. 1970. Some aspects of the reproductive biology of *Actinia equina* (Cnidaria: Anthozoa). *Journal of the Marine Biological Association of the United Kingdom* **50**, 253–64.
- Child, A.R. & Solomon, D.J. 1977. Observations on morphological and biochemical features of some cyprinid hybrids. *Journal of Fish Biology* **11**, 125–31.

- Chintiroglou, C.C. & Sirmsiridou, M. 1997. Biometric investigations of the cnidae of the sea anemone *Actinia equina mediterranea* Form I *sensu* Schmidt, 1972. *Israel Journal of Zoology, Jerusalem* **43**, 5–11.
- Cocks, W.P. 1850. Contributions to the fauna of Falmouth. *Reports of the Cornwall Polytechnic Society* **17**, 94–5.
- Coffroth, M.A., Lasker, H.R., Diamond, M.E., Bruenn, J.A. & Bermingham, E. 1992. DNA fingerprinting of a gorgonian coral, a method of detecting clonal structure in a vegetative process. *Marine Biology* **114**, 317–25.
- Colebrook, J.M. & Robinson, G.A. 1965. Continuous plankton records. Seasonal cycles of phytoplankton and copepods in the North Eastern Atlantic and North Sea. *Bulletin of Marine Ecology, Edinburgh* **6**, 23–139.
- Crisp, D.J. 1964. The effects of the severe winter of 1962–63 on marine life in Britain. *Journal of Animal Ecology* **33**, 165–210.
- Dakin, W.J. 1952. *Australian seashores*. Sydney: Angus & Robertson.
- Dalyell, J.G. 1848. *Rare and remarkable animals of Scotland*. London: Van Voorst.
- Delle Chiaje, S. 1825. *Memorie sulla storie e notomia degli animala senza vertebre del Regno di Napoli*. Napoli.
- Donoghue, A.M., Quicke, D.L.J. & Brace, R.C. 1985. Biochemical-genetic and acrorhagial characteristics of pedal disc colour phenotypes of *Actinia equina*. *Journal of the Marine Biological Association of the United Kingdom* **65**, 21–33.
- Dunn, D.F. 1975. Reproduction of the externally brooding sea anemone *Epiactis prolifera* Verrill, 1869. *Biological Bulletin* **148**, 199–218.
- Elmhirst, R. & Sharpe, J.S. 1920. On the colours of two sea anemones, *Actinia equina* and *Anemonia sulcata*. Part I. Environmental. Part II. Chemical. *Biochemical Journal* **14**, 48–57.
- Endler, J.A. 1977. *Geographic variation, speciation, and clines*. New Jersey: Princeton University Press.
- Fautin, D.G. 1991. Developmental pathways of anthozoans. *Hydrobiologia* **216**, 143–9.
- Fujii, H. 1987. The predominance of clones in populations of the sea anemone *Anthopleura asiatica* (Uchida). *Biological Bulletin* **172**, 201–11.
- Gashout, S.E. & Ormond, R.F.G. 1979. Evidence for parthenogenetic reproduction in the sea anemone *Actinia equina* L. *Journal of the Marine Biological Association of the United Kingdom* **59**, 975–87.
- Gosse, P. 1860. *Actinologia Britannica: a history of the British sea anemones and corals*. London: Van Voorst.
- Gravenhorst, J.L.C. 1831. Tergestina oder Beobachtungen und Untersuchungen uber Vorkommen, Lebensweise, Erscheinungs- und Fortpflanzungszeit der einzelnen Arten, III. Coelenteraten. *Arbeiten aus dem Zoologischen Institut der Universität Wien* **5**, 333–62.
- Gravier, C.J. 1916. Sur la faune actinienne de l'île San Thome (Golfe de Guinée). *Comptes Rendus de l'Académie des Sciences a Paris* **162**, 847–9.
- Griffiths, R.J. 1977a. Thermal stress and the biology of *Actinia equina* L. (Anthozoa). *Journal of Experimental Marine Biology and Ecology* **27**, 141–54.
- Griffiths, R.J. 1977b. Temperature acclimation in *Actinia equina* L. (Anthozoa). *Journal of Experimental Marine Biology and Ecology* **28**, 285–92.
- Hadrys, H., Balick, M. & Schierwater, B. 1992. Applications of random amplified polymorphic DNA (RAPD) in molecular ecology. *Molecular Ecology* **1**, 55–63.
- Hall, S.J., Todd, C.D. & Gordon, A.D. 1982. The influence of ingestive conditioning in the prey species selection in *Aeolidia papillosa* (Mollusca: Nudibranchia). *Journal of Animal Ecology* **51**, 907–21.
- Hall, S.J., Todd, C.D. & Gordon, A.D. 1984. Prey-species selection by the anemone predator *Aeolidia papillosa* (L.): the influence of ingestive conditioning and previous dietary history, and a test for switching behaviour. *Journal of Experimental Marine Biology and Ecology* **82**, 11–33.
- Hand, C. 1955a. The sea anemones of central California, Part II. The endomyarian and mesomyarian anemones. *Wasmann Journal of Biology* **13**, 37–99.
- Hand, C. 1955b. The sea anemones of central California, Part III. The acontiarian anemones. *Wasmann Journal of Biology* **13**, 189–251.
- Haylor, G.S., Thorpe, J.P. & Carter, M.A. 1984. Genetic and ecological differentiation between sympatric colour morphs of the common intertidal sea anemone *Actinia equina*. *Marine Ecology Progress Series* **16**, 281–9.

- Herndl, G. 1984. Differences in feeding behaviour between *Actinia equina* and *Actinia bermudensis* (Actiniaria, Coelenterata) with a short note on intraspecific differences in feeding behaviour in *A. equina*. *Zoolische Anzeiger, Jena* **212**, 353–61.
- Hoffman, R.J. 1983. Temperature modulation of the kinetics of phosphoglucose isomerase genetic variants from the sea anemone *Metridium senile*. *Journal of Experimental Zoology* **227**, 361–70.
- Hoffman, R.J. 1987. Short term stability of genetic structure in populations of the sea anemone *Metridium senile*. *Marine Biology* **93**, 499–507.
- Hughes, R.N. 1989. *A functional biology of clonal animals*. London: Chapman & Hall.
- Hunt, A. & Ayre, D.J. 1989. Population structure in the sexually reproducing sea anemone *Oulactis muscosa*. *Marine Biology* **102**, 537–44.
- Hutchison, C.A., Newbold, J.E., Potter, S.S. & Edgell, M.H. 1974. Maternal inheritance of mammalian mitochondrial DNA. *Nature* **251**, 536–8.
- Jennison, B.L. 1978. Gametogenesis and reproductive cycles in the sea anemone *Anthopleura elegantissima* (Brandt, 1835). *Canadian Journal of Zoology* **57**, 403–11.
- Jennison, B.L. 1983. Reproductive biology of three species of sea anemones from the central Atlantic Coast of Florida. *Florida Science* **46**, 168–78.
- Johnston, G. 1847. *A history of the British zoophytes*. 2nd edn. London: Van Voorst.
- Karl, S.A. & Avise, J.C. 1993. PCR-Based assays of Mendelian polymorphisms from anonymous single copy nuclear DNA. Techniques and applications for population genetics. *Molecular Biology and Evolution* **10**, 342–61.
- Kruger, L.M. & Griffiths, C.C. 1996. Sources of nutrition in intertidal sea anemones from the south western Cape, South Africa. *South African Journal of Zoology* **31**, 110–119.
- Lacy, R.C. 1982. Niche breadth and abundance as determinants of genetic variation in populations of mysophagous Drosophilid flies (Diptera: Drosophilidae). *Evolution* **36**, 1265–75.
- Larkman, A.U. 1980. Ultrastructural aspects of gametogenesis in *Actinia equina* L. In *Developmental and cellular biology of coelenterates*, P.Tardent & R.Tardent (eds). Amsterdam: North Holland, 61–6.
- Larkman, A.U. 1983. An ultrastructural study of oocyte growth within the endoderm and entry into the mesoglea in *Actinia fragacea* (Cnidaria, Anthozoa). *Journal of Morphology* **178**, 155–77.
- Larkman, A.U. 1984a. An ultrastructural study of the establishment of testicular cysts during spermatogenesis in the sea anemone *Actinia fragacea* (Cnidaria, Anthozoa). *Gamete Research* **9**, 303–27.
- Larkman, A.U. 1984b. The fine structure of granular amoebocytes from the gonads of the sea anemone *Actinia fragacea* (Cnidaria, Anthozoa). *Protoplasma* **122**, 203–21.
- Larkman, A.U. & Carter, M.A. 1980. The spermatozoon of *Actinia equina* L. var. *mesembryanthemum*. *Journal of the Marine Biological Association of the United Kingdom* **60**, 193–204.
- Larkman, A.U. & Carter, M.A. 1982. Preliminary ultrastructural and autoradiographic evidence that the trophonema of the sea anemone *Actinia fragacea* has a nutritive function. *International Journal of Invertebrate Reproduction* **4**, 375–9.
- Larkman, A.U. & Carter, M.A. 1984. The apparent absence of a cortical reaction after fertilization in a sea anemone. *Tissue and Cell* **16**, 125–30.
- Lavie, B. & Nevo, E. 1981. Genetic diversity in marine molluscs: a test of the niche-width variation hypothesis. *Marine Ecology* **2**, 335–42.
- Lavie, B. & Nevo, E. 1986. Genetic diversity of marine gastropods: contrasting strategies of *Cerithium rupestre* and *Cerithium scabridum*. *Marine Ecology* **28**, 99–103.
- Lewontin, R.C. 1974. *The genetic basis of evolutionary change*. New York: Columbia University Press.
- Linnaeus, C. 1758. *Systema naturae per regna tria naturae secundum, classes, ordines, genera, species, cum characteribus, differentibus, synonymis, locis. Editio decimo reformata*, 2 vols. Holmia, Laurentius Salvius.
- Littlejohn, M.J., Watson, G.F. & Loftus-Hills, T.J. 1971. Contact hybridisation in the *Crinia laevis* complex (Anura: Leptodactylidae). *Australian Journal of Zoology* **19**, 85–100.
- Longhurst, A.R. & Pauly, D. 1987. *Ecology of tropical oceans*. London: Academic Press.
- Lubbock, R. 1980. Clone specific cellular recognition in a sea anemone. *Proceedings of the National Academy of Sciences* **77**, 6667–9.
- Lubbock, R. & Allbut, C. 1981. The sea anemone *Actinia equina* tolerates allogeneic juveniles but alters their phenotype. *Nature* **293**, 474–5.
- Lynch, S.M. 1996. *Empirical aspects of allozyme based ecological genetics and taxonomy of Actiniidae and other marine invertebrates*. PhD thesis, University of Liverpool, Port Erin, Isle of Man.

- Mackay, T.F.C. 1980. Genetic variance, fitness and homeostasis in varying environments: an experimental check on the theory. *Evolution* **34**, 1219–22.
- Manuel, R.L. 1981. *British Anthozoa*. London: Academic Press.
- Manuel, R.L. 1988. *British Anthozoa* (revd). Leiden: E.J.Brill.
- Mariscal, R.N. 1970. The nature of the symbiosis between Indo-Pacific anemone fishes and sea anemones. *Marine Biology* **6**, 58–65.
- Mayr, E. 1963. *Animal species and evolution*. Cambridge, Mass.: Harvard University Press.
- McCommas, S.A. & Lester, L.J. 1980. Electrophoretic evaluation of the taxonomic status of two species of sea anemone. *Biochemical Systematics and Ecology* **8**, 289–92.
- McFadden, C.S., Grosberg, R.K., Cameron, B.B., Karlton, D.P. & Secord, D. 1997. Genetic relationships within and between clonal and solitary forms of the sea anemone *Anthopleura elegantissima* revisited: evidence for the existence of two species. *Marine Biology* **128**, 127–39.
- Milne-Edwards, H. 1857. *Histoire naturelle des corallieres ou polypes proprement dits*. Paris.
- Monteiro, F.A., Russo, C.A.M. & Solé-Cava, A.M. 1998. Genetic evidence of the asexual origin of small individuals found in the coelenteron of the sea anemone *Actinia bermudensis* McMurrich. *Bulletin of Marine Science* **63**, 257–64.
- Monteiro, F.A., Solé-Cava, A.M. & Thorpe, J.P. 1997. Extensive genetic divergence between populations of the common intertidal sea anemone *Actinia equina* from Britain, the Mediterranean and the Cape Verde Islands. *Marine Biology* **129**, 425–35.
- Moran, C., Wilkinson, P. & Shaw, D.D. 1980. Allozyme variation across a narrow hybrid zone in the grasshopper, *Caledia captiva*. *Heredity* **44**, 69–81.
- Nei, M. 1972. Genetic distance between populations. *American Naturalist* **106**, 283–92.
- Nei, M. 1987. *Molecular evolutionary genetics*. New York: Columbia University Press.
- Noy, R., Lavie, B. & Nevo, E. 1987. The niche-width hypothesis revisited: genetic diversity in the marine gastropods *Littorina punctata* (Gmelin) and *L. neritoides* (L.). *Journal of Experimental Marine Biology and Ecology* **109**, 109–16.
- Orr, J., Thorpe, J.P. & Carter, M.A. 1982. Biochemical genetic confirmation of the asexual reproduction of brooded offspring in the sea anemone *Actinia equina*. *Marine Ecology Progress Series* **7**, 227–9.
- Ottaway, J.R. 1973. Some effects of temperature, desiccation and light on the intertidal sea anemone *Actinia tenebrosa* Farquhar (Cnidaria: Anthozoa). *Australian Journal of Marine and Freshwater Research* **24**, 103–26.
- Ottaway, J.R. 1977. Predators of sea anemones. *Tuatara* **22**, 213–21.
- Ottaway, J.R. 1978. Population ecology of the intertidal sea anemone *Actinia tenebrosa*. I. Pedal locomotion and intraspecific aggression. *Australian Journal of Marine and Freshwater Research* **29**, 787–802.
- Ottaway, J.R. 1979a. Population ecology of the intertidal sea anemone *Actinia tenebrosa*. III. Dynamics and environmental factors. *Australian Journal of Marine and Freshwater Research* **30**, 41–62.
- Ottaway, J.R. 1979b. Population ecology of the intertidal sea anemone *Actinia tenebrosa*. II. Geographical distribution, synonymy, reproductive cycle and fecundity. *Australian Journal of Zoology* **27**, 273–90.
- Ottaway, J.R. 1980. Population ecology of the intertidal sea anemone *Actinia tenebrosa*. IV. Growth rates and longevities. *Australian Journal of Marine and Freshwater Research* **31**, 385–95.
- Ottaway, J.R. & Kirby, G.C. 1975. Genetic relationships between brooding and brooded *Actinia tenebrosa*. *Nature* **255**, 221–3.
- Ottaway, J.R. & Thomas, I.M. 1971. Movement and zonation of the intertidal sea anemone *Actinia tenebrosa* Farquhar. (Cnidaria: Anthozoa) under experimental conditions. *Australian Journal of Marine and Freshwater Research* **22**, 63–78.
- Parker, G.H. 1917. Pedal locomotion in *Actinia* ns. *Journal of Experimental Zoology* **22**, 111–24.
- Paterson, H.E.H. 1981. The continuing search for the unknown and unknowable: a critique of contemporary ideas on speciation. *South African Journal of Science* **77**, 113–19.
- Paterson, H.E.H. 1982. Perspective on speciation by reinforcement. *South African Journal of Science* **78**, 53–7.
- Paterson, H.E.H. 1985. The recognition concept of species. *Transvaal Museum Monographs* **4**, 21–9.
- Pax, F. 1907. *Vorarbeiten zu einer Revision der Familie Actiniidae*. Inaugural Diss., Breslau.
- Perrin, M.C. 1993. *Aspects of the ecology and genetics of Actinia colour morphs*. PhD thesis, University of Liverpool, Port Erin, Isle of Man.

- Polteva, D.G. 1963. Regeneration and somatic embryogenesis of *Actinia equina* in different stages of ontogenetic development. *Acta Biologica Academiae Scientiarum Hungaricae Budapest* **14**, 199–208.
- Quicke, D.L.J. & Brace, R.C. 1983. Phenotypic and genotypic spacing within an aggregation on the anemone, *Actinia equina*. *Journal of the Marine Biological Association of the United Kingdom* **63**, 493–515.
- Quicke, D.L.J. & Brace, R.C. 1984. Evidence for the existence of a third, ecologically distinct morph of the anemone, *Actinia equina*. *Journal of the Marine Biological Association of the United Kingdom* **64**, 531–4.
- Quicke, D.L.J., Donoghue, A.M. & Brace, R.C. 1983. Biochemical-genetic and ecological evidence that red-brown individuals of the anemone *Actinia equina* comprise two morphs in Britain. *Marine Biology* **77**, 29–37.
- Quicke, D.L.J., Donoghue, A.M., Keeling, T.F. & Brace, R.C. 1985. Littoral distributions and evidence for differential post-settlement selection on the morphs of *Actinia equina*. *Journal of the Marine Biological Association of the United Kingdom* **65**, 1–20.
- Rees, T.D. 1984. *The population ecology and behaviour of Actinia equina*. PhD thesis, University of Nottingham, Nottingham.
- Risso, A. 1826. *Histoire naturelle des principales productions de l'Europe meridionale et particulièrement de celles des environs de Nice et des Alpes maritimes*. Vol. 5. Paris.
- Ross, D.M. 1983. Symbiotic relations. In *The biology of Crustacea*, Vol. 7. *Behaviour and ecology*, F.J. Vernberg & W.B. Vernberg (eds). New York: Academic Press, 163–212.
- Rostron, M.A. & Rostron, J. 1978. Fecundity and reproductive ecology of a natural population of *Actinia equina* L. (Cnidaria: Anthozoa). *Journal of Experimental Marine Biology and Ecology* **33**, 251–9.
- Rubenstein, D.I. & Koehl, M.A.R. 1977. The mechanisms of filter feeding: some theoretical considerations. *American Naturalist* **111**, 981–4.
- Russo, C.A.M. & Solé-Cava, A.M. 1991. Genetic variation and differentiation between populations of a tropical sea anemone (*Bunodosoma caissarum*). *Revista de Biología Tropical*. **39**, 41–6.
- Russo, C.A.M., Solé-Cava, A.M. & Thorpe, J.P. 1994. Population structure and genetic variation in two tropical sea anemones (Cnidaria, Actiniidae) with differing reproductive strategies. *Marine Biology* **119**, 267–76.
- Schaefer, W. 1981. Fortpflanzung und Sexualität von *Cereus pedunculatus* und *Actinia equina* (Anthozoa: Actiniaria). *Helgoländer Wissenschaftliche Meeresuntersuchungen* **34**, 451–61.
- Schmidt, H. 1971. Taxonomie, Verbreitung und Variabilität von *Actinia equina* Linné 1766 (Actiniaria; Anthozoa). *Zeitschrift für Zoologische Systematik und Evolutionsforschung, Frankfurt am Main* **9**, 161–9.
- Schmidt, H. 1972. Prodrömus zu einer monographie der mediterranen Aktinien. *Zoologica* **42**, 1–120.
- Schopf, T.J.M. & Gooch, J.L. 1971. A natural experiment using deep-sea invertebrates to test the hypothesis that genetic homozygosity is proportional to environmental stability. *Biological Bulletin* **141**, 401 only.
- Sebens, K.P. 1981. The allometry of feeding, energetics and body size in three sea anemone species. *Biological Bulletin* **161**, 151–71.
- Sebens, K.P. 1984. Agonistic behaviour in the intertidal sea anemone *Anthopleura xanthogrammica*. *Biological Bulletin* **166**, 457–72.
- Sebens, K.P. 1986. Community ecology of vertical rock walls in the Gulf of Maine, USA: small scale processes and alternative community states. In *The ecology of rocky coasts: essays presented to J.R. Lewis*, P.G. Moore & R. Seed (eds). New York: Columbia University Press, 346–71.
- Serov, O.L., Zakijan, S.M. & Kulichov, V.A. 1978. Allelic expression in intergeneric fox hybrids (*Alopex lagopus* x *Vulpes vulpes*). III. Regulation of the expression of the parental alleles at the Gpd locus linked to the X chromosome. *Biochemical Genetics* **16**, 145–57.
- Shaw, P.W. 1988. *Ecological genetics of anthozoans*. PhD thesis, University of Wales, Swansea.
- Shaw, P.W. 1989. Seasonal patterns and possible long-term effectiveness of sexual reproduction in three species of sagartiid sea anemones. In *Reproduction, genetics and distributions of marine organisms*, J.S. Ryland & P.A. Tyler (eds). Fredensborg, Denmark: Olsen & Olsen, 189–99.
- Shaw, P.W., Beardmore, J.A. & Ryland, J.S. 1987. *Sagartia troglodytes* (Anthozoa: Actiniaria) consists of two species. *Marine Ecology Progress Series* **41**, 21–8.
- Shick, J.M. 1991. *A functional biology of sea anemones*. London: Chapman & Hall.

- Shick, J.M. & Lamb, A.N. 1977. Asexual reproduction and genetic population structure in the colonising sea anemone *Haliplanella luciae*. *Biological Bulletin* **153**, 604–17.
- Skibinski, D.O.F. & Ward, R.D. 1981. Relationship between allozyme heterozygosity and rates of divergence. *Genetical Research* **38**, 71–92.
- Skibinski, D.O.F., Ahmad, M. & Beardmore, J.A. 1978. Genetic evidence for naturally occurring hybrids between *Mytilus edulis* and *M. galloprovincialis*. *Evolution* **32**, 354–64.
- Smith, B.L. & Potts, D.C. 1987. Clonal and solitary sea anemones (*Anthopleura*) of western North America: population genetics and systematics. *Marine Biology* **94**, 537–46.
- Solé-Cava, A.M., Russo, C.A.M., Araujo, M.E. & Thorpe, J.P. 1994b. Cladistic and phenetic analysis of allozyme data for nine species of sea anemones of the family Actiniidae (Cnidaria: Anthozoa). *Biological Journal of the Linnean Society* **52**, 225–39.
- Solé-Cava, A.M. & Thorpe, J.P. 1987. Further genetic evidence for the reproductive isolation of the green colour morph of the common intertidal sea anemone *Actinia equina*. *Marine Ecology Progress Series* **38**, 225–30.
- Solé-Cava, A.M. & Thorpe, J.P. 1989. Biochemical correlates of genetic variation in marine lower invertebrates. *Biochemical Genetics* **27**, 303–12.
- Solé-Cava, A.M. & Thorpe, J.P. 1991. High levels of genetic variation in natural populations of marine invertebrates. *Biological Journal of the Linnean Society* **44**, 65–80.
- Solé-Cava, A.M. & Thorpe, J.P. 1992. Genetic divergence between colour morphs in populations of the common intertidal sea anemones *Actinia equina* and *Actinia prasina* (Anthozoa: Actiniaria) in the Isle of Man. *Marine Biology* **112**, 243–52.
- Solé-Cava, A.M., Thorpe, J.P. & Kaye, J.G. 1985. Reproductive isolation with little genetic divergence between *Urticina* (= *Tealia*) *felina* and *U. eques* (Anthozoa: Actiniaria). *Marine Biology* **85**, 279–84.
- Solé-Cava, A.M., Thorpe, J.P. & Todd, C.D. 1994a. High genetic similarity between geographically distant populations in a sexually reproducing sea anemone species with low dispersal capabilities. *Journal of the Marine Biological Association of the United Kingdom* **74**, 895–902.
- Somero, G.N. & Soule, M. 1974. Genetic variation in marine fishes as a test of the niche variation hypothesis. *Nature* **249**, 670–72.
- Stebbins, G.L. 1950. *Variation and evolution in plants*. New York: Columbia University Press.
- Stephenson, T.A. 1929. On methods of reproduction as specific characters. *Journal of the Marine Biological Association of the United Kingdom* **16**, 131–72.
- Stephenson, T.A. 1935. *The British sea anemones, Vol II*. London: The Ray Society.
- Templeton, A.R. 1989. The meaning of species and speciation: A genetic perspective. In *Speciation and its consequences*, D.Otte & J.A.Endler (eds). Sunderland, Mass.: Sinauer Associates, 3–27.
- Templeton, R. 1836. A catalogue of the species of rayed animals found in Ireland. *Annals and Magazine of Natural History* **9**, 301–5.
- Thorpe, J.P. 1979. Enzyme variation and taxonomy: the estimation of sampling errors in measurements of interspecific genetic similarity. *Biological Journal of the Linnean Society* **11**, 369–86.
- Thorpe, J.P. 1982. The molecular clock hypothesis: Biochemical evolution, genetic differentiation and systematics. *Annual Review of Ecology and Systematics* **13**, 139–68.
- Tugwell, G. 1856. *A manual of sea anemones commonly found on the English coast*. London: Van Voorst.
- Turner, B.J., Elder, J.F., Laughlin, T.F. & Davis, W.P. 1990. Genetic variation in clonal vertebrates detected by simple-sequence DNA fingerprinting. *Proceedings of the National Academy of Sciences* **87**, 5653–7.
- Van Valen, L. 1965. Morphological variation and the width of the ecological niche. *American Naturalist* **99**, 337–90.
- Ward, R.D. & Skibinski, D.O.F. 1985. Observed relationships between protein heterozygosity and protein genetic distance and comparisons with neutral expectations. *Genetical Research* **45**, 315–40.
- Williams, G.C. 1975. *Sex and evolution*. Princeton: Princeton University Press.
- Young, G.A., Yule, A.B. & Walker, G. 1988. Adhesion in the sea anemones *Actinia equina* L. and *Metridium senile* (L.). *Biofouling* **1**, 137–46.
- Zamer, W.E. 1986. Physiological energetics of the intertidal sea anemone *Anthopleura elegantissima* I. Prey capture, absorption efficiency and growth. *Marine Biology* **92**, 299–314.
- Zamer, W.E. & Hoffman, R.J. 1989. Allozymes of glucose-6-phosphate isomerase differentially modulate pentose-shunt metabolism in the sea anemone *Metridium senile*. *Proceedings of the National Academy of Sciences* **86**, 2737–41.

THE MORTALITY OF INTERTIDAL CIRRIPEDES

MARGARET BARNES

*The Scottish Association for Marine Science, Dunstaffnage Marine Laboratory,
P.O. Box 3, Oban, Argyll, PA34 4AD, Scotland*

Abstract Intertidal cirripedes are readily available on rocky shores. They are found in large numbers and, in most cases, are easily accessible. They have, therefore, been widely used in marine ecological studies. In their intertidal habitat, during their lifetime, they face physical and biotic pressures which may impede their growth or sometimes destroy them completely. The protective measures developed by barnacles to counteract physical factors such as ice scour and exposure to waves have been reviewed. The removal of cyprids and newly settled barnacles by algal whiplash or bulldozing by grazing organisms has been considered. The smothering of juveniles and adults by overgrowing competitors is a biological interaction that cannot be regarded as predation but is still important in the cirripede habitat. Predation, in the true sense of the word, has been dealt with systematically from hydrozoans through fish and birds to man. Community studies that probably started on European shores have been extended worldwide.

Introduction

The sessile habit of adult cirripedes makes them easy to observe, to count, and to manipulate. The accessibility and abundance of those occurring in the intertidal zone on rocky shores means that they have been used in many studies of marine ecology. Darwin (1851, 1854) was aware of the strong intertidal preference and emersion tolerance of many species but he made no mention of their predators nor what depends on them or controls their distribution. The first community studies considering the causes of densities and distribution were probably made on European shores (see Foster 1987). These studies have since been extended worldwide and have covered reasons for diversity and stability of the communities of which the barnacles are a part. Emphasis has been placed on the role of predators, competitors, and physical factors that affect recruitment and survival (Foster 1987, and references therein).

Predation is one of the biotic pressures directed at barnacles and this may come from a variety of organisms as will be seen later in this review. A brief summary of the predators of *Semibalanus balanoides* is given by Stubbings (1975). There are, however, other causes of barnacle mortality. During its life after the embryo is released from the egg an intertidal barnacle goes through seven planktonic stages—nauplii stages I to VI and a cyprid which is the settling stage—after which metamorphosis occurs and the young barnacle grows and matures. The life span depends on the species, but is also affected by environmental conditions. At any stage in its life cycle predation may have a pronounced effect. Predators may consume the ovary and/or eggs while still protected by the adult shell; the planktonic stages are an important item in the food web. For example, the planktonic larvae of cirripedes are preyed on by fish and filter-

feeding organisms such as the benthic predators, *Mytilus edulis* and the ascidian *Styela gibbsii*. Differences in rate of predation may be owing to defence mechanisms of the larvae such as spines on the larvae or chemical deterrents. The spined larvae of *Pollicipes polymerus*, however, had a low survival rate (Cowden et al. 1984). The anthozoans, *Edwardsia longicornis* and *E. danica* feed on zooplankton, mainly cyprids of *Balanus* sp. (Ellehaug 1978).

On intertidal shores small adults may be bulldozed by grazing organisms, such as limpets or encroached upon by, for example, mussels. Juvenile barnacles can be removed by the whiplash of algal fronds. In some cases faster growing organisms such as bryozoans or sponges, may overgrow and smother the barnacles. There may also be intraspecific competition caused by gregarious settling of cyprids and the density of juveniles which causes hummock formation and subsequent self-destruction. The whole range of biotic pressures acting on sessile, solitary individuals may have forced some species through evolutionary time to seek marginal habitats such as the upper shore where physical and environmental conditions become a hazard.

Incidences covering many of the causes of the destruction and death of barnacles will be reviewed in what follows. It is not intended to consider parasites and diseases that may affect cirripedes. The parasites of *Balanus eburneus* and *Semibalanus balanoides* in New York harbour have been reviewed by Arvy & Nigrelli (1969). These authors also include an account of the parasites and diseases of other cirripedes. Barnacles are a common fouling organism and a great deal of time and effort has been expended on trying to control their effect on marine structures and shipping (see Christie & Dalley 1987, Thompson et al. 1994). Johnson & Strathmann (1989) found that settlement of some barnacle cyprids could be affected on surfaces that had previously been occupied by predators of adult barnacles (see also Standing 1976, Raimondi 1988). Low molecular weight substances that prevented settlement of barnacle cyprids have been detected in homogenates of some octocorals (Standing et al. 1984, Rittschof et al. 1985, Keifer et al. 1986, Gerhart et al. 1988, Sr Vitalina et al. 1991). The muscles of adult barnacles can be affected by toxic material as shown by R. Endean and co-workers (Endean & Henderson 1969, Endean et al. 1969, 1974a,b, Endean & Rifkin 1975). In recent years oil spills have caused devastation of many intertidal rocky communities with the consequent effect on barnacles (Southward & Southward 1978). Prevention of fouling and the effects of oil spills are without the scope of the present review.

When necessary the names of cirripedes have been changed to agree with the revision of balanomorph barnacles by Newman & Ross (1976, 1977). For gastropods, the specific names *Purpura* and *Thais* have been replaced by the more modern name *Nucella*. In the literature the common nudibranch found on British shores has been referred to by various names: *Lamellidoris bilamellata* (Farran 1909, Swennen 1961), *Doris bilamellata* (Barnes & Powell 1954), *Onchidoris fusca* (Barnes & Powell 1951, 1954, Marcus 1961, Miller 1961, Swennen 1961, Hadfield 1963, Thompson 1964, Potts 1970), *Onchidoris bilamellata* (Marcus 1961, Connell 1970, Thompson 1976, Crampton 1977, Todd 1979, 1981, Todd & Doyle 1981, Thompson & Brown 1984, Chia & Koss 1988). Thompson & Brown (1984) quote other synonyms. The name used in this review will be *Onchidoris bilamellata* irrespective of that used by the author(s) of the papers quoted. In general, the latin names used for fishes are those given in the original papers. The few exceptions have been noted.

Protective characteristics

Avoidance of predation

The responses of mobile invertebrates following exposure to or contact with potential predators has been well documented (see Palmer et al. 1982 and references therein). Sessile invertebrates, such as cirripedes, have no such recourse and are limited in the methods of avoidance that can be used. The presence of a hard shell, which increases in thickness, and probably strength, with age and firm adhesion to the substratum, will help to prevent physical removal of a whole animal, for example, by grazing predators. The structure of the shell as well as its thickness may deter predators that drill the shell of their prey in order to gain access to the soft parts.

In order to protect their soft parts barnacles must attempt to keep their opercular valves enclosed, which entails withdrawal of the cirri and so prevents them from feeding. The protective withdrawal and closure reaction of cirripedes in response to shading was first mentioned by Coldstream in 1836 and quoted by Gwilliam (1963). The beginning of an analysis of the various factors involved in the shadow reflex from a neurophysiological viewpoint in two acorn and two stalked barnacles—*Semibalanus cariosus*, *Balanus eburneus*, *Pollicipes polymerus* and *Lepas anatifera*—was started by Gwilliam (1962, 1963, see also later papers by Gwilliam and by Ozawa et al. 1977). Differences in the recordings from the circumoesophageal connectives in the two types of barnacle may have to do with the detailed distribution of motor cells. Adaptation that occurs just prior to the motor output stage would, however, allow the barnacles to ignore repeated shadows of little consequence that must occur constantly during feeding, but still permit them to receive information in the central nervous system about changing light levels in the environment. This has become known as the shading or shadow reflex and can be elicited by approaching prey.

Withdrawal of barnacle cirri may also be caused by physical stimuli or contact with other organisms. The time the cirri are withdrawn depends on the stimulus (Palmer et al. 1982). These authors found that when *Balanus glandula* was contacted by potential predators such as gastropods, *Nucella emarginata* and *N. lamellosa*, and asteroids, such as *Leptasterias hexactis* and *Pycnopodia helianthoides*, the cirri remained withdrawn and the opercular valves closed for a longer time than when contacted by non-predators including algae such as *Fucus distichus*. Such a prolonged response is probably important for a species whose predators depend on chemical cues to determine whether shelled prey, such as barnacles, are alive and worth attacking. By reducing the release of metabolites, prolonged withdrawal and closure probably increases the chance of being overlooked by predators that rely entirely on chemical cues. The shorter closure time with non-predatory species shows that it is not a generalized response, for example to all gastropods, since the herbivorous gastropod *Tegulo pulligo* does not increase closure time.

Palmer et al. (1982) did not try to determine the cues used by barnacles but suspected that they were chemical. One barnacle with a starfish attached did not renew cirral activity when the starfish was removed—three tubefeet remained attached to the opercular valves of the barnacle. The cirri remained withdrawn and the operculum closed for 45 min. Within 8 min of the tubefeet being removed with a scalpel normal beating was resumed. It appeared that the residual chemical stimulants released by the adherent tubefeet inhibited re-opening. Sensory hairs on the occludent edges of the mantle may detect such cues when the barnacle's

operculum is retracted, although the initial withdrawal may have been the result of physical contact with beating cirri (Palmer et al. 1982).

Answers to some of the problems encountered in discussing predation require knowledge of the ways animals choose their diets, select the appropriate foraging technique, foraging location, and the modification of such choices according to the changing circumstances. The optimal foraging theory is devoted to securing such knowledge (Hughes 1980). A sessile organism is at a disadvantage as food has to come to it; it cannot seek out prey as mobile predators do.

Prey can reduce predation pressure either by avoiding encounters with predators or by escaping after a contact has been made. Within these two main categories mobile prey can seek refuge by hiding in crevices, under boulders or seaweed (Nelson & Vance 1979, Sih 1987). Again sessile prey such as barnacles are at a disadvantage; they cannot resort to these methods. Barnacles react to shading by approaching predators by tightly closing their opercular valves; they can keep the operculum closed for extended periods if necessary. The form of the shell may be influenced by predation. The conical form of *Chthamalus anisopoma*, which is restricted to the Gulf of California, may become bent so that the rim of the operculum is orientated perpendicular to the substratum rather than parallel to it. This form has been induced as a defence against predation by *Acanthina angelica* which normally preys on barnacles by covering them with its body and penetrating the operculum (Lively 1986, Levinton 1995). A similar defence mechanism may occur in other *Chthamalus* sp. (M.T. Burrows, pers. comm.).

Drilling gastropods are common predators of intertidal barnacles and an important cause of mortality. Features of the barnacle shell may, therefore, have been selected in order to reduce vulnerability to drilling. Such features may be channels within the wall plates, strong external sculpturing of the wall plates and a reduction in their number (Palmer 1982, 1983). The tubular wall plates of the Balanidae and Tetraclitidae may have evolved because channels increase the thickness of the shell and the distance to be drilled but not the amount of material to be removed. The depth to which a gastropod can drill may be limited by the distance to which it can extend its accessory boring organ (Palmer 1982). Stanley & Newman (1980), however, argue that porous wall plates primarily permit more rapid growth—less energy expended producing shell material—and therefore an increased ability to combat competition. For most intertidal barnacles, however, mortality as a result of predation is significantly greater than that due to competition (Connell 1961a,b, 1970). Thus, morphological adaptations against predation become more important. Porous wall plates favour rapid growth of juveniles which is an advantage in order to reach a size-refuge from predation.

Barnacles are vulnerable at the margins between the wall plates and external sculpturing of the plates may make the sutures more difficult to locate. Gastropods, for which there are sufficient data, recognize sutures more easily on the smooth shells of *Balanus glandula* than on the heavily “thatched” shells of *Semibalanus cariosus* (Palmer 1982). Sutures are the places where barnacle shells are most likely to fail on impact. Reduction in the number of wall plates reduces the number of sutures and so the vulnerability to crushing by predators is reduced (Barnes et al. 1970).

Strength of shells

Many papers have been published since Darwin (1854) on the formation and growth of shells from as early as Bahls (1903) to Bourget’s (1987) review of the composition, structure,

and growth of barnacle shells, and even later (Karande & Udhayakumar 1989). The shell consists of irregularly deposited calcite crystals in an organic matrix with aragonite in the calcareous base of some warm-water species. The amount of organic matter and minor chemical elements varies according to species and the environmental conditions. One of the main functions of the shell is to combat the physical forces exerted on it and to protect the soft parts of the body from adverse conditions including predation (see Bourget 1987 and references therein).

The construction of the shell may take one of several forms according to the species (Barnes et al. 1970). These authors developed an apparatus which was essentially a small guillotine to test the resistance of shells of various species to crushing of the wall plates. The shells of nine species of common barnacles were tested and Barnes et al. (1970) have tabulated the size range, shell structure and general distribution of these species. They also illustrated the structure of the junctions between the wall plates as seen in polished cross sections of the shells. Crisp (1958) from his field experience rated the resistance to mechanical stress of *Chthamalus stellatus* (probably *C. montagui*) and *Balanus perforatus* as equal and better than *B. crenatus* and *B. improvisus* which he considered better than *Semibalanus balanoides*; *Elminius modestus* was rated as the most fragile. Barnes et al. (1970) agreed that "large" *Chthamalus stellatus* (probably *C. montagui*) have relatively the strongest shells. Allowing for size differences and comparing those of moderate and similar size they found little difference between *Balanus perforatus*, *B. crenatus*, and *Semibalanus balanoides* while *Balanus improvisus* and *Elminius modestus* were similar to each other and less resistant than the others.

Murdock & Currey (1978) tested the strength of a shell when loaded on the top, that is on the rim of the opercular opening, using an Instron table model testing machine. They used *Semibalanus balanoides* and *Balanus balanus* and found that shells of the latter were 3—13 times as strong as shells of the former depending on which variables were considered. They decided that the difference in strength of these shells was probably due to the general architecture of the shells rather than the microstructure or the properties of the shell material.

Compression and tension experiments have been done by Gubbay (1983) on the shells of several British barnacles while Karande & Udhayakumar (1989) have tested the compressive and adhesive strength of seven barnacles from Bombay shores. These last authors and Gubbay (1983) emphasize the need for some uniform approach in obtaining and comparing data on shell strength. Even the habitat from which animals of the same species are taken can affect the result, as in the case of *Tesseropora rosea* (Otway & Anderson 1985).

Barnes et al. (1970) and Murdock & Currey (1978) related shell strength to the degree of wave action experienced by the barnacles tested. Murdock & Currey (1978) also considered possible adaptations in shell design to reduce risk of predation. Palmer (1982) discussed the possibility of a connection between the number of wall plates and the degree of predation caused by boring gastropods. In testing the compressive and adhesive strengths of barnacles Gubbay (1983) again used an Instron table model testing machine. The species tested were *Balanus balanus*, *B. perforatus*, *B. crenatus*, *Elminius modestus*, *Chthamalus montagui*, *Semibalanus balanoides*, and *Verruca stroemia*. The first two species were rated the strongest in the compression tests, the next four were intermediate, and the last, owing to the asymmetry of the shell, was the weakest. It is of interest that *Semibalanus balanoides* is about three times stronger when crowded than when solitary and also slightly stronger than solitary *Balanus balanus*.

Newman et al. (1967) considered that calcification of the base of a barnacle led to better adhesion but the tension experiments carried out by Gubbay (1983) did not confirm this.

Gubbay (1983) found greater tenacity in animals with a membranous base. When pulling up species with a membranous base the membrane gradually stretched before the final sudden detachment. No such intermediate stage was seen when testing animals with a calcareous base; they remained firmly attached until suddenly detached at the failure point. All the species tested were much weaker under tension than under compression. This is a vulnerable point exploited by some barnacle predators which rasp the shells and pull them off a rocky surface.

The results of the tension experiments showed a reversal of the order of strength indicated above. Under tension *B. balanus* and *B. crenatus* were the weakest with *Elminius modestus* and *Semibalanus balanoides* showing a greater adhesion to the substratum. Even so Luckens (1976) records the dislodgement of *Elminius plicatus* in New Zealand by wave action. Barnes et al. (1970) and Murdock & Currey (1978) record *Semibalanus balanoides* as having less shell strength than *Balanus balanus* although the former species experiences much greater wave action in its intertidal habitat. It also usually grows in dense aggregations on the rock surface and this increases its resistance to compression as shown by Gubbay's (1983) experiments. The tension experiments show that *Semibalanus balanoides* is more firmly attached to the rocky surface. Denny (1982) showed that in the pressure changes associated with breaking waves there are significant negative pressures or tension transients. *S. balanoides* is well suited to cope with these conditions.

Shell strength and resistance to erosion are thought to depend on the layering of the shell and the microcrystalline arrangements. The spread of cracks may be reduced by the inclusion of organic matter in the crystalline matrix. Resistance to wave shock is probably increased when the organic matter is in fibres or sheets separated by crystalline layers as in chthamalids. Hollow canals in some Balanoidea or secondarily filled canals such as in *Balanus perforatus* and *Tetraclita*, together with the sheets of organic matter may reduce shell erosion and boring by predators (Bourget 1987).

Physical factors

The significance of physical environmental factors on the distribution of littoral organisms and their predators on rocky intertidal shores has been reviewed and discussed on several occasions (see Underwood 1985 and references therein). For example, *Nucella lapillus*, a predator of the barnacle *Semibalanus balanoides* is known to shelter in crevices during gales and periods of cold weather (Connell 1961a). Menge (1978a,b) studied the degree of exposure to wave action and desiccation on the intensity of predation by *Nucella lapillus* on barnacles on the eastern coast of the USA. When comparing two sites near Bass Point in Australia—one protected and the other exposed—Moran (1980) found natural physical disturbance to be the major factor in structuring the community of 29 species. Predation was of less importance than physical stress on the exposed site and had virtually no effect on species distribution on the protected site.

Prolonged aerial exposure can cause die-back of *Chthamalus* spp. on Santa Cruz Island (Seapy & Littler 1982). Heavy rainfall and inundation by sediment as a consequence is equally detrimental to *Tetraclita squamosa rubescens* (Seapy & Littler 1982). A newly established group of *Policipes polymerus*, the largest measuring 6 mm rostrum-carinal length, was seen in a rock fissure; two days later it had been smothered by beach sand (Hoffman 1989). On the shores of New Hampshire, USA the lower limit of mussels, *Mytilus edulis* and barnacles, *Semibalanus balanoides* is approximately the height of the surrounding sand

in summer. Movement and abrasion by sand can erode and remove the barnacles and produce bare patches (Daly & Mathieson 1977, see also Lewis 1964). *Chthamalus stellatus stellatus* and *Balanus amphitrite communis* are found in the Gulf of Mannar and Palk Bay near Mandapam Camp. The barnacles are numerous on the sides of jetties and pillars but those growing on flat boulders become smothered and killed by the movement of the sandy substratum (Rao & Sundaram 1972–4). Extreme cold and ice conditions as well as the pounding by waves can also take their toll on intertidal shores.

Ice scour

Ice forms close to the shores in such places as Cumberland Sound and Frobisher Bay on Baffin Island and may be up to seven feet thick or more if there is ice movement during the winter. In places, the entire shore may be completely covered by ice if the thickness of the sea ice is greater than the tidal amplitude. When the amplitude is greater than the thickness of the sea ice only the upper part of the shore becomes frozen and an ice foot is formed at the water's edge (Ellis 1955, Ellis & Wilce 1961). At low tide during the winter, ice floating on the sea close to the shore abrades the exposed surface of the shore below the ice foot (Fig. 1).



Figure 1 Disko, Greenland; showing the frozen shore, ice foot, sea ice and floes in May. (Courtesy of Dr G.Høpner Petersen).

In these conditions animals on the upper shore are killed by freezing and ice cover and those on the lower shore below the ice foot are abraded by the sea ice. *Semibalanus balanoides* which occurs on Arctic shores such as in Cumberland Sound and Frobisher Bay on Baffin Island, the Canadian Arctic Archipelago, Labrador, and parts of Greenland is affected by such ice conditions (Ellis 1955, Ellis & Wilce 1961). Not all the barnacles are, however, removed from below the ice foot. Høpner Petersen (1962) does not think that ice floes could push barnacles off the rocks as the sea ice is soft during the thaw and could not easily exert the necessary pressure. Barnacles growing in crevices and on the sides of boulders probably survive and become the basis of future populations. The rocky shores in the Halifax region of Nova Scotia are not usually exposed to ice scour but abnormal conditions in 1987 demonstrated how severe such scouring can be in clearing organisms from the shore (McCook & Chapman 1997).

On the rocky shores of the Gulf of St Lawrence, Canada, ice occurs regularly and the dominant perennial organisms are found almost exclusively in cracks or crevices or at the base of boulders (Bergeron & Bourget 1986, Gosselin & Bourget 1989). Ice scour kills most of the barnacles settling outside crevices but since only a small proportion settle on exposed surfaces the annual mortality due to ice scouring is less than would be expected. On the New England coast ice mortality is higher at similar levels on the shore as these shores offer less protection by way of crevices.

Effect of waves

Intertidal organisms are repeatedly exposed to the forces of incoming and breaking waves (Figs 2, 3) and such forces are important to the structure of exposed communities (Dayton 1971, Denny 1985).

A telemetry system for measuring the direction and magnitude of forces exerted on intertidal organisms by breaking waves has been devised by Denny (1982). He used the system to measure wave force on epoxy replicas of the barnacle *Semibalanus cariosus*. An incoming wave exerts the greatest pressure directed into the rocky surface and shoreward but during the backwash the barnacle experiences both lift (a force normal to and away from the rock) and a drag force parallel to the rock.

The total force exerted on an intertidal organism by breaking waves and the backwash (Figs 2, 3) depends on the velocity of the water and its acceleration. The force due to velocity (drag and lift) increases in proportion to the animal's structural strength as the animal increases in size (Denny et al. 1985). This then cannot act as a mechanical limitation to size. Force due to the water's acceleration increases faster than the animal's structural strength as the animal grows. This, therefore, is a potential mechanical limit to size. Denny et al. (1985) produced a model that predicted the probability that an organism would be destroyed by wave force. They also measured the shear strength of the barnacles *Semibalanus cariosus*, *Balanus glandula* and *B. nubilus* giving values of $3.29 \times 10^5 \text{ N m}^{-2}$, $4.17 \times 10^5 \text{ N m}^{-2}$ and $3.41 \times 10^5 \text{ N m}^{-2}$, respectively. These values are similar to those given by Yule & Walker (1984a) for *Semibalanus balanoides*, who found that the force required to remove small animals (up to 14 days after settlement) was $1.672 \times 10^5 \text{ N m}^{-2}$, while $9.252 \times 10^5 \text{ N m}^{-2}$ was required to remove large animals (4–19 months after settlement). Denny et al. (1985) concluded that the size of these barnacles is not limited by the mechanical factors being considered. Etter (1996), however, suggests that slower

THE MORTALITY OF INTERTIDAL CIRRIPEDES



Figure 2 Maine, USA; force of incoming waves.



Figure 3 Maine, USA; showing backward surge after breaking waves in a narrow channel causing drag on the organisms attached to the vertical walls.

growth rates of *Nucella lapillus* when foraging time is restricted are consistent with the idea that wave action on exposed coasts depresses growth by limiting foraging time or efficiency.

When *Chthamalus fragilis* was removed from marsh grass and allowed to re-attach to polystyrene, Dougherty (1990) found the strength of adhesion averaged $1.05 \times 10^5 \text{ N m}^{-2}$ with a range of 0.14×10^5 to $2.79 \times 10^5 \text{ N m}^{-2}$. These results are comparable with those of 1.47×10^5 to $3.81 \times 10^5 \text{ N m}^{-2}$ found by Yule & Crisp (1983) for exploring cyprids of *Semibalanus balanoides* on slate. Yule & Walker (1984b, 1987) give 0.6×10^5 to $3.0 \times 10^5 \text{ N m}^{-2}$ for cyprids on slate, glass, or plastic. For juvenile barnacles Yule & Walker (1984a) give $1.7 \times 10^5 \text{ N m}^{-2}$ and for adults 0.8–20.8 N m^{-2} on various substrata.

The movement of seaweeds especially the whiplash of algal fronds caused by waves can cause early mortality of newly settled barnacles (Grant 1977). Furoid whiplash can inhibit settlement of *S. balanoides* on New England shores (Menge 1976).

A major disturbance on intertidal boulder shores can be caused by waves (Shanks & Wright 1986), particularly those generated by storms. Small boulders are more frequently disturbed than larger ones and any barnacles on the smaller boulders may be damaged or crushed by the rolling of the boulders against each other. Fewer animals survive on small boulders than on larger ones (Sousa 1979). *Elminius modestus* has not replaced *Semibalanus balanoides* or *Chthamalus* sp. on wave-beaten shores and Crisp (1958) has suggested that this may be because *Elminius* is more fragile than the other species and suffers from the crashing waves or pounding by pebbles.

Wave-borne debris can be a hazard to intertidal organisms on exposed shores (Connell 1970, Dayton 1971, Shanks & Wright 1986). Drift logs accumulate on the outer shores of Washington and Vancouver Island as well as in many areas around the San Juan Islands. Battering by these logs destroys the intertidal organisms (Dayton 1971). Pentcheff (1991) compared the resistance of *Balanus glandula* to crushing by wave-borne debris at two places on San Juan Island. At one site the opercular valves were sunk below the upper rim of the wall plates whereas at the second site the opercular valves protruded above the wall plates. When pressure is applied in the second case force is exerted on the body of the animal and is transmitted as a hydrostatic pressure which tends to separate the wall plates. In the first case the rim of the wall plates is the first part of the shell to feel the force and the pressure of the impact is transmitted to the substratum. A chipped rim of a wall plate is not likely to expose the soft parts of the animal. Gubbay (1983) found that crowding of animals, in his case *Semibalanus balanoides*, reduced damage due to crushing. Similarly Shanks & Wright (1986) found that a "continuous sheet" of *Chthamalus fissus* was more resistant to crushing than solitary animals.

The self-destruction of crowded barnacles which form clumps of elongated shells that are fragile and not very securely adhering to the substratum can be encouraged by wave action. The break-up of such clumps is well known, and the mortality in such cases can be up to 90%, see for example, Barnes & Powell (1950), Connell (1959b) and Potts (1970) for *Semibalanus balanoides* in the UK and Woods Hole, USA; Bertness (1989) and Bertness et al. (1991) for *S. balanoides* at Rhode Island, USA; Connell (1959b) for *Chthamalus stellatus* in southwest Ireland and *Balanus glandula* at Santa Barbara and on San Juan Island, USA; Shelford (1930) for *Semibalanus cariosus* in Puget Sound after 1–2 yr; Bokenham (1938) and Branch (1976) for *Megabalanus algicola*, *Chthamalus dentatus* and *Tetraclita serrata* in South Africa; as well as Grant (1977) and Farrell (1989). Once break-up of the clumps begins wave action rapidly removes the shell remains.

Biological interactions (other than predation)

There are occasions when the mortality of barnacles is caused by interactions with other intertidal organisms that cannot be regarded as true predation in the recognized sense of the word. In such cases the barnacles may be forcibly removed or actually smothered by other organisms. The barnacles do not, however, form part of the diet of those offending organisms.

Prevention of settlement and/or removal by algae

In experimental work on the settling of cyprids and growth of juvenile barnacles, cages or screens are often used. Such artificial barriers may reduce the flow of water and current speeds and this can affect settlement. This was specifically mentioned in experiments with *Elminius modestus* (Schmidt & Warner 1984, see also Edwards et al. 1982).

The presence of a fucoid canopy on a rocky shore can affect the establishment of a *Semibalanus balanoides* community (Lewis 1964). Hawkins (1983) discusses the detrimental and beneficial effects of such fucoid canopies on the settlement and survival of young barnacles on the rocky shores of the Isle of Man. The reduction of desiccation stress under canopies is an advantage to newly metamorphosed *S. balanoides* but, as noted above, sweeping of fucoids in water can remove settling cyprids. On exposed shores fucoid sweeping can be a disadvantage at all levels (Lewis 1964) but on sheltered shores inhibition is only obvious in the low *Fucus serratus* zone where water movement is likely to be greatest. On high sheltered shores settlement of cyprids is still reduced especially by *F. vesiculosus* but the effect is less pronounced than enhancement of post-settlement survival (Hawkins 1983). Hartnoll & Hawkins (1985) also found in the Isle of Man that clumps of *F. vesiculosus* could dislodge up to 80% of settling *Semibalanus balanoides* cyprids.

On the Olympic Peninsula, USA, on shores exposed to the Pacific Ocean, the barnacles *S. cariosus*, *Chthamalus dalli* and *Pollicipes polymerus* occur in scattered patches while *Balanus glandula* dominates the upper levels of the shore. Here Dayton (1971) did not find significant differences in barnacle settlement except in areas of high desiccation where barnacle recruitment and survival was better under *Fucus distichus* than in cleared areas. Interference due to the seaweed was probably not as important as on European shores because *F. distichus* is a smaller plant than *F. vesiculosus* and does not form such heavy sweeping canopies. In South Africa, however, seaweed sweeping can affect *Chthamalus dentatus* and *Tetraclita serrata* (Bokenham 1938).

The reactions between barnacles, algae, and limpets are often complex and difficult to separate (Dayton 1971, Connell 1972, Choat 1977, Hawkins 1981, 1983, Hawkins & Hartnoll 1982, Underwood et al. 1983, Branch 1984, Hartnoll & Hawkins 1985). On the mid-intertidal rocky shore at Pelican Point, northwest of Puerto Peñasco, Mexico, in the Gulf of California, the main species are the barnacle *Chthamalus anisopoma*, the limpet *Collisella strongiana* and the brown alga, *Ralfsia*. Dungan (1986) found that grazing by the limpet limited algal abundance and indirectly increased the abundance of *Chthamalus anisopoma*. He did not detect any direct effect of *Collisella* on *Chthamalus* (Dungan 1986).

At levels of intermediate wave exposure on the shores of New South Wales the main species found were the barnacle *Tessieropora rosea*, the limpets *Cellana tramoserica* and *Patelloida latistrigata* and a predatory whelk, *Morula marginalba* (Underwood et al. 1983). When the barnacles become too big for the whelk it eats the *Patelloida latistrigata* thereby allowing growth of algae to the detriment of the barnacles.

On New England shores the common herbivore, *Littorina littorea*, grazes on *Enteromorpha* so making areas available to barnacle settlement. In areas that are not grazed barnacle settlement is inhibited. *Littorina* are also known physically to remove juvenile barnacles (Dexter 1947, Petraitis 1983, 1987). Mussels are also affected by this intense herbivory. *Littorina* indirectly depresses the establishment of mussels by reducing the density of barnacles which in turn affects mussel recruitment. Cyprid larvae have been found in the faeces of *L. littorea*; it has been suggested that the *Littorina* inadvertently ingest barnacle spat and cyprids while grazing (Petraitis 1987). Hayes (1929) found moults of cirri of *Semibalanus balanoides* in the oesophagus and stomach of *Littorina*. The association between *Chthamalus stellatus* and *C. depressus* is also influenced by *Littorina* (Bosch & Moreno 1986).

Secretions from seaweeds can be harmful to barnacle larvae and adults in confined areas such as tide pools. Sea water appears to offer ideal conditions for algal tannins; the alkaline pH favours tannin extraction from algal tissues. *Semibalanus balanoides* is suppressed in pools dominated by *Ralfsia verrucosa* (Conover & Sieburth 1966). *Semibalanus balanoides* is also affected by *Ulva lactuca*. If in contact with the barnacle *Ulva* can cause smothering but mortality also occurred when the *Ulva* and barnacles were not in contact suggesting that the alga secretes a toxic substance (Magre 1974).

Smothering and overgrowing

Farrell (1988) found overgrowth by algae to be a major source of mortality of *Chthamalus dalli* on the Oregon coast of the USA in areas where limpets were excluded or had been removed. *Balanus glandula* did not, however, seem to be harmed by such overgrowth. On Australian shores, Denley & Underwood (1979) found that algal overgrowth killed the barnacles *Tesseropora rosea* and *Tetraclitella purpurascens*, but Jernakoff (1985b) showed that adult *Tesseropora rosea* could withstand overgrowth for as long as a year probably because of the small limpet, *Patelloida latistrigata* which could graze between the barnacles and so removed the algae.

On New South Wales rocky shores *Gelidium pusillum* may occasionally overgrow *Tesseropora rosea* (Jernakoff 1983, 1985b, 1986, Jernakoff & Fairweather 1985). In some cases barnacles are not completely overgrown; the opercular valves are not covered. In such cases whelks, *Morula marginalba* and *Nucella orbata* are attracted to the barnacles. Jernakoff (1985b) found that overgrowth of *Tesseropora rosea* by ulvoid algae did not cause more mortality of the barnacles than was seen in the control areas. These overgrown barnacles may survive for long periods without feeding but with the seasonal decline of the algal cover feeding is resumed. While the perennial *Gelidium pusillum* and associated silt are detrimental to juvenile barnacles, adults may be able to survive.

Algae settling later than the barnacles *Chamaesipho brunnea*, *C. columna*, *Elminius plicatus* and *Balanus trigonus* rapidly overgrow the barnacles on New Zealand shores (Luckens 1970a). At higher levels *Tetraclitella purpurascens* can survive for longer periods as can *Chamaesipho brunnea* at the highest levels. The seaweeds, *Ulva* species, *Petalonia fascia*, and *Colpomenia sinuosa* grow between the barnacles and the resultant silting and overgrowing causes some barnacles to die (Luckens 1970a). *Chamaesipho columna* can be overgrown by *Xenotrobus pulex* at low levels (Luckens 1976).

At Port Philip Bay, Victoria, Australia, Russ (1982) found a basic hierarchy in the overgrowing by the taxonomic groups: ascidians = sponges > bryozoans > barnacles, and special mention was made of *Elminius modestus* of <15 mm high being overgrown by

colonial ascidians, sponges, and encrusting bryozoans. The early settling and fast growth rate of *Elminius modestus* on British shores seems to cause much of the initial mortality of *Chthamalus montagui* whereas encroaching, older *Semibalanus balanoides* causes later mortality of both *Elminius* and *Chthamalus* (Hui 1983). At Leigh in New Zealand, Luckens (1975b) found dense clumps of elongated and fragile *Epopella plicata* overgrowing and smothering *Chamaesipho columna*; eventually the *Epopella* clumps break away. Wagh & Bal (1970a) found *Megabalanus tintinnabulum* associated with several algal species and sponges covering the shells of *Chirona (Striatobalanus) amaryllis*. Coelenterates were also found in dense colonies on the shells of both these barnacles on Bombay shores.

Hoshiai (1958, 1959, 1960) found that *Balanus albicostatus albicostatus* and *Chthamalus challengerii* could be covered by *Mytilus edulis* and, lower on the shore, by *Crassostrea gigas*. On plates exposed at various depths at Shimoda, Pacific coast of Japan, the earliest colonizers were the barnacle *Balanus trigonus* and the spirorbid *Dexiospira foraminosus* followed by the ascidian *Diplosoma mitsuurii* and *Crassostrea nippona*. These early colonists were overgrown by colonial ascidians, bryozoans, and sponges. On deeper plates *Megabalanus volcano*, *M. rosa*, and *Balanus trigonus* increased coverage in 37 months after initial immersion but *Crassostrea nippona* was regarded as a persistent climax community in succession because it could easily settle on the shells of the barnacles. Hoshiai (1965) found *Chthamalus challengerii* overgrown by Melobesioideae sp. and smothered and eventually killed by *Chondria* sp. and *Dictyota* sp.

At Helgoland in the German Bight, *Balanus crenatus* is an early settler in the spring followed by *Elminius modestus*, *Balanus improvisus* and colonial ascidians, *Botryllus schlosseri*. This last species tends to overgrow the barnacle populations. Mussels also soon cover the barnacles as do hydrozoans (*Laomedea* spp). Later in the season ascidians, *Ciona intestinalis* and *Asciidiella aspera* begin to dominate the barnacles (Harms & Anger 1983). *Elminius modestus* can, under some circumstances overgrow *Semibalanus balanoides* causing the latter to become silted up and smothered (Crisp 1960).

The bryozoan, *Schizoporella unicornis*, is abundant on pier piles at Beaufort, North Carolina, and grows over barnacles smothering them so that they can no longer extend their cirri and feed. The sheets of *Schizoporella* are raised in humps in some places and under these are the remains of dead barnacles. There is a strong smell of hydrogen sulphide from decaying flesh when the barnacles are exposed confirming that they had been smothered and not eaten (see, e.g. McDougall 1943, Cory 1967, Branscomb 1976).

Mytilus edulis determines the lower limit of *Semibalanus balanoides* both by overgrowing and smothering any already settled barnacles and occupying primary space which then becomes unavailable to barnacles (Peterson 1979). On the east coast of America barnacles covered by mussels may survive for varying periods but after two months of complete coverage most were dead (Menge & Sutherland 1976). In Delaware Bay there is a heavy settlement of *Balanus improvisus* in the first year on clear areas but mussels, *Mytilus edulis*, eventually take over and in the second year the barnacles are rare (Dean & Hurd 1980). In the Gulf of St Lawrence, the greater proportion of *Semibalanus balanoides* cyprids (97%) settle in crevices. They not only avoid exposed surfaces but also show reduced settlement in the presence of mussels (Bergeron & Bourget 1986).

In Chile, the highest chthamaloid is *Jehlius cirratus*, up to 18 mm basal diameter. This outcompetes *Chthamalus scabrosus* where they overlap—*Jehlius* overgrows *Chthamalus* 100% of the time ($n=52$). *Jehlius* can also overgrow *Balanus laevis* ($n=23$). Although it was not actually observed there is no reason why *Jehlius* should not also overgrow *Notobalanus flosculus* (Paine 1981).

In the Gulf of California at Pelican Point, near Puerto Peñasco, *Chthamalus anisopoma* reaches a maximum diameter of 5–7 mm, matures in about six weeks and reproduces throughout the year with main settlement in summer. *Tetraclita stalactifera confinis* reaches sexual maturity in its second year, and reproduces during late summer with one period of settlement between August and October. Dungan (1985) and Malusa (1986) found that crowding by *Chthamalus* greatly reduced the survival of the *Tetraclita*. Only four out of 92 *Tetraclita* survived compared with 45 out of 90 when *Chthamalus* were removed. The *Tetraclita* were surrounded and frequently undercut or overgrown by *Chthamalus* (Dungan 1985).

At Millport, Scotland, *Semibalanus balanoides* may smother or undercut *Chthamalus stellatus* (probably also *C. montagui*) in seasons when the growth of *Semibalanus* is most rapid (Connell 1959a, 1961b). At Beaufort, the density of young barnacle populations is so great that they invariably smother each other and many dead shells are found under living juveniles (McDougall 1943).

Chthamalus spp. have a thick shell that may protect them from predation by boring but they may be overgrown by *Arthropropyrenia balanophila* or “hidden under a thicker tarry lichen (unidentified)” (Cranwell & Moore 1938). These authors also found *Megabalanus tintinnabulum* var. *concinus* overgrown by sertularians and polyzoans.

In 1963 Paine (1974) observed a horizontal bare patch in what had been a continuous mussel bed on the Olympic Peninsula, Washington. This was adjacent to an area where *Pisaster ochraceus* had been removed. *Pollicipes polymerus* settled in spring 1964. These were counted and measured occasionally until they disappeared in June–August 1970. When they disappeared they were smaller than the largest on adjacent areas, so their demise was not due to natural old age. During the observational period the patch was invaded by adult mussels, *Mytilus californianus*, up to 8 cm in shell length. This crowding constricted and killed organisms with a flexible stalk such as *Pollicipes polymerus* and within six years the solid mussel cover was restored. When the rocky surface is almost vertical the mussel cannot exist and communities of *P. polymerus* thrive.

Megabalanus stultus is a barnacle inhabiting the hydrocoral *Millepora complanata* in Barbados. Of the *Millepora* examined, 9.2% were colonized with a mean of 2.58 barnacles per colony. Adult barnacles were contiguously distributed. There was a positive correlation between the abundance of millepore colonies on reefs and the frequency of colonies bearing barnacles. This was an indication that barnacle larvae were attracted to settlement sites in proportion to the density of host millepore colonies. These newly metamorphosed barnacles grew at a rate of about 1.1 mm month⁻¹ and reached about 19 mm in 18 months. Recruitment was low compared with densities of recruits of shore barnacles. Of the annual recruits, 74% were found on the current year’s growth. Settlement mortality was lowest in this region, where the density of millepore predatory zooids was lowest, but higher on the second year millepore growth. Dead barnacles became overgrown by the hydrocoral. The mortality of those barnacles surviving to adulthood was probably owing to old age (Lewis 1992).

Bulldozing and grazing

The physical removal of barnacles as a result of bulldozing by larger animals or the disturbance caused by grazing herbivores is not predation in the usual meaning of the word but it is important when considering the mortality of barnacles. The association of barnacles, limpets and algae is complex (see, for example, Dayton 1971, Branch 1984). It is difficult

to separate the physical interference from what is sometimes true predation. The problem has, therefore, been considered in the relevant sections that follow on predation.

Predation

Coelenterata, Anthozoa

Waste pellets of 50 large and about 150 small sea anemones, *Metridium senile*, were examined and found to contain, among other things, barnacle nauplii and cyprids. Pellets from small *Metridium* contained 5% barnacle nauplii and they were frequently present in those from larger *Metridium*. Barnacle cyprids formed 10% and 15% of the pellets from small and large *Metridium*, respectively (Purcell 1977).

Ctenophora, Tentaculata

The ctenophore, *Mnemiopsis leidyi*, in the York River estuary, Virginia, USA was found to feed on barnacle larvae among other plankton. Food items found in stomodaea of *M. leidyi* included bivalve larvae, barnacle nauplii and annelid larvae in many more instances than would have been expected from their relative abundance in plankton samples. Of 2494 stomodaea containing food about 16% contained barnacle nauplii, the longest of which was 0.8 mm (Burrell & Van Engel 1976).

Platyhelminthes, Turbellaria

A flatworm, superficially similar to *Stylochus zanzibaricus* suspected by Skerman (1960) to be a predator of barnacles, was found by Luckens (1970b) at Asamushi, Japan. At low tide the worm was found inside dead barnacle shells. On the shore the worm was not seen feeding on *Chthamalus challengerii* but a rock well-covered with the barnacles if placed where *Chthamalus* were scarce or absent would attract worms from the surrounding areas. Such a rock 20 cm in diameter attracted 40 or more flatworms in 1–2 days. In the laboratory the worms were never seen to feed during the day; they spent the time in empty barnacle shells. At night, however, suitable food disappeared. When fed on *C. challengerii* the worms turned dark brown to black owing to dark masses of ingested food but gradually became paler until after a week they appeared exactly like starved ones. The barnacles that had been eaten were pale and easily distinguished from those that had died for other reasons, except in the smallest and youngest barnacles. At night, a worm extended over the top of a barnacle immediately moved away when illuminated to reveal an open eaten barnacle. No damage to the barnacle plates was seen in this or any of the other eaten barnacles. Worms ate on an average, two barnacles a night. Skerman (1960) found higher proportions of *Balanus amphitrite cirratus* and *B. trigonus* were affected by *Stylochus* than the smaller *Elminius modestus* possibly owing to the size of the opercular opening and the size of the flatworm. He also only found these flatworms during the summer as did Luckens (1970b) at Asamushi. Whenever the worm was present it could eat a large number of barnacles and was not forced to retreat

downshore (as did other predators) in summer as long as any small moist barnacle shell was available for shelter.

Two flatworms, *Stylochus tripartitus* and *Notoplana inquieta* are important predators of *Balanus pacificus* (Hurley 1975, 1976). They enter the barnacles through the opercular valves and digest the soft parts while inside the barnacle shell. Both flatworms were found inside partially ingested barnacles in the field and *Stylochus* readily eats them in the laboratory. Hurley (1975) found that the peaks of flatworm abundance coincided with peaks of barnacle mortality. In the field *Stylochus* consumed 0.015 g barnacle tissue g of flatworm tissue⁻¹ day⁻¹ and in the laboratory five separate worms consumed 0.033 g, 0.086 g, 0.081 g, 0.040 g, and 0.032 g of barnacle tissue g of flatworm tissue⁻¹ day⁻¹. These calculations are based on an "average" flatworm of approximate length 0.4 cm and weight 4.6 mg (Hurley 1975).

Hurley (1976) examined the behaviour of *S. tripartitus* of about 1 cm length and a *Balanus pacificus* of about 2 cm basal diameter in running sea water with time lapse photography and a dissecting microscope. The flatworm first climbed up the side of the barnacle to the opercular valves and inserted its pharynx between the barnacle wall and the opercular valve near the opercular muscles. The flatworm then crawled backwards along the side of the barnacle and remained in the angle between the substratum and the barnacle. The pharynx stayed in place over the edge of the shell wall. This position was retained for several hours; the barnacle made several unsuccessful attempts to remove the pharynx. During this time the barnacle became weaker, the opercular valves gaped and the cirri extended and beat only erratically. When the opercular valves could no longer close the flatworm climbed back up the side of the barnacle and entered it through the gap between the opercular valves. The flatworm then fed on the barnacle and remained in the shell of the dead barnacle until it began to feed on another barnacle. This behaviour is similar to that reported by Skerman (1960) for *Stylochus zanzibaricus* and by Branscomb (1976) for *S. ellipticus* preying on *Balanus improvisus*. Branscomb (1976), however, noticed that the pharynx may be inserted either between the opercular valves or between one of the valves and one of the wall plates. Fluids were also observed being pumped into the barnacle and tissue being pumped out in turn. Usually a second fold of the pharynx was then inserted into the barnacle. Within 90 min the barnacle gaped and the worm entered.

In the Patuxent River estuary heavy settlements of the barnacles *B. improvisus* and *B. eburneus* do not persist for the whole season. The high mortality may be caused by predation and competition for space. The flatworm *Stylochus ellipticus* is commonly found in and around the shells of recently dead barnacles; often up to 90% mortality is noted (Cory 1967). A similar mortality associated with *Eustylochus meridionalis* was noticed at Beaufort by McDougall (1943). This flatworm readily killed and ate barnacles (Pearse & Wharton 1938). In Chesapeake Bay the initial settlement of *Balanus* sp. was in early May and the settling of *Stylochus ellipticus* also began in the first week of May. Christensen (1973) found a predation rate of 1.34 barnacles killed worm⁻¹ week⁻¹. These worms had never eaten oysters, their other main prey. Prey selection suggested "ingestive conditioning" (see also Landers & Rhodes 1970). Known barnacle-eating worms appeared to have a preference for barnacles but known oyster-eating worms did not establish the same preference and fed on barnacles when oysters were not available. Only rarely did oyster-eating worms feed on barnacles when oysters were present. Some worms can become conditioned to the lack of oysters but not to the lack of barnacles; barnacles appear to be the preferred prey.

Development patterns on plain and mimic panels were similar with respect to species composition (Dean 1981) near Delaware Bay. *Balanus improvisus* and *Mytilus edulis* were

the first to colonize. There followed high mortality of barnacles caused by overgrowth by mussels and occasionally by *Stylochus ellipticus*.

Flat worms and the nemertean worm *Emplectonema* can be major barnacle predators according to Paine (1981). Flatworms, *Notoplana australis*, may prey on *Tesseropora rosea* (Fairweather 1987). Hoffman (1989) found *Emplectonema gracile* on at least six occasions foraging among juvenile *Pollicipes polymerus* (1 mm rostrum-carinal length). The worms were often wrapped round the peduncles many of which had lost their capitulum (see also Bernard 1988, Barnes 1996).

Annelida, Polychaeta

The polychaete *Galeolaria caespitosa* will overgrow and kill newly settled spat of *Tesseropora rosea* and *Tetraclitella purpurascens* (Denley & Underwood 1979). It also restricts growth in patches where the barnacles settled first and were not immediately overgrown by the worm. Often empty shells of *Tesseropora rosea* were found under the tubes of *Galeolaria* when masses of the tubes were removed from the rocks. Connell (1961a) and Potts (1970) observed the polychaete *Eulalia viridis* feeding on *Semibalanus balanoides* and *Hipponoë gaudichauda*, was found by Willey (1910) penetrating between the valves of *Lepas anserifera*.

Arthropoda, Malacostraca

Crabs are capable of attacking such prey as barnacles by crushing the shells and consuming the soft parts with their claws or mouthparts (Menge 1983). Their activity may be regulated by the time of day, temperature, salinity or season (Ropes 1968), as, for example, on New England shores where the three crabs *Carcinus maenas*, *Cancer borealis*, and *C. irroratus* are found (Menge 1983). The stomach contents of crabs usually show that a variety of prey are devoured. Ropes (1968) found remains of mussels and barnacles in some stomachs of *Carcinus maenas* suggesting that one food may have been eaten incidentally with the other. In laboratory tests, however, the crabs used their chelae to remove individual barnacles from clumps adhering to wood or glass and ate them. The consumption of barnacles was, therefore, not dependent on the presence of another food such as mussels.

Juvenile *C. maenas* have a preference for the barnacle *Semibalanus balanoides* over gastropods on the rocky shores of the Bay of Fundy although adult crabs preferred gastropods (Rangeley & Thomas 1987). These authors used five groups of crabs in their predation experiments namely, juvenile males and females (carapace width 21–29 mm in each case), medium size males and females (carapace width 41–49 mm in each case) and large males (carapace width 61–69 mm). No large females were available. *S. balanoides* and three common gastropods (*Nucella lapillus*, *Littorina littorea*, and *L. obtusata*) were used as prey. The crabs were allowed to feed for 12 h during the night. The results are shown in Table 1. There was no significant difference in the proportion of barnacles to gastropods preyed on by juvenile male and female crabs. There were, however, significant differences between juvenile and adult crabs. The crabs were able to open or crush barnacles of any size but the weight of food obtained was less than that obtained from gastropods. The total weight of barnacle prey in the diets of adult crabs was low (Table 1) but accounted for over 50% in the diets of juveniles.

Table 1 *Carcinus maenas*: percentage of barnacles in diet and comparison between percentage of total weight of gastropods and barnacles prey (after Rangeley & Thomas 1987.)

	<i>Carcinus maenas</i>				
	Juvenile		Medium		Large Male
	Male	Female	Male	Female	
% barnacles in diet	83	72	14	11	15
Gastropod prey % total wt.	33	48	96	96	97
Barnacle prey % total wt.	67	52	4	4	3

Large crabs crushed or scraped groups of barnacles off the rocks and used their maxillipeds to clean the shell fragments of meat. Juvenile crabs attacked individual barnacles and often removed the soft parts through the opercular opening without damaging the outer shell. *Semibalanus balanoides* provides sufficient nutriment for young crabs while they are growing rapidly but larger crabs require more gastropods and must switch prey and forage lower on the shore.

In Delaware Bay, USA, two xanthid crabs (*Panopeus herbsti* and *Neopanope texana sayi*) were capable of destroying the barnacle *Balanus improvisus* (McDermott 1960). The barnacles were crushed by the chelipeds of the crab and ripped off the oyster shells to which they were attached. The same two crabs (≈ 25 mm carapace width) destroyed 97 barnacles in 14 h, 100 in 24 h, and 200 in 6 days. The respective rates of 83, 50 and 17 barnacles crab⁻¹ day⁻¹ obviously decrease as the crabs become satiated. Over 6 days 300 *B. improvisus* can be destroyed by six *Neopanope texana sayi*; this represents a rate of 8.5 barnacles crab⁻¹ day⁻¹.

Cancer pagurus can be a voracious predator of operculate barnacles on both European and Japanese shores (Vasserot 1983). The walls of the barnacles are again crushed by the pincers of the crabs. Very young *C. pagurus* attack *Balanus perforatus* from above and tear away pieces of the operculum; the whole body of the barnacle is extracted through the orifice. Young crabs can pulverize a group of *B. perforatus* of equal volume to themselves in 24 h. *Carcinus maenas* and, to a lesser degree, adult *Pagurus bernhardus* only attack barnacles after several days fasting and small barnacles such as *Elminius modestus* are preferred. Vasserot (1983) suggests that it would be of interest to determine which species of *Cancer* preferred which barnacles and to distinguish the geographic zones. Several species of *Cancer* co-exist on the west coast of America where *C. magister*, the Dungeness crab, preys on barnacles. From 10°S to about 30°S there are four species of *Cancer* and further south there are three.

The stone crab, *Homalaspis plana* is common along the western coast of South America. These were used by Morales & Antezana (1983) in their investigations and had carapace widths ranging from 100–120 mm. They collected the crabs from Los Piqueros beach, Valparaiso between August and January. Examination of the stomach contents of 122 crabs captured in the field revealed that 77 had food remains in their stomachs. Of these 23 (30%) contained remains of *Balanus laevis*. This crab is also able to break the walls of the giant barnacle, *Megabalanus psittacus* found on the coasts of Chile (Vasserot 1983).

Navarrete & Castilla (1988) studied the foraging activities of two carnivorous intertidal crabs from Chile, *Acanthocyclus gayi* and *A. hassleri*. The crabs are morphologically similar and their principal prey are mussels, gastropods, and barnacles. The least preferred prey is the barnacle *Jehlius cirratus* although it is one of the most abundant organisms

in the field. The consumption rates of both crabs are similar when feeding on *J. cirratus*. The same techniques are used by both crabs when attacking barnacles. Small barnacles are held by the master chela of the crab and detached from the substratum. No remains of the barnacle shell are left on the rocks. To feed *in situ* the crab inserts its small chela through the opercular valves of the barnacle and tears away the soft parts. Sometimes the large chela is also used to break the wall plates of the barnacle. This method is usually used on large barnacles and some shell remains or even whole empty barnacle shells are left on the substratum.

Barnacles were found in 11% of the stomachs of *Cancer magister* (carapace width >50 mm) in Kachemak Bay in Cook Inlet, Alaska (Feder & Paul 1980). In smaller *C. magister* (carapace width 22–44 mm) 28% of the stomachs contained barnacle remains. In the same Bay the king crab, *Paralithodes camtschatica*, had barnacle remains in 14% of the stomachs examined. In Kamishak Bay, also in the Cook Inlet, in November the king crabs were feeding almost exclusively (81%) on *Balanus crenatus* and the stomachs contained the equivalent of $11.2 \pm \text{SD } 7.4$ barnacles crab⁻¹. Near Kodiak Island, Alaska, Jewett & Feder (1982) examined 809 *Paralithodes camtschatica* and found food in 713 (88%) stomachs. *Balanus crenatus* formed 19.2% ww of the food and the frequency of occurrence was 24.8%. Another crab found in the Cook Inlet, the snow crab *Chionoecetes bairdi* was collected by Paul et al. (1979). In October, of 715 crabs caught 428 (60%) contained food in their stomachs and of these 76 contained *Balanus* spp. As with *Carcinus maenas* feeding on *Semibalanus balanoides* in the Bay of Fundy (Rangeley & Thomas 1987), barnacles are again important to crabs in their early stages of rapid growth.

There is an important commercial fishery in Oregon for *Cancer magister* and culture of this crab has been investigated. Reed (1969) found that *Balanus glandula* nauplii were a suitable food for the crab zoeae whereas *Mytilus edulis* larvae were not.

The intertidal pedunculate barnacles may also be prey of small pagurid crabs (Barnes 1996). Bernard (1988) found that numerous small (<1 mm) *Pollicipes polymerus* present on peduncles of adults and on cleared quadrats virtually disappeared within six weeks of settlement, probably due to predation by small crabs and polychaetes. Hui (1983) thought predation by crabs might be a reason for the contraction of the peduncle in *P. pollicipes* and the predominance of tight clumps of the barnacle in crevices. Barnes & Reese (1960) also considered the tight “rosette” habit of *P. polymerus* to be a protection from predation.

Arthropoda, Chilopoda

Centipedes, *Scolioplanes maritimus*, were observed at night on the shore at Port Erin feeding on barnacles. The hind ends of three centipedes were seen projecting from between the opercular plates of an apparently intact *Semibalanus balanoides*, but its soft parts had been reduced to a slime. A maximum of six centipedes were seen on any one barnacle (Blower 1957).

Arthropoda, Pterygota

According to Burger et al. (1980) *Oedoparena glauca* is the first known dipterous predator of intertidal barnacles. It is about 5–9 mm long and occurs from central California to Alaska. In 1966, fly pupae were found in empty shells of *Balanus glandula* on the central Californian

coast. There are earlier records of association between Diptera and barnacles on European coasts such as the work of Mercier (1921) who found the larvae of *Limnophora aestuum* living in barnacles and believed them to be feeding on the barnacles. Burger et al. (1980), however, followed the life history of *Oedoparena glauca* in detail.

In nature *O. glauca* preferentially selects *Balanus glandula* on which to deposit eggs doing so on the inner surface of the test or the opercular valves. The eggs have a pair of flanges that may help to secure them to the barnacle. Eggs were not deposited on *Chthamalus fissus* but in the laboratory small larvae would invade that barnacle suggesting that the first instar larvae could move from one barnacle to another. First instar larvae from eggs hatching during a low tide could enter a barnacle through the micropylar opening between the opercular valves before the tide returned. When feeding, the opening between the opercular valves of *Balanus glandula* varied from 2.1–4.55 mm and the *Oedoparena glauca* larvae contained in the barnacle were 3.2–9.8 mm long. In *Chthamalus fissus* the opening was less, 1.05–2.45 mm long, and the larvae were 1.7–5.6 mm long. As a larva grows it requires larger prey and because *Balanus glandula* is larger at maturity than *Chthamalus fissus* larger larvae were found in the former barnacle. The larva moved slowly when searching for new prey but when a barnacle operculum was found, the mouth parts of the larva moved rapidly. If the micropylar opening was found the mouth parts were lodged in it and the larva so anchored until entry could be completed when the opercular valves opened at the next high tide. Usually only one of these larger larvae was present per barnacle. The larva apparently feeds on the basal part of the barnacle but not initially on the muscles controlling the opercular valves; they were still able to open. This allows periodic flushing of the prey and also allowed the larva to leave after completion of feeding. During this time the cirri were affected and the barnacle could not feed. In a weakened state and with its tissues ultimately all consumed death was inevitable. *Oedoparena glauca* larvae were found in 11.0–12.5% of barnacles in the mid- and low-tide levels but only in 5% on the upper shore.

Mollusca, Gastropoda, Archaeogastropoda

The zonation on the rocky intertidal shores is usually determined by physical factors (upper limit) and biological interactions (lower limit), see for example Branch (1976) and Dye (1988). The association of barnacles and limpets has been observed on many occasions and although it may not always be true predation in the usual recognized meaning of the word the presence of limpets can be detrimental to barnacles particularly in the very early stages (Underwood 1979). Connell (1959b, 1961a) reported that most of the early mortality of newly metamorphosed *Semibalanus balanoides* at Millport, Scotland, occurred underwater and that it was caused by limpets. Potts (1970) observed *Patella vulgata* destroying barnacles in Kent, England. *P. cochlear* prevents barnacles settling and Branch (1975) found cyprids and small barnacles in the gut of the limpet. *Balanus algicola* only becomes established on South African shores in the absence of *Patella cochlear*.

Farrell (1988) found that on the Oregon coast of USA there was an increase in abundance of *Balanus glandula* in areas where limpets had been removed or excluded. *Chthamalus dalli*, however, appears to be more resistant to limpet grazing activity perhaps because of its smaller size. On the shores limpets were abundant with densities of $>2000 \text{ ind.m}^{-2}$ of which about 65% were *Lottia digitalis* (= *Collisella digitalis*) and 35% were *Lottia strigatella*. There is no evidence that *Collisella strongiana* removes *Chthamalus anisopoma* from the substratum (Dungan 1986, 1987, but see also Sutherland & Ortega 1986, Ortega 1987).

Cellana tramoserica can dislodge, crush, and sometimes ingest newly settled *Tesseropora rosea* at Cape Banks, New South Wales (Denley & Underwood 1979). Because *Tetraclitella purpurascens* tend to settle on conspecifics or in crevices and confined areas they are not so much affected by limpets. When the settlement is extremely heavy survival is lower than in areas with reduced densities because *T. purpurascens* can squash and smother each other. In both species, when the barnacles reach a shell diameter of 3–4 mm (from 1 to 2 months old) they are large enough to be unaffected by the activities of limpets. Underwood et al. (1983) mention two other ways in which limpets may affect barnacles; they may alter patterns of water flow on a small scale or exude chemicals that may have a deleterious effect on barnacles.

Dayton (1971) examined the effects of limpets on barnacle populations on the Pacific coast of the Olympic Peninsula and on San Juan Island, Washington, USA. These areas represented a variety of physical exposures. The barnacles *Semibalanus cariosus* and *Pollicipes polymerus* occur in scattered patches while *Balanus glandula* dominate on the upper level. *Chthamalus dalli* may also be present. He found the effects of limpets on the initial settlement of barnacles to be quite “dramatic”—his word. Limpets interfered by eating, pushing off, and dislodging the cyprids or newly metamorphosed barnacles from the substratum. Four species of limpets were present in the areas studied—*Acmaea digitalis*, *A. paradigitalis*, *A. pelta*, and *A. scutum*. In general, limpet interference is more effective on San Juan Island shores than on the outer coast of the Olympic Peninsula. The rock on the former shores is smoother than the siltstone of the outer coast and so the bulldozing of limpets is more effective. The populations of *A. pelta* and *A. scutum* are denser on San Juan shores than on the outer coast and particularly the latter is both bigger and more active than *A. digitalis* or *A. paradigitalis*. In several experimental tests, Dayton (1971) found a reduction in the number of *Balanus glandula* and *Semibalanus cariosus* in the presence of limpets and in the absence of *Nucella* spp. Survival of *Chthamalus dalli* was, however, increased in the presence of limpets because of the removal by them of the bigger *Balanus glandula* and *Semibalanus cariosus* even though the limpets were detrimental to the initial recruitment of *Chthamalus*.

Miller & Carefoot (1989) examined the interaction between limpets and juvenile barnacles at Bamfield, Vancouver Island. *Lottia digitalis* was the grazing limpet and *Balanus glandula*, *B. crenatus*, and *Semibalanus cariosus* were the barnacles. The limpet may ingest and/or bulldoze the juvenile barnacles. In the field shallow depressions in the rocky surface offer some protection against bulldozing and the presence of large adult barnacles deter grazing by limpets. One week old barnacles on a smooth surface suffered a 35–42% mortality whereas in depressions it was only 25%. *Balanus glandula* and *B. crenatus* reached a size refuge at a basal area of 5–7.6 mm²; *Semibalanus cariosus* reached a refuge at a smaller basal area because of its stronger adhesion to the substratum. The total mortality of all barnacles on open surfaces and in depressions at two shore levels during the whole study are given in Table 2.

Miller & Carefoot (1989) studied the mechanism by which limpets kill barnacles. Of 435 barnacles of all species removed by limpets 26% were found in the faeces of the limpets, that is ingested by the limpets, and 74% were bulldozed. Table 3 gives the fate of the barnacles. In the two species with calcareous bases, *Balanus glandula* and *B. crenatus* 57% and 66% of the shells, respectively, were fragmented possibly indicating weak plate junctions (see Barnes et al. 1970). Only 23% of *Semibalanus cariosus*, with a membranous base, were fragmented and this species might have stronger plate junctions. *Chthamalus dalli*, however, also with a membranous base was mostly fragmented (49%) when bulldozed by limpets. Observations of *Balanus glandula* growing in grooves on pipes showed that 58% removed by *Lottia digitalis* had been ingested. Most of these ingested barnacles were

Table 2 Total mortality of barnacles on open surfaces and in depressions at high and low levels. Numbers of replicates=10. (From Miller & Carefoot 1989.)

Number of limpets present	Location	Mortality, % \pm SE		Average
		High level	Low level	
0	Surface	17 \pm 10	14 \pm 4	15
	Depression	21 \pm 14	14 \pm 4	17
2	Surface	51 \pm 4	13 \pm 4	32
	Depression	32 \pm 4	13 \pm 4	22
4	Surface	72 \pm 4	15 \pm 4	43
	Depression	45 \pm 6	16 \pm 6	30
6	Surface	75 \pm 2	36 \pm 12	55
	Depression	57 \pm 4	21 \pm 4	39

Table 3 Condition of shells of barnacles bulldozed by *Lottia digitalis* as they grazed on single-species barnacle populations on rocks in the laboratory. Whole=barnacle shell intact; crushed=shell compressed (usually laterally) but in one piece; fragmented=shell plate separated, sometimes in pieces. (From Miller & Carefoot 1989.)

Barnacle	n	Condition of shells, %		
		Whole	Crushed	Fragmented
<i>Balanus glandula</i>	168	24	19	57
<i>Balanus crenatus</i>	78	13	21	66
<i>Semibalanus cariosus</i>	13	39	38	23
<i>Chthamalus dalli</i>	63	29	22	49

fragmented (67%) or crushed (26%) and only a few (7%) passed whole through the gut of the limpets. Barnacles not in the faeces were in a slightly better condition: 45% fragmented, 27% crushed, and 28% whole. All the barnacles were in grooves, so the limpets can remove barnacles from depressions by ingestion but the narrowness of the grooves hindered bulldozing. Microscopic examination indicated that the limpet shell was not the only means of removing barnacles. Of seven observed removing barnacles in the field, two were bulldozed by the shell of the limpet, two were bulldozed by the foot, two were pushed off by the mouth, and one of 0.9 mm² basal area was pushed off by the tentacle.

Lottia gigantea can be up to 8 cm long and they are able to remove any intruders in their area including barnacles. Stimson (1970) found exoskeletons of small newly settled barnacles in the faeces of *Lottia* indicating that they had been rasped off as the limpet grazed. *Lottia* removed *Chthamalus fissus* of 3 mm basal diameter from one-third of an area covered by the barnacle in the first month. Later all but about 20% of the barnacles had gone. One *Lottia* was seen pushing and crushing a large *Balanus glandula*.

Measurements of refuge size in *Balanus* spp. correspond to a basal diameter of 2.7–3.6 mm (Miller & Carefoot 1989) which is similar to the range of 2–4 mm estimated by Dayton (1971) for *B. glandula* and 3–4 mm estimated by Denley & Underwood (1979) for *Tesseropora rosea* attacked by *Cellana tramoserica*.

A second spatial refuge may be the proximity of adult barnacles, for example Miller & Carefoot (1989) found that juvenile barnacles situated more than 4 mm from an adult barnacle suffered up to 60% mortality in their first week of settlement. This was six times the mortality encountered in areas near to adults where *Lottia digitalis* could not graze. This contrasts with the limpet *Patelloida latistrigata* which does not grow big enough to be excluded from among the barnacles *Tesseropora rosea* on NSW shores, so it can graze or bulldoze juvenile barnacles in the spaces between the adults throughout its life (Jernakoff 1983, 1985a).

Mollusca, Gastropoda, Stenoglossa

The ability to detect chemical changes in their environment is found in many groups of animals. The mechanisms of chemoreception in gastropod molluscs have been reviewed by Kohn (1961). He considered chemoreception in this group of animals to have been first discovered in the seventeenth century by the Dutch naturalist, Swammerdam. Detection of prey by chemoreception or by chance contact is a first necessity to a predator. In order to feed on the soft tissues of prey, such as barnacles, predators have to obtain access through the barnacle shell. Many predators bore holes through the wall plates or the opercular valves, others prise open the opercular valves, some paralyse the barnacle by injecting a venom which causes the animal to gape, while some drag the whole animal complete with shell off the rocky surface.

Interest in the penetration of calcareous shells by organisms dates back for thousands of years (Jensen 1951). This author credits Aristotle with observing the capacity of predatory gastropods to bore holes in the shells of prey. There is now a vast amount of literature on the penetration of calcareous material. In 1961, Carriker listed the organisms capable of attacking calcareous exoskeletons of other organisms; these included representatives of algae, fungi, bacteria and "at least 7 animal phyla". Plants and lower invertebrates may use chemical means, whereas chemical, or mechanical, or a combination of the two may be used by higher invertebrates (Carriker 1961). It is not intended in this review to report in detail all the work that has been done over the years on this subject. Everything has been well summarized and reviewed by M.R.Carriker and his co-workers (for example, Carriker 1961, 1981, Carriker et al. 1974, Carriker & Williams 1978, and the references contained in these papers, see also Fretter & Graham 1962) (see also pp. 198–9).

Anachis species

Anachis rugosa on the Pacific coast of Costa Rica does not often overlap with the distribution of *Tetraclita stalactifera* but in areas where other barnacles are absent it preys on young *Tetraclita*. It is probably more significant as a predator of *Chthamalus panamensis* (Villalobos 1980).

Anachis boivini is included in a list of herbivorous and carnivorous gastropods found in Costa Rica but nothing is mentioned about predation by it (Ortega 1987).

Acanthina species

Acanthina species are widely distributed from the Pacific coast of Costa Rica to the Monterey Bay region on the Pacific coast of USA including the Gulf of California. *Acanthina* species and their prey are summarized in Table 4.

Table 4 *Acanthina* species feeding on cirripedes.

Predator	Prey	Place	Reference
<i>Acanthina angelica</i>	<i>Tetraclita stalactifera</i>	Gulf of California	Paine 1966b, Malusa 1985
<i>Acanthina angelica</i>	<i>Chthamalus anisopoma</i> <i>Chthamalus anisopoma</i>	Gulf of California	Dungan 1986, 1987, Lively 1986
<i>Acanthina angelica</i>	<i>Chthamalus</i> sp. <i>Tetraclita squamosa</i> <i>Balanus amphitrite</i>	San Felipe	Paine 1966b
<i>Acanthina brevidentata</i>	<i>Chthamalus</i> sp.	Pacific coast of Costa Rica	Paine 1966b
<i>Acanthina brevidentata</i>	<i>Chthamalus fissus</i>	Pacific coast of Costa Rica	Sutherland & Ortega 1986, Ortega 1987
<i>Acanthina brevidentata</i>	<i>Tetraclita stalactifera</i>	Nicoya Peninsula, Costa Rica	Villalobos 1980
<i>Acanthina punctulata</i>	<i>Balanus glandula</i> <i>Chthamalus fissus</i>	Santa Cruz Island	Menge 1974
<i>Acanthina punctulata</i>	<i>Chthamalus dalli</i> <i>Balanus glandula</i> <i>Pollicipes polymerus</i> (in Lab.)	Monterey Bay, California	Sleder 1981
<i>Acanthina spirata</i>	<i>Balanus glandula</i> <i>Chthamalus fissus</i>	Southern California	Perry 1985, 1987
<i>Acanthina spirata</i>	<i>Tetraclita rubescens</i>	Carmel, Monterey Peninsula, California	Villalobos 1979b
<i>Acanthina spirata</i>	<i>Balanus glandula</i>	Monterey Bay, California	Perkins 1974
<i>Acanthina spirata</i>	<i>Balanus glandula</i> <i>Chthamalus</i> sp. <i>Pollicipes polymerus</i>	Goleta Point, California	Murdoch 1969
<i>Acanthina spirata</i>	<i>Balanus glandula</i>	California	Connell 1985a

As an alternative to boring, some predators obtain entry to the prey's shell by forcing its shell margin between the valves of the prey (e.g. Paine 1962). Once entry has been attained the proboscis is inserted to consume the soft parts of the barnacle. This habit of "wedging" (Malusa 1985) has been enhanced in some Thaididae, such as *Acanthina*, by an extension of the predator's shell margin into a labial spine or tooth. In *A. angelica* the labial spine may be short or long and the attack on prey was related to the length of spine and prey size. As prey size increased the snails switched from wedging to drilling, the change taking place earlier in short-spined snails than long-spined ones. Short-spined snails were usually found associated with small barnacles but long-spined ones were found more often with larger barnacles. At Puerto Peñasco, Gulf of California, *A. angelica* less than 25 mm long had short spines (<3.5 mm). Larger *A. angelica* may have short or long spines. The length is not fixed and Malusa (1985) quotes experiments in which the spine length was controlled by the prey size. When consistently offered small barnacles the spine of *A. angelica* will be significantly shorter in about 3 months. The reverse is also true, if large barnacles are regularly offered—the spine will increase in length. This ensures that the

correct relationship between length of spine and size of prey is maintained. Paine (1966b) regarded gastropods with a labial spine as feeding specialists and that the spine itself was not involved in prey penetration but was used to anchor the predator to the substratum.

A. angelica is widely distributed in the upper Gulf of California. Paine (1966b) observed it at San Felipe and Puerto Peñasco and regarded it as a “barnacle specialist” because out of 432 records of prey only two were not barnacles. At San Felipe the gastropod was found eating *Chthamalus* sp., *Balanus amphitrite*, and *Tetraclita squamosa*. The feeding intensity on these three cirripedes was 54%, 62%, and 40%, respectively. The reduced intensity may reflect the greater difficulty in gaining access to the larger and thicker shelled *Tetraclita*. If the nourishment gained per unit time were greater for the larger prey then *Tetraclita* might be the optimal food (Paine 1966b). On the opposite shore of the Gulf at Puerto Peñasco a similar situation was evident except that the spines on the *Acanthina angelica* were of different lengths. Predators with short spines, 3 mm or less long, were eating *Chthamalus* and those with long spines, 6–10 mm long, were attacking *Tetraclita*. In the latter case about 35% of the sightings were of the spine actually inside the opercular cavity of the barnacle and only 25% were feeding through the opercular valves. In the remaining cases, both the spine and the point of drilling were removed from the opercular opening. In some cases the spine was hooked around or in one barnacle while the gastropod was drilling on a second one. It seems that in long-spined *Acanthina angelica* the spine is used for support and is not directly involved in drilling (Paine 1966b).

The function of the spine of *A. angelica* and its feeding behaviour were also studied by Malusa (1985). Gastropods with short and long spines were given three sizes of barnacle prey. The method of attacking the prey was related to the length of the spine. Contrary to Paine's (1966b) observations, Malusa (1985) observed the spine being used as a wedge to force apart the opercular valves; he called this “wedging”. Drilling through the test or opercular valves was an alternative method of attack. Short-spined predators switched to drilling at a smaller prey size than the long-spined predators. Short-spined predators were usually associated with small barnacles such as *Chthamalus anisopoma* and long-spined ones with larger barnacles, such as *Tetraclita stalactifera*. Malusa (1985) gives details of the mode of attack and behaviour of *Acanthina angelica* after encountering a barnacle. He found wedging by the spine in 100% of the cases of small barnacles, 87% with medium sized and only 43% with large ones. As in other *Acanthina* species there is evidence that *A. angelica* may possess a paralyzing toxin.

Chthamalus anisopoma is a common prey of *Acanthina angelica* (Dungan 1986, 1987) and the two shell morphs of the barnacle are found on the intertidal rocky shores of the northern Gulf of California (Lively 1986). The typical morph has a conical shape characteristic of acorn barnacles. The atypical morph is bent so that the rim of the operculum is in a plane perpendicular to its base rather than parallel to it. This morph is restricted to the northern Gulf of California (Lively 1986). This bent form may be more resistant to desiccation than the conical form. It also has added protection from predation by *Acanthina* because the orientation of the operculum prevents a downward thrust of the spine.

On the Pacific coast of Costa Rica, Sutherland & Ortega (1986) found *Tetraclita panamensis* and *Chthamalus fissus* on open surfaces together with the carnivorous gastropod, *Acanthina brevidentata*. Near crevices the density of *Chthamalus fissus* was always low. It seemed that *Acanthina* sheltered in crevices and emerged during low tides and formed feeding fronts near the borders of live barnacles. The density of *Acanthina* averaged 68.3 m⁻² during this time and *Chthamalus fissus* virtually disappeared. Large *Chthamalus* of more than 2–3 mm basal diameter transferred to this area also disappeared

within 6–10 days. In contrast, survival of barnacles was high when the predator was excluded. A similar situation was found by Ortega (1987).

Paine (1966b), on the basis of 80 observations of *Acanthina brevidentata* at two stations on the Pacific coast of Costa Rica, said that 75% were feeding mainly on *Chthamalus fissus* as well as small individuals of other cirripede species. *Acanthina brevidentata* has a well formed spine—about 1 mm long in individuals of 2 cm length. The predator penetrated barnacles by drilling; no evidence of use of the spine was seen.

A. punctulata is common on the upper intertidal zone of the Californian coast up to the Monterey Bay area which is probably the northern limit of its known range (Sleder 1981). Earlier studies of this gastropod were carried out on Santa Cruz Island in southern California by Menge (1974). She was mainly concerned with two *Littorina* species that were the diet of this gastropod. The barnacles, *Balanus glandula* and *Chthamalus fissus*, were taken when the preferred prey was not available. *Acanthina punctulata* consumes its prey by boring a hole in the shell and rasping out the flesh. When numbers of prey were compared 34% were barnacles and 66% littorinids but the barnacles only formed 10% of the diet biomass. Menge (1974) had the impression that it took less time to consume a barnacle than a littorinid but obviously much less biomass was obtained.

At Pacific Grove, Monterey, about half of the shore (49%) consists of bare rocks or rocks bearing *Chthamalus* and *Balanus* species. Of the *Acanthina*, 37% occur there at low tide. Tide pools account for about 23% of the area sampled by Sleder (1981) and 30% of the *Acanthina*. *Chthamalus* sp. and *Balanus glandula* formed part of the diet of *Acanthina punctulata*. The gastropod appeared to use its spine in a hammering action on the opercular opening of the barnacle. After 15 min of this treatment the barnacle appeared paralysed and allowed easy access to the predator's proboscis. There were no drilling marks and no damage to the opercular valves of the barnacle suggesting that a toxin had been applied to the operculum. Sleder (1981) demonstrated that an extract of the hypobranchial gland of *Acanthina* applied to the margin of the operculum or injected into the mantle cavity of *Chthamalus dalli* could paralyse the barnacle. *Acanthina punctulata* (probably *A. spirata*) secretes a toxin from its hypobranchial gland that it transfers to barnacles through their opercular valves causing paralysis of the prey and thereby assisting in predation (Sleder 1981). Toxic cholin esters have been reported by Bender et al. (1974) from the hypobranchial gland of *A. spirata* and from *Nucella emarginata*. Because barnacles provide a relatively small diet biomass for *Acanthina punctulata* it seems reasonable that the predator should make use of an alternative method of entry rather than having to spend time drilling the shell.

A. spirata is common in the rocky intertidal zone from Tomales Bay, California to northern Baja California (Perry 1985). It possesses a distinct labial spine on the aperture lip. Perry (1985) found that *A. spirata* used its shell spine in a ramming and forcing motion to fracture or open the opercular valves of *Balanus glandula* and *Chthamalus fissus*. The shell spine seems advantageous over drilling for attacking barnacles. Gastropods with spines have a lower handling time and feed at a greater rate than those without a spine that have to drill. Attacking *Balanus glandula* takes more than twice as long as when the gastropod attacks *Chthamalus fissus* but there is no difference in the number of spine thrusts to force entry. When feeding on *Balanus glandula*, *Acanthina spirata* ingests a greater dry weight per unit handling time than with *Chthamalus fissus*. The ability to drill when necessary allows *Acanthina spirata* with broken spines to continue feeding during spine repair. In tests made on *A. spirata* with and without spines in no case was drilling of the barnacle prey found when spines were present (Table 5). When spines were absent access to the prey was by drilling holes in the

Table 5 Results of *Acanthia spirata* attacks with and without spines on cirripede prey. (After Perry 1985.)

	Spine present		Spine absent	
	<i>Balanus glandula</i>	<i>Chthamalus fissus</i>	<i>Balanus glandula</i>	<i>Chthamalus fissus</i>
Number of tests	40	43	46	149
Number of times opercular valves remained intact	40	26	23	66
Number of times opercular valves were broken	0	17	0	0
Number of times opercular valves were drilled	0	0	23	83

opercular valves but never in the wall plates. The attacks not using the spine or drilling (50% in *Balanus glandula* and 44% in *Chthamalus fissus*) must have involved a third mechanism—probably the use of a paralytic toxin. Perry (1985) provides an excellent discussion on the evolutionary aspects of “spine-feeding” and a comparison of the predatory behaviour on barnacles.

Perry (1987) applied the optimal foraging theory to *Acanthina* feeding on *Balanus glandula* and *Chthamalus fissus* under conditions of satiation and starvation. *Acanthina spirata* is less selective when abundance of the higher ranking prey, *Balanus glandula*, is low. Satiated animals preferentially choose *B. glandula*—the more profitable as regards ash free dry weight of barnacle per unit handling time. When starved the gastropod will attack both barnacles equally but because *Acanthina spirata* is more successful at attacking *Chthamalus fissus* than *Balanus glandula*, 76% compared with 70%, respectively, more of the former are taken. There are fewer attacks on *B. glandula* because of a decrease in the gastropod’s success which is related to an energetic disadvantage as it passes from a satiated condition to one of starvation.

Predators can allow persistence of two prey populations if they switch their attacks among the prey in a particular way (Connell 1985a). If the number of attacks on a prey species is great when the predator is abundant relative to the prey and vice versa such a “switching” behaviour can reduce fluctuations in the numbers of prey populations. Such behaviour was found by Murdoch (1969) when *Acanthina spirata* was feeding on *Mytilus edulis* and *Balanus glandula* in the laboratory.

Murdoch (1969) records *Acanthina spirata* as usually preying on *Chthamalus* species when available in the field and occasionally on small *Pollicipes polymerus*. Perkins (1974) estimated that *Acanthina spirata* proportional to its weight will consume 111 mg of barnacle tissue per month. The high density of *A. spirata* at some places on the Monterey Peninsula reduces the survival of young *Tetraclita rubescens*, but at other places—such as Carmel—the number of predators is low and the *Tetraclita* density is high (Villalobos 1979b).

Concholepas concholepas

Guisado & Castilla (1983) record *Concholepas concholepas* as “the most important gastropod shellfish in the world and the mollusc of greatest commercial importance in

Chile". It is found on the coast of Chile and southern Peru from the intertidal zone down to about 40 m depth. It can reach a maximum size of about 19 cm and of 1277 examined many at Las Cruces, Chile, were in association with the barnacles *Chthamalus cirratus* (43%) and *Balanus laevis* (28%).

After a Marine Reserve was established near Valdivia in southern Chile in 1978, the population of *Concholepas* was protected from human predation and as a result the barnacle population of *Jehlius cirratus* and *Chthamalus scabrosus* in the Reserve actually decreased. The combined percentage cover of barnacles and the percentage of bare rock in the Reserve increased from 1978–80 probably owing to increased grazing of algae by an herbivorous limpet. From 1980 onwards large *Concholepas* became more frequent and the barnacle cover decreased to about 60% while the amount of bare rock reached 30% (see also Moreno et al. 1986, Durán & Castilla 1989).

Drupa species

Taylor (1976) lists 23 species of predatory muricid gastropods that are common on the intertidal rocky shores of Aldabra Atoll (Table 6). Most species of *Nucella* and *Morula* feed by drilling sedentary or semi-mobile prey. *Drupa* species do not drill.

Drupa species are abundant in exposed habitats of the Indo-Pacific coral reefs (Taylor 1983). *D. ricinus* sometimes preys on barnacles. One individual of *D. rubusidaeus* contained the remains of a barnacle at Guam. Also at Guam, barnacles formed 19% of the diet of *D. clathrata clathrata*. Other common predatory gastropods taking barnacles are *Morula* spp. (Muricidae), *Nucella*, etc. (Muricidae), *Engina* (Buccinidae) and *Peristernia* and *Leucozonia* (Fascioliariidae). The muricids found on the Atoll that include barnacles in their diet are given in Table 6. The Muricidae are the major group of predatory gastropods to have exploited the intertidal habitat and, together with *Littorina* species and *Nerita* species, they have generally evolved in response to intertidal conditions. Menge (1974) has divided the feeding process in drilling muricids into a number of distinct phases of which the last—drilling and eating—may take several hours. This represents a high proportion of the total time available and so muricids are highly prey-selective.

Subtidal *Urosalpinx* is attracted to metabolites of prey species secreted into the water (Wood 1968, Pratt 1974). *Acanthina* and some other intertidal species find their prey by

Table 6 Frequency (%) of cirripedes in diets of some muricid gastropods at all the places examined on Aldabra Atoll (after Taylor 1976). *n*=number of attacks examined

Predator	<i>n</i>	Prey		
		<i>Tetraclita squamosa rufotinca</i>	<i>Tetrachthamalus obliteratus</i>	<i>Lithotrya valentiana</i>
<i>Nucella aculeata</i>	236	3.8	10.2	3.4
<i>Nucella savignyi</i>	28	14.3	3.6	—
<i>Nucella fusconigra</i>	374	2.4	48.4	7.8
<i>Nucella rudolphi</i>	322	45.3	0.3	2.8
<i>Morulaanaxeres</i>	17	—	82.4	—
<i>Morula granulata</i>	386	0.3	6.5	0.3
<i>Morula marginatra</i>	277	—	77.8	11.1
<i>Drupella cariosa</i>	21	—	4.8	—

random foraging at low water (Menge 1974). For *Drupa* species selection takes place at high water (Taylor 1976); this species has a small foot with an accessory boring organ.

Fasciolaria species

Paine (1963) gives eight sympatric predatory gastropods of which only one, *Fasciolaria hunteria*, preys on barnacles, *Chthamalus* sp., in western Florida. The Fasciolariidae lack any drilling apparatus and penetrate prey by forcibly inserting the proboscis into the prey with mild rasping of the radula or use of the shell margin.

Lepsiella species

Lepsiella vinosa is found in the mangroves of southern Australia where it feeds on the barnacles *Balanus amphitrite* and *Elminius modestus* (*E. adelaide* in Bayliss 1993) and only takes other prey when barnacles are not available (Bayliss 1982). In patches of high density, more than 25 *Balanus amphitrite* m⁻¹ pneumatophore, *Lepsiella* concentrates on *Balanus amphitrite* irrespective of the relative abundance of the two barnacle species. At less than 25 *B. amphitrite* m⁻¹ pneumatophore it feeds on both species but prey selection in moderately dense patches was not random and was influenced by the feeding history of the *Lepsiella*. In tests *Lepsiella* which had fed on the more abundant species, *Elminius modestus*, selected this species at a higher rate than expected in subsequent surveys. This suggested that there had been "ingestive conditioning" in the field and supports a switching hypothesis. The switching response was, however, asymmetrical. *Lepsiella* switched to *Balanus amphitrite* when it was the more abundant species, irrespective of prior training. *Lepsiella* trained on *Elminius* or when starved, switched to *Elminius* when it was more abundant but those trained on *Balanus amphitrite* did not. There was also asymmetry in the feeding rate irrespective of the prey barnacle, but with *Lepsiella* trained on *Balanus amphitrite* there was a marked reduction in feeding rate when *B. amphitrite* was less abundant (Bayliss 1982).

Lepsiella vinosa is the major predator in the mangrove areas of Port Adelaide in most years (Bayliss 1993). In some years, however, large numbers of the gastropod *Bedera paivae* migrate from the mudflats to feed on the barnacles on the mangrove pneumatophores. This phenomenon is rare and in most years there is little predation by this gastropod.

Lepsiella vinosa is also a common intertidal gastropod on the exposed rocky shores of Victoria, Australia. Its main prey are mussels and littorinids but some *Chthamalus antennatus* are eaten (Ward & Quinn 1988).

Sometimes a barnacle may have such a thick or strong wall that, after reaching a critical size, it withstands boring by predators. Such is the case of *Chthamalus* sp. at Poor Knights Islands, New Zealand (Cranwell & Moore 1938). *Elminius modestus*, however, at West Tamaki Head, New Zealand, may be bored in the wall plates or the opercular valves by *Lepsiella scobina* (Luckens 1976). *L. scobina* preys on *Elminius* spat and *Chamaesipho brunnea* on the shore at Leigh, New Zealand (Luckens 1970a). The numbers of *Lepsiella scobina* increased as the barnacles *Chamaesipho columna* increased to above 2 mm basal diameter. With a density of 6 predators dm⁻² the proportion of live *C. columna* greater than 2 mm basal diameter fell to 5–10% (Luckens 1976).

Three species of barnacle *C. brunnea*, *C. columna* and *Epopella plicata* occupy much of the intertidal zone at Goat Island Bay, Leigh. Preferential predation by *Lepsiella scobina* restricts *Chamaesipho brunnea* to the upper shore (Luckens 1975b). At lower levels on the shore, where *C. brunnea* and *C. columna* compete with each other, predation by *Lepsiella*

scobina on the former barnacle species forces it to higher levels. The distributions of *Chamaesipho columna* and *Epopella plicata* overlap completely and the latter can even overgrow and smother the former. When the *Epopella* becomes dense it forms clumps and may break away; increasing density of *Lepsiella* also favours survival of *Chamaesipho columna*. Luckens (1975a) found *Lepsiella scobina* preying on several species of barnacles—*Chamaesipho brunnea*, *C. columna*, *Balanus trigonus*, *Elminius modestus*, *Epopella plicata* and *Tetraclita purpurascens*. In most cases the cirripedes had been bored by the predator although no positive proof of this was found in *Chamaesipho columna*. The opercular valves appeared undamaged but whether they were forced apart before or after smothering by *Epopella* is not known. *Elminius*, *Epopella*, and *Tetraclita* were usually bored through the opercular valves, often at the junction, but sometimes the holes were in the wall plates when these could be reached. In very tightly packed aggregations this was not always possible. Luckens (1975a) did numerous experiments on the behaviour, feeding rates, and relationship of predator and prey size and her paper should be consulted for the details.

Morula ferruginosa

Chthamalus anisopoma is a small acorn barnacle that is found in the mid-intertidal region of the Gulf of California (Lively & Raimondi 1987). It is commonly found in dense aggregations and rarely exceeds 7 mm diameter. *Morula ferruginosa* is a small gastropod about 12 mm long that is found in the same region and which preys selectively on an intertidal mussel, *Brachidontes semilaevis* (maximum length about 10mm). This mussel overlaps with the *Chthamalus* and in the absence of predation by *Morula ferruginosa* the mussel has a negative effect on the barnacle. On the other hand, predation of the mussels benefit the barnacle. Lively & Raimondi (1987), however, have found that *M. ferruginosa* will consume barnacles when mussels are not available in the autumn through to spring. *M. ferruginosa* is, therefore, a “switching predator” and its effect on barnacles is dependent on the season (Lively & Raimondi 1987).

Morula marginalba

The biology and ecology of the organisms living in the intertidal zone of the rocky shores of New South Wales, Australia, and the interactions between them have been extensively studied by the group of workers originally based at the University of Sydney (Denley & Underwood 1979, Creese 1982, Fairweather & Underwood 1983, Jernakoff 1983, 1985a,b, 1986, Underwood et al. 1983, Fairweather et al. 1984, Moran et al. 1984, Fairweather 1985, 1986, 1987, 1988a,b,c,d,e, Jernakoff & Fairweather 1985, Moran 1985a,b,c, Underwood & Fairweather 1985). The barnacle, *Tesseropora rosea*, is found from Queensland to eastern Victoria (Endean et al. 1956) and is common on rocky shores exposed to wave action. If not subjected to predation by *Morula marginalba*, this barnacle may live for 8–10 yr and reach a size of 3 cm diameter, although 2–4 yr is more usual in the mid-intertidal region (Caffey 1985).

M. marginalba is one of the important predators on these shores (Fig. 4). It sometimes forms large aggregations and these are usually in crevices, shallow pools or in depressions in the rocky surface at low tide levels. When feeding, *M. marginalba* leave the shelter of crevices, for example, and may become subjected to wave action on exposed shores (Jernakoff & Fairweather 1985, Moran 1985b, Underwood 1985). Fairweather & Underwood (1983) give *Catomerus polymerus*, *Chthamalus antennatus*, *Chamaesipho columna*, *Tetraclitella*



Figure 4 Caloundra, Queensland, Australia; *Morula marginalba* feeding on *Tetraclita* (now *Tesseropora*) *rosea*. (Courtesy of Professor W. Stephenson, Drs R. Edean and R. Kelly; with permission of *The Australian Journal of Marine and Freshwater Research*, plate published in Vol. 7, 1956).

purpurascens, and *Tesseropora rosea* as possible prey but the last is the main one consumed by *Morula marginalba*. This predator can significantly affect the distribution and abundance of barnacles (Caffey 1985). Feeding aggregations of *Morula* can kill all the barnacles in a local area of the shore while leaving those in nearby areas untouched (Denley & Underwood 1979, Fairweather & Underwood 1983, Underwood et al. 1983).

Creese (1982) noted that *M. marginalba* may prey directly on *Patelloida latistrigata*, a small intertidal limpet living among the barnacles, *Tesseropora rosea*, and gaining some protection from them. When *Morula* consumes the barnacles it removes a source of refuge for the limpets.

M. marginalba alternates between feeding or sheltering in response to daytime low tides. Only during high tides is foraging initiated (Fairweather & Underwood 1983). The habit of *Morula* sheltering in crevices during adverse conditions leads to areas of clear space emanating from crevices when conditions become favourable and *Morula* emerges and starts feeding again. In one experiment Fairweather (1988a) found “haloes”, as he called them, of $70.7 \pm \text{SD } 52.3$ cm ($n=37$) diameter around crevices with *Morula* and $19.8 \pm \text{SD } 10.4$ cm ($n=10$) diameter when no *Morula* were present in the crevice. Densities of live barnacles were negatively correlated with the presence of *Morula* being, for example, 2000 barnacles m^{-2} before an advancing front of *Morula* and only 156 barnacles m^{-2} behind it. Such patterns were found over the whole rocky surface and seemed to result in a widening of the bare space around crevices. This again suggests a relationship between feeding of *Morula* and a decline in the number of prey around crevices.

Table 7 Densities of species (no. 100 mm⁻²) in areas with (Control) and without (Removal) of *Morula marginalba* at the beginning and end of experiment. (After Fairweather et al. 1984.)

Species	Removal (<i>Morula</i> absent)		Control (<i>Morula</i> present)	
<i>Tesseropora rosea</i>				
Dec. 1978	52	89	89	87
Jan. 1980	41	68	0	0
Ratio Jan./Dec.	0.79	0.78	–	–
<i>Chthamalus antennatus</i>				
Dec. 1978	7.3	16.5	8	9.5
Jan. 1980	11.5	27.5	0	1
Ratio Jan./Dec.	1.55	1.97	–	0.18
<i>Chamaesipho columna</i>				
Dec. 1978	432	408	310	370
Jan. 1980	370	373	273	306
Ratio Jan./Dec.	0.87	0.91	0.88	0.83

The alga *Gelidium* may act as a shelter for *Morula* against desiccation but it also protects *Tesseropora rosea* from predation (Jernakoff & Fairweather 1985). Normally *Morula* predate barnacles by drilling through the opercular valves but when the barnacle is covered with *Gelidium* this is apparently not possible. All barnacles eaten that were partially covered by *Gelidium* had been drilled through a bare patch on a side plate instead of the operculum. Jernakoff & Fairweather (1985) found a significantly greater proportion of *Tesseropora* consumed by *Morula* when the barnacles were incompletely covered by the alga than when they were completely covered. Of the partially covered barnacles all those consumed ($n=26$) had been drilled through the side walls of their shells. Of 438 dead barnacles without algal protection only 7.4% were drilled through the side walls. The predatory behaviour of *Morula* must have been affected by the presence of the alga. *Morula* drills a hole in the prey's shell with the radula, a process that may take several hours, and then feeds through the hole (Fairweather & Underwood 1983, Fairweather 1985).

Fairweather et al. (1984) made preliminary experiments by removing *M. marginalba* from two sites on the shore, leaving control sites undisturbed, and blocking any crevices with concrete on a third site, thus removing any shelter for *Morula* from desiccation or exposure to waves and indirectly, therefore, reducing the number of predators present. Within a year in the areas where *Morula* was absent, the *Tesseropora* had declined slightly but in control areas where *Morula* was present the barnacles had all gone (Table 7). *Chthamalus antennatus* was also lost in areas where *Morula* was present but had increased in the absence of *Morula* presumably due to survival of the original population and further recruitment during the experimental period. *Chamaesipho columna* had decreased slightly in all plots indicating that *Morula* had a pronounced affect on the survival of this barnacle. These initial experiments suggest that *Chamaesipho columna* is not a preferred prey of *Morula* (Table 7).

Fairweather et al. (1984) examined the effect of predation on any interaction between the two major barnacles, *Tesseropora rosea* and *Chamaesipho columna*; the former, larger barnacle was removed from some sites. Where *Tesseropora rosea* was removed *Morula* did not affect *Chamaesipho* even though its preferred prey was not available. Removal of *Tesseropora* by *Morula*, or manually, presumably created space onto which further

Table 8 Mean (\pm SD) sizes of *Morula marginalba* feeding on different barnacles on one particular shore ($n=50$). Mean (range) of dry flesh weight (mg) of prey sampled over the sizes eaten by *Morula* ($n>20$) for each species. (After Moran et al. 1984.)

Prey	Mean (range) dry flesh wt. (mg) of prey	<i>Morula marginalba</i> , mean size (\pm SD) (mm)
<i>Chamaesipho columna</i>	5 (0.5–6)	11.6 (1.8)
<i>Tetraclitella purpurascens</i>	13 (1.5–40)	12.6 (1.7)
<i>Chthamalus antennatus</i>	18 (1.0–25)	14.4 (2.0)
<i>Tesseropora rosea</i>	99 (0.9–200)	14.6 (2.8)

recruitment of *Chamaesipho* was possible. Fairweather (1988b) examined the relationship of *Morula* with its intertidal prey *Tesseropora rosea* and *Chamaesipho columna* (as *C. tasmanica*) during five years. These barnacles represented about 85% of the potential prey. *Morula* was seen feeding on barnacles at all the sites examined. Increase in numbers of barnacles was mainly in autumn and winter—the reproductive season (Caffey 1985) while activity of *Morula* (12–18 mm > 2 yr old) was mainly in the warmer months and represented an invasion of *Morula* rather than recruitment. A decrease in the number of *Morula* was probably not due to mortality as tagged ones could be found in other areas (Fairweather 1988d). The unpredictable movements of *Morula* have also been described by Moran (1985c). Invading *Morula* can eliminate whole populations of barnacles. Some areas, however, may be free of predation for long periods. Fairweather (1988d) found that *Morula* moved from areas where prey was scarce or there was no shelter, such as crevices.

Moran (1985b) gave prey species of barnacles as *Tesseropora rosea*, *Chamaesipho columna*, and *Tetraclitella purpurascens*, in that order, near Sydney, NSW. Moran (1985a) studied the effect of sizes of predator and prey using *Morula marginalba* as predator and *Tesseropora rosea* as prey. There was no simple relationship. *Morula* of 15-mm aperture length ate 4.15 as many adult barnacles as did a *Morula* with a 12-mm aperture but there was no significant difference in the rates at which the two sizes of *Morula* ate juvenile barnacles. However, in all cases the feeding rates increased with prey density. Both sizes of *Morula* ate more juveniles than adults, 4.2 times as many for 12-mm *Morula* and 2.3 times for 15-mm *Morula*.

Fairweather & Underwood (1983) measured similar handling times at 21°C in the laboratory and in the field for *Morula* feeding on *Tesseropora*. Moran (1985a) working at a seawater temperature of 16.5°C quotes his own work saying that *Morula* feeds 1.8–2.5 times faster at 21°C than at 16.5°C. He estimated that handling times for juvenile *Tesseropora* were 1.7–2.2 times those measured directly by Fairweather & Underwood (1983). These results are in agreement when corrected for temperature differences. Fairweather (1985, 1986) observed *Morula* eating *Tesseropora* on all sampling occasions and taking adults in preference to juveniles. The latter were taken when they were about 3–4 months old by which time the number of adult barnacles was decreasing. At this size (aperture about 3.5 mm long, about 4 months old) *Tesseropora* is becoming sexually mature.

One of the things affecting the growth of *Morula* is the prey on which it feeds (Table 8) rather than variations in the habitat (Moran et al. 1984). On the particular shore where this work was done the mean size of *Morula* was positively correlated with the mean weight and maximum weight of prey taken. This result is not merely due to increased frequency of observation of predators on prey needing longer handling times because all these

barnacles need relatively long handling times by *Morula* (Fairweather & Underwood 1983). Sampling on a variety of beaches, Moran et al. (1984) showed the same trend. Size of adult *Morula* was greater on shores dominated by larger prey species. The rate at which *Morula* approached their asymptotic size on a diet of *Chamaesipho columna* was slower than for other diets, e.g. *Tessoropora*. It seems, once again, that although *Chamaesipho columna* is taken by *Morula* it is a less-preferred prey. On the rocky shores of NSW *Morula* reduces the abundance of some prey, e.g. barnacles (Underwood et al. 1983, Fairweather et al. 1984). Other prey are less-preferred and are, therefore, relatively unaffected.

Muricanthus nigritus

In the northern part of the Gulf of California small *Muricanthus nigritus* live in cobble patches where barnacles are abundant. At a shell length of 2–6 cm the predator is found taking barnacles in 34% of the observations made; above 6 cm length the diet switches to gastropods. Up to a length of 5 cm *Muricanthus* will drill barnacles, but at lengths above 5 cm use of the shell predominates (Paine 1966b).

Neothais species

Neothais nesiotis occurs high in the intertidal zone on Easter Island and was observed feeding on the barnacle *Chthamalus belyaevi* in 45% of the cases examined by Kohn (1978). At Leigh in New Zealand the mortality rates of barnacles increased sharply if *Neothais scalaris* was able to prey on them (Luckens 1970a, Paine 1971). *N. scalaris* did not appear to bore either *Chamaesipho brunnea* or *Epopella plicata*. Many of the latter had their opercular valves stained purple presumably by secretion from the purple gland of *Neothais*. Such staining was found on living barnacles and inside the tops of the wall plates of dead ones (Luckens 1975a). *N. scalaris* was never found to bore *Chamaesipho brunnea*, *Epopella plicata* and *Elminius modestus*. On rare occasions *Megabalanus decorus* was bored. Maximum densities of *Neothais* were at low tide level. It was only found feeding high on the shore if the weather was damp or waves were breaking well up on the shore. *Neothais* should be wetted at least 50% of the time. Luckens (1975a) provides extensive experimental information on the relative sizes of prey and predators and the feeding rates of predators about which it is impossible to give all the details in this review.

Nucella bronni, *N. clavigera* and *N. freycineti*

Nucella bronni and *N. clavigera* from near Asamushi and *Nucella freycineti* from near Hachinohe, Aomori Prefecture, Japan, feed on large barnacles, such as *Tetraclita squamosa*, *Megabalanus tintinnabulum* and *Semibalanus cariosus*, where these are available (Luckens 1970b).

Nucella dubia

On the rocky shores of the Cape Peninsula, South Africa, *Nucella dubia* is found in the middle and upper balanoid zone. Cirripedes are one of its major prey. It feeds predominantly on *Chthamalus dentatus* (42%), *Tetraclita serrata* (16%), and *Octomeris angulosus* (9%) (Branch 1975, 1976, 1978, McQuaid 1985). McQuaid (1985) and Palmer (1982) found

boring of its prey by *Nucella dubia* was uncommon. Barnacles were attacked through the operculum possibly by the injection of a toxin.

Chthamalus dentatus occurs highest on the shore being replaced by *Tetraclita serrata* at lower levels. *Octomeris angulosus* is found in exposed areas but is not numerically dominant. *Chthamalus* settles in April and September and rapidly reaches its maximum size of 10 mm diameter. The settling density may be as high as 120000 m⁻², but by the adult stage it is about 35000 m⁻² owing to loss due to overcrowding. At lower levels it is also heavily preyed on by *Nucella dubia* (Branch 1976). *Tetraclita serrata* grows to about 25 mm diameter and is less often preyed on by *Nucella dubia*. This barnacle can, therefore, extend further down the shore where *Chthamalus* would be eradicated by *Nucella*. *N. dubia* will prey on *Patella granularis* if barnacles are absent, but *Chthamalus*, in particular, remains the preferred prey.

According to McQuaid (1985), *Tetraclita serrata* was the most commonly consumed prey (60%) while *Octomeris angulosus* was rarely taken (<5%) in the region where he worked. *Nucella* from 10–27 mm length were found feeding on *Tetraclita* and there was no correlation between size of predator and prey. There was no significant difference between feeding rates in the upper and lower mid-balanoid zone or between large and small *Nucella*. Sometimes small *Nucella* were seen to take only part of a large barnacle in preference to eating smaller *Tetraclita*. McQuaid (1985) gives average feeding rates from some caging experiments. These rates were 0.02 barnacle *Nucella*⁻¹ day⁻¹ or a predation rate of 1.72 barnacles m⁻² day⁻¹. Based on 20×20 cm quadrats with a mean density of 1375 barnacles m⁻² the predation represented 3.88% of the barnacle population month⁻¹ or 46.56% yr⁻¹. The *Nucella* density was taken as 866 m⁻².

McQuaid (1985) found that predation on sessile *Tetraclita serrata* was greater than on mobile prey such as *Littorina africana knysnaensis*. This supports the suggestion of Branch (1984) that in the intertidal zone sessile invertebrates are generally more influenced by predators than are mobile ones. Branch (1978) says that *Nucella dubia* drills into barnacles through the operculum and that thin-walled *Chthamalus* is particularly vulnerable. As noted above, however, McQuaid (1985) suggested that barnacles were rarely drilled but were attacked by the injection of a toxin between the opercular valves (see also Palmer 1982).

Nucella canaliculata, *N. emarginata*, *N. lamellosa*, *N. lima*

Four *Nucella* species occur on the rocky intertidal of the western coast of America and Canada from California to Alaska. All are predators of cirripedes (see, for example, Connell 1970). The lives of these predators and prey are so interwoven that it is impossible to consider each one separately. Table 9 is an attempt to summarize the position and to indicate the relevant literature. The four species of *Nucella* are *N. canaliculata*, *N. emarginata*, *N. lamellosa*, and *N. lima* and they predate selectively on barnacles. Palmer (1982) investigated the feeding of these predators on four barnacles, *Semibalanus cariosus*, *Balanus glandula*, *B. nubilus* and *Chthamalus dalli*, but only had enough data to consider the first two in detail. He was essentially interested in where the predators gained entry through the barnacle shell. The sites were found as distinct holes or as circular or subcircular cavities of recently exposed shell. Even when the soft parts had been completely consumed the drill holes were often incomplete. In the results shown in Table 10 he did not distinguish between complete and incomplete holes. The results imply that penetrating barnacles between, rather than through, lateral plates is more beneficial to the predator. In an adult *B. glandula* (basal diameter about 14 mm) the overlap of adjacent wall plates is about 1 mm wide and is slightly less than the

Table 9 *Nucella* species as predators on cirripede prey with references containing details. 1, Barnes 1996; 2, Bernard 1988; 3, Butler 1979; 4, Connell 1970; 5, Connell 1972; 6, Dayton 1971; 7, Emlen 1966; 8, Hart & Palmer 1987; 9, Murdoch 1969; 10, Paine 1966a; 11, Palmer 1982; 12, Palmer 1983; 13, Palmer 1984; 14, Palmer 1990; 15, Perkins 1974; 16, Sebens & Lewis 1985; 17, Spight 1973; 18, Spight 1981; 19, Spight 1982; 20, Stickle, 1973; 21, Villalobos 1979b; 22, West 1986.

Prey	Predator			
	<i>Nucella canaliculata</i>	<i>Nucella emarginata</i>	<i>Nucella lamellosa</i>	<i>Nucella lima</i>
<i>Balanus glandula</i>	3,4,6,8,13,17,18	3,4,6,7,8,9,10,11, 12,13,14,15,17,18, 19,22	6,8,17,20	8,11
<i>Balanus nubilus</i>	—	11	—	11
<i>Chthamalus dalli</i>	6,12,13	6,11,12,13,14	6,12,13,19	11
<i>Chthamalus fissus</i>	—			
<i>Semibalanus cariosus</i>	6,17,18	4,5,6,7,11,12,13	3,4,6,16,17,20	11
<i>Tetraclita rubescens</i>	—	21,22	—	—
<i>Pollicipes polymerus</i>	12	1,2,13,22	1,2,12	—

Table 10 Frequencies with which four *Nucella* species drill various places on the shell of the prey *Balanus glandula* (*B. gl.*), and *Semibalanus cariosus* (*S. car.*). After Palmer (1982).

Region	Site on shell	<i>N. canaliculata</i>		<i>N. emarginata</i>		<i>N. lamellosa</i>		<i>N. lima</i>	
		<i>B. gl.</i>	<i>S. car.</i>	<i>B. gl.</i>	<i>S. car.</i>	<i>B. gl.</i>	<i>S. car.</i>	<i>B. gl.</i>	<i>S. car.</i>
Opercular valves	Not at suture	3	0	19	1	14	1	20	0
	At suture	1	0	89	3	4	2	45	1
	Total	4	0	108	4	18	3	65	1
Middle of wall plate	Not at suture	1	12	3	5	4	25	5	0
	At suture	18	38	10	3	29	23	18	1
	Total	19	50	13	8	33	48	23	1
Base of wall plate	Not at suture	2	8	11	0	14	23	13	0
	At suture	4	6	5	0	9	9	7	0
	Total	6	14	16	0	23	32	20	0
Total observations		29	64	137	12	74	83	108	2

thickness of the wall plate at the mid-point (Barnes et al. 1970). In the overlap there is a slight space between opposing plates and here there is some tissue. According to Huang & Mir (1971, 1972), *Nucella haemastoma* possess a strong toxin and so complete penetration is not necessary as long as there is contact with body tissue into which the toxin can be injected. This is probably true for the four *Nucella* species considered in this section. Once effective, the toxin relaxes the main body and the tissue can be consumed through the gaping opercular valves as these can no longer be held tightly closed. If a hole is drilled in a wall plate and the toxin injected then the hole need not be large enough for the buccal mass to enter—again the relaxing of the animal causes the opercular valves to gape and

the predator can consume the prey through them. This finding contrasts with those of earlier workers who thought that the opercular valves had to be forced apart (e.g. Moore 1938, Largen 1967b, Morgan 1972, Barnert 1979).

Balanus glandula was often drilled through the opercular valves whereas *Semibalanus cariosus* was rarely drilled there. Three of the predators, *Nucella lamellosa*, *N. canaliculata* and *N. emarginata* were consistently more successful when they attacked the largest *Semibalanus cariosus* at a suture (41.0%) than when they attempted to drill through the wall plate (12.2%). When drilling larger barnacles handling time by the predator may be reduced and the successful penetration higher when attacking the plate margins. *Nucella emarginata* and *N. lima* when attacking *Balanus glandula* are more like each other than they are to *Nucella canaliculata* or *N. lamellosa* (Table 10); the former two predators feed in the upper and mid-intertidal region and handling time is limited. This does not explain why *N. canaliculata* and *N. lima* differ in their attack of *Semibalanus cariosus* (Table 10, see also Hart & Palmer 1987). A trade-off of decreased handling time and an increased risk of dislodgement may become important depending on the normal distribution of the predators. If a predator is raised further off the ground or is less stable when attacking the opercular valves then decreased handling time may not be sufficient to outweigh the risk of dislodgement lower on the shore (Palmer 1982).

Palmer (1984) considered this system of predators and prey to be a good one in which to study foraging behaviour. He also used these prey animals to determine the growth rates of three *Nucella* species (Palmer 1983). In this work he grew three size classes of each predator in experimental cages at two tidal heights and used four size classes of prey, *Semibalanus cariosus* and *Balanus glandula*, as food. *Nucella emarginata* was also fed on *Chthamalus dalli*. The three predators used were *Nucella emarginata*, *N. canaliculata*, and *N. lamellosa*. Rates of body growth depended on predator size, prey size and prey species. Intermediate sized *Balanus glandula* promoted the most rapid growth of all sizes of the predators except large *Nucella canaliculata*. These competing predators therefore have the same highest ranked prey. Of prey responsible for slower growth, those encountered more frequently in the normal habitat of the predators produce more rapid growth than those rarely encountered. For some predators the ranking of prey species changes with size of predator. For example, *Balanus glandula* and *Chthamalus dalli* of a similar size promoted comparable growth in small *Nucella emarginata* but in larger *N. emarginata* growth was faster with *Balanus glandula* than *Chthamalus dalli*. Large *Balanus glandula* promoted relatively faster growth for large predators than small ones in all those *Nucella* species tested. In *N. canaliculata* and *N. emarginata* more rapid growth was associated with fitness. Prey promoting rapid growth resulted in an earlier age of maturity in young predators and a high rate of egg capsule production in mature predators (Palmer 1983).

Stickle (1973) examined *N. lamellosa* collected from among *Semibalanus cariosus*. The abundance of *S. cariosus* varied seasonally but was usually plentiful from September to November and low in December to July with most barnacles being large and high in the intertidal zone. The new barnacle settlement was in early July. The availability of barnacles of suitable size and distribution for predation by *Nucella lamellosa* regulated the nutrient acquisition of the *Nucella*. Thus the increase in visceral mass, gonad-digestive gland, and the capsule-albumin gland indices between August and September were probably related to the presence of barnacles of optimum size for predation (Stickle 1973). Usually populations of *Semibalanus cariosus* on the San Juan Islands are dominated by animals of 2–9 mm diameter. Occasionally, there are peaks of animals greater than 20 mm diameter; these are caused by the death of the predators (Sebens & Lewis 1985).

By measuring the diameters of successful drill holes and knowing the unsuccessful drill attempts and the relationship of shell length to hole diameter, Palmer (1990) was able to determine the ability of hatchlings of *Nucella emarginata* (1.1–5.3 mm shell length) to attack and consume barnacles, *Balanus glandula* and *Chthamalus dalli*, of various sizes (1.0–6.0 mm opercular diameter). The smallest *Nucella emarginata* (1.45 mm shell length) were able to consume a few of the largest barnacles offered (6.0 mm opercular opening) but such attacks were successful less than 10% of the time. At least a 50% success was attained by *N. emarginata* of 5 mm shell length on nearly all sizes of barnacles offered. Although attacked with equal frequency larger barnacles were less likely to be drilled successfully and the average growth rate of the young *N. emarginata* decreased with increasing barnacle size mainly due to decrease in successful attacks. Attacks at sutures and on the operculum by hatchlings were more successful than attacks elsewhere on the shell wall.

Bertness (1977) found that thaid size gradients on the shore are in response to similar size gradients in their major prey, *Balanus* and *Semibalanus* species. An energetically efficient size relationship of predator to prey is therefore introduced and resource partitioning results. This study was extended by Butler (1979). He showed from field observations on three *Nucella* species, *N. emarginata*, *N. lamellosa* and *N. canaliculata* on the Pacific coast of north America and *N. orbata* in Australia, that the relationship between size distribution and intertidal height or subtidal depth was very variable. Butler (1979) argued that when there is a size gradient it is produced by responses of the *Nucella* species to factors such as shelter, temperature, desiccation and food.

On San Juan Island, Puget Sound, three intertidal barnacles, *Balanus glandula*, *Semibalanus cariosus*, and *Chthamalus dalli* are the prey of *Nucella emarginata*, *N. lamellosa*, and *N. canaliculata*. Larvae of *Balanus glandula* settle throughout the intertidal zone but, except where predators are absent in quiet bays, the barnacle only survives to reach maturity in a narrow zone at the top of the shore (Connell 1970, 1972). *Nucella emarginata* and *N. lamellosa* could account for all the mortality of *Balanus glandula* on the low shore in mid to late summer. In the autumn the predators move upwards and the increased predation is probably enough to eliminate barnacles on the middle and upper shore within the next year. The breeding population of *B. glandula* in the upper shore “refuge” is sufficient to replace itself there and on the mid and lower shore. The barnacles on these levels can be regarded as a regular food supply for *Nucella emarginata*. Because of the dependability of the food supply at the upper shore levels, Connell (1970) says *N. emarginata* has evolved to specialize there. *Semibalanus cariosus* on the same shores may be eaten by *Nucella lamellosa* within 12–15 months, but if the barnacles are protected from the predator by cages for two years and the cages then removed *N. lamellosa* ignores the 2-yr old barnacles and only consumes the younger ones. The older barnacles have reached a size-refuge.

According to Dayton (1971) *Nucella* will selectively kill most of the *Balanus glandula* by the end of the first summer after settlement by which time *Chthamalus dalli* density will have increased. Dayton (1971) followed mixed size classes of *Balanus glandula* and *Semibalanus cariosus*. *Nucella canaliculata* and *N. emarginata* killed all 320 *Balanus glandula* within 10 days after a protecting cage was removed. Later all 47 *Semibalanus cariosus* with a basal diameter of less than 10 mm were also killed; *S. cariosus* of 13–19 mm basal diameter having presumably reached a size-refuge. *Nucella lamellosa* will, however, feed on large *Semibalanus cariosus* in the very low intertidal zone where they may only be exposed every two weeks by the lowest tides (Connell 1972).

Spight (1973, 1981, 1982) studied the various effects of barnacle prey on the populations of *Nucella* species in the Puget Sound area including the existence of *Nucella emarginata*

and *N. lamellosa* together on the same shore (Spight 1982); the effect of food on the shape of the *N. lamellosa* shell (Spight 1973), and the co-existence of the three *Nucella* species on a limited food supply (Spight 1982). *N. emarginata* and *N. lamellosa* are both intertidal, both depend on barnacles and mussels for food but they are found at different levels and have different life histories. *N. emarginata* is small (22–26 mm adult size), reaching maturity in one year and only a few (about 5%) survive for two years. It remains on the upper shore above the 0.6 m level. *N. lamellosa* is bigger (30–60 mm adult size), has a long juvenile period of four years and breeds once a year for several successive years. It is usually on the low shore (+0.6 m to -0.3 m). When the density of *Balanus glandula* is reduced young *Semibalanus cariosus* become available and many of these survive for a year or more. In natural conditions *Nucella lamellosa* grows at 0–1 mm month⁻¹ during spring and 2–3 mm month⁻¹ in summer. *N. emarginata* and *N. canaliculata* grow 2–3 mm month⁻¹ in spring and 0–1 mm month⁻¹ in summer. All three *Nucella* are, however, opportunists and when unlimited food is available (in the laboratory) seasonal and interspecific differences disappear. Temporal differences in the field must arise from spatial segregation rather than differences in activity or because barnacle availability differs from one area to another (Spight 1981).

Navarrete (1996) and Wieters & Navarrete (1998) investigated the variable predation and feeding preferences of *Nucella canaliculata* and *N. emarginata* on the Oregon coast. The prey available were *Mytilus trossulus* and the barnacle *Balanus glandula*. They found that the preference ranking of different prey species changed among some populations of *Nucella*. If mussels were absent from year to year then they were ignored when newly offered to *Nucella* spp. If, however, the mussels were seasonally abundant or only available within scattered patches then they were eaten but barnacles remained the preferred diet. The ability of *Nucella* spp to “learn” to handle prey more efficiently and eventually to choose prey according to past dietary experience has been shown by other workers (Hughes & Dunkin 1984b, Palmer 1984, West 1986, Burrows & Hughes 1991). Navarrete & Menge (1996) also showed that *N. canaliculata* and *N. emarginata* possess some degree of “ingestive conditioning” (*sensu* Wood 1968). After about 70 days *Nucella* spp. not accustomed to mussels were able to handle and consume them confirming observations made by Murdoch (1969) and Burrows & Hughes (1991).

Further south on the Pacific coast on the Monterey Peninsula, *Tetraclita rubescens* becomes prey for *Nucella emarginata* (Villalobos 1979b, West 1986). West’s (1986) data suggest that selection of prey by *N. emarginata* does not simply reflect the abundance of the prey species available. At one site seven prey species were consumed of which four were barnacles; at a second site five prey species were attacked but only three were barnacles. *Chthamalus* species (both *C. dalli* and *C. fissus* combined), *Balanus glandula*, and *Tetraclita rubescens* were taken at both sites with the addition of *Pollicipes polymerus* at the first site. *Nucella emarginata* was found to feed on *Balanus glandula* in preference to *Chthamalus fissus* (Connell 1961b). The acorn barnacles were always drilled between the paired tergal or paired scutal valves. None were seen drilled between a tergal and scutal pair. In a few cases West (1986) found that the opercular plates seemed to have been forced open without drilling in contrast to the observations of Palmer (1982, see earlier). West (1986) found that *Pollicipes polymerus* was always drilled laterally between the rostral and scutal valves. *P. polymerus* was also mentioned as a prey by West (1986) and Murdoch (1969) at Goleta Point and at Pacific Grove. This stalked barnacle was also consumed by *Nucella emarginata* and *N. lamellosa* at sites on Vancouver Island where areas had been cleared of other organisms in an attempt to study recolonization of an area by *Pollicipes* (Bernard 1988, Barnes 1996).

Nucella haemastoma floridana

Nucella haemastoma floridana is a destructive predator of the American oyster in the Gulf of Mexico. It also preys on the barnacles *Chelonibia patula* and *Balanus* spp. (Cake 1983). The prey barnacles in this area normally occur as epifauna associated with crabs: *Chelonibia* on blue crabs and *Balanus* spp. on hermit crabs. Blue crabs infested with *Nucella* carried about 9.4 times as many live barnacles as did infested hermit crabs (Table 11). The number of *Nucella* on blue crabs was inversely proportional to the number of barnacles whereas the opposite was true on hermit crab. This is a function of the total shell space available for foraging *Nucella* to attack. When a blue crab's carapace was heavily infested (>50% coverage) with live barnacles the lack of space limited the predation by *Nucella*. When live barnacles were present on hermit crab shells 179 (91.8%) of 195 *Nucella* mounted the shells: 63.6% in the presence of *Nucella* and 28.2% in the absence of *Nucella*. In the absence of live barnacles these percentages were reduced to 5.6% and 2.6%, respectively. The *Nucella* attracted to such epifaunal barnacles remained on them until the preferred prey (oysters) were available. Foraging *Nucella* are negatively geotactic and when placed under water they will always move upwards, unless suitable food is encountered in the water, so mounting the crab or hermit crab shells is not unusual.

Table 11 Infestation of crabs and hermit crabs by *Nucella haemastoma floridana* feeding on barnacles. (After Cake 1983.)

	Blue crabs	Hermit crabs
No. of drill infested crabs	99	233
No. of drills	203	299
Mean no. drills crab ⁻¹	2.0 ± 2.1	1.3 ± 0.8
(range)	(1–17)	(1–6)
No. of barnacle infested crabs	99	103
No. of live barnacles	8099	896
No. of barnacles crab ⁻¹	81.8 ± 33.8	8.7 ± 18.8
(range)	(12–287)	(0–120)

Nucella heyseana

Nucella heyseana is abundant in the shallow waters of the western and northern Sea of Japan. It is a common predator on rocky areas and occupies a similar ecological habitat to *N. lapillus* in Atlantic shallow water regions. The diet of *N. heyseana* is varied and includes the barnacle *Chthamalus dalli* although *Mytilus trossulus* is preferred (Gul'bin & Shadrin 1991). Feeding aggregations of the mature predator can move in the intertidal zone at a speed of 3–5 m day⁻¹ and consume 90–95% of their prey (Gul'bin & Shadrin 1991). Some prey are drilled but in barnacles the proboscis is inserted between the opercular plates. In areas where *Nucella heyseana* is abundant the barnacles rarely reach their maximum size and so the population is always young and *N. heyseana* maximizes the population productivity of its prey in the intertidal zone.

Nucella lapillus

In the literature pertaining to the predation of barnacles this gastropod has been referred to as *Purpura lapillus*, *Nucella lapillus* and *Thais lapillus*. In order to avoid confusion the name *Nucella lapillus* is used in what follows. *N. lapillus* belongs to that group of gastropods which occupies and often dominates many rocky shores from the highest to the lowest levels. It is found on the shores of Europe and eastern North America (Connell 1961b, 1970, Lewis 1964, Largen 1967a, Bayne & Scullard 1978, Underwood 1979, 1985, Hughes 1985, Hughes & Burrows 1990, Burrows & Hughes 1991). Its principal prey are the barnacles *Semibalanus balanoides*, *Chthamalus* species and *Elminius modestus* (see, for example, Fischer-Piette 1934, Moore 1938, Connell 1961a,b, Largen 1967b, Hughes & Dunkin 1984a, Burrows 1985). The predation by *Nucella lapillus* on the distribution and abundance of barnacles has been reviewed by Connell (1972, 1975). This predation may be sufficient to eliminate barnacles from the lower shore but at higher levels submersion time may be insufficient for consumption of a barnacle and so the barnacles can grow sufficiently to reach a size refuge (Underwood 1979).

N. lapillus often cease feeding and aggregate at certain times of the year. They aggregate and shelter in crevices during gales or periods of cold weather (Moore 1938, Connell 1961a). Complex patterns of aggregation in summer, winter, and before reproductive activity have been described by Feare (1971). Summer aggregations suggested a link with feeding as they were found on mussels and barnacles, *Semibalanus balanoides*. Feare (1971) found an average of 91.8% of *Nucella lapillus* feeding within groups compared with 34.5% outside groups. Winter aggregation is probably a defence mechanism to reduce chances of dislodgement in inclement weather. The holding power of *Nucella* was not reduced at low temperatures but if physically removed they were unable to regain a foothold at 5°C (Feare 1971).

Largen (1967a) determined the influence of water temperature on the feeding rate of *N. lapillus* on barnacles. The rate increased from 0.4 barnacle *Nucella*⁻¹ week⁻¹ at 3°C to 16.0 barnacles *Nucella*⁻¹ week⁻¹ at 20°C. At 27–28°C the *Nucella* become comatose.

Menge (1978a,b) followed the activities of *N. lapillus* on several shores of different degrees of exposure to determine the effects of wave action and desiccation of its intensity of predation on its prey, particularly *Semibalanus balanoides*, on the eastern coast of North America. Reduction of predation on such shores was not due to an absence of *Nucella* but rather that wave shock reduced foraging and kept the predators sheltering in crevices. On sheltered shores desiccation during low tides possibly influenced the activity of *Nucella* (see also Dayton 1971, Menge & Sutherland 1976).

The most common prey of *Nucella* are mussels and barnacles (for example, see Hughes & Dunkin 1984a,b.). Hughes & Dunkin (1984a) give the cirripede prey as *Semibalanus balanoides*, *Chthamalus stellatus* (probably including *C. montagui*) and *Elminius modestus*. *Nucella* maintained for 2–3 months on either the first of these barnacles or mussels, *Mytilus edulis*, causes them to increase their tendency to attack the familiar prey when subsequently offered both—a result of ingestive conditioning (Hughes & Dunkin 1984b). According to Hughes (1985) ingestive conditioning was first demonstrated by Wood (1968).

Dunkin & Hughes (1984) maintained *Nucella lapillus* on mussels for 60 days to reduce prior effects of ingestive conditioning and handling skills. When dealing with barnacles these “inexperienced” *Nucella* preferred the largest presented to them. Juvenile and adult *Nucella* maintained on barnacles—called “experienced”—preferred intermediate sized barnacles that correlated with the size of *Nucella*. “Inexperienced” *Nucella* penetrated

barnacles more often by drilling than forcing them open; the reverse was true for “experienced” *Nucella*. After consuming 6–8 consecutive prey “inexperienced” *Nucella* began to force the barnacles open in preference to drilling them. “Experienced” predators forced open all barnacles of about 2 mm opercular diameter but only 20% of those of about 6 mm opercular diameter. Barnacles of 4–5 mm opercular diameter were the size preferred by “experienced” *Nucella*; they could force them open in 50% of the attacks made. Barnacles were inspected for about 20 min by *Nucella* if they were eventually rejected and for about 30 min if they were to be consumed. The time required to obtain penetration and to consume the contents depended on the opercular diameter of the barnacle. Those with opercular diameters of 2.5–2.7 mm required 4–26 h handling time. Because of the mode of attack, “experienced” *Nucella* handled barnacles faster than “inexperienced” ones. The yield of food per unit handling time could be increased by a factor of about 1.2 for barnacles with an opercular diameter of 7 mm to about 200 for barnacles with a 2 mm opercular diameter. Minimizing handling time is important if there is a risk in nature of the predator being displaced by a competitor or dislodged for any reason. Barnacles of about 5 mm opercular diameter were estimated by Dunkin & Hughes (1984) to be slightly more profitable to a *Nucella* experienced with barnacles than mussels of 17.5 mm length but less profitable to one experienced with mussels. *N. lapillus* may switch, therefore, between diets mainly of barnacles or mussels if the abundance of prey of similar food value is drastically changed (Dunkin & Hughes 1984). The switching ability of *Nucella* was recorded by Morgan (1972) after a *Semibalanus balanoides* population was destroyed.

Burrows & Hughes (1991) found that *Nucella lapillus* feeding on *Semibalanus balanoides* spent a longer time foraging than when feeding on mussels; also extended bouts of attacks were probable. In diverse conditions foraging time was reduced and a smaller size of barnacle was taken. This reduced the gain per prey item by 40% (Hughes & Burrows 1990). This represents a decrease in energy intake per item of 20% using the estimates of handling time given by Dunkin & Hughes (1984) and Hughes & Dunkin (1984a).

Nucella lapillus foraged among barnacles for 1–3 tidal cycles on an exposed shore, moving about 160 mm between low tides and then about 460 mm to a resting place, probably a crevice. They rested there for 2–4 tidal cycles before foraging again. About 4–5 barnacles (50 mg AFDW of flesh) were consumed per foraging bout (Hughes & Drewett, 1985). These foraging distances are of the same order (100 mm per tide) as those found by Connell (1961a). In summer at Millport, Scotland, *Nucella* fed about 60% of the time (Connell 1961a).

In the absence of *Semibalanus balanoides*, and when not protected from *Nucella* by cages, a few *Chthamalus stellatus* (probably mixed with *C. montagui*) were evidently eaten (Connell 1961b). *Nucella*, however, prefers a larger barnacle and so a switch is made to *Semibalanus balanoides*. This preference is also illustrated by Barnett (1979) and Burrows (1985). Burrows (1985) found that *Nucella* showed no preference between *Chthamalus stellatus*, *C. montagui* and *Semibalanus balanoides* at upper shore levels. On the midshore, however, *Chthamalus montagui* was consumed much less frequently than the other two. *Semibalanus balanoides* was taken in preference to *Elminius modestus* in laboratory experiments except when *Nucella* had been starved for a long time (Barnett 1979). The predator’s attack was by forcing in *Elminius* and by drilling in *Semibalanus*; the drilling was usually at the occludent margin of the opercular valves (Barnett 1979). Moore (1938), however, did not find any drilled shells; the opercular valves of both *Chthamalus* and *Semibalanus* were forced apart. It may be that purpurin is used by *Nucella* to relax and kill its prey. Largen (1967b) examined the shells of small barnacles that had been preyed on

by newly hatched *Nucella*. The shells all showed drilling on the wall plates or operculum; the normal forcing open by *Nucella* was not seen. It suggests that the very young *Nucella* lack the strength to force open the opercular valves even of small barnacles.

On Cape Ann, Massachusetts, *N. lapillus* feeds mainly on barnacles and showed a tendency to remain on them between tides or in crevices or under seaweed. During a day, a *Nucella* may travel up to 240mm (Dexter 1943, 1947). Jillson (1981) demonstrated the overlap of prey size available and eaten by *Urosalpinx* and *Nucella* on sheltered shores. The former's diet consisted of 35% barnacles and 65% mussels. *Nucella* consumed 76% barnacles in a habitat where the relative availability of barnacles was 55%. Both these predators ate smaller than average sized barnacles, failing to take advantage of the larger prey present. In the absence of *Urosalpinx* on exposed shores *Nucella* showed a prey size selection but no prey species preference. Competition between the two predators on sheltered shores is reduced by their preferential feeding on different prey species (Jillson 1981).

Menge (1976) followed the diet of *Nucella* in several areas of New England shores for 3 years. As found by other workers the main prey are mussels and barnacles. Of 1265 *Nucella* observed feeding in all areas only six were eating other prey. He also found that the composition of the diet can vary from year to year depending on the abundance of the preferred prey. When necessary *Nucella* can switch from a diet of 89% barnacles in one summer to a diet of 88.6% mussels in a summer two years later.

It has been shown that some predators, including *Nucella* take shelter when exposed to extreme environmental conditions. Menge (1983) points out that predation intensity often increases along local gradients of decreasing harshness of the environment. This is due to the increase in number and effectiveness of the individual predators. On relatively protected intertidal rocky shores of northern New England a group of predators, including three species of crabs, two of seastars, and one *Nucella* species, form a predator guild. These predators prevent mussel or barnacle populations from outcompeting the red alga, *Chondrus crispus*. Of these predators *Nucella lapillus* is apparently the only functionally important one in the mid-tidal zone according to Menge (1983) although others occur in the lower zone (Menge 1976, 1978a,b, 1982a, Edwards et al. 1982).

On the northern shore of the Gaspé Peninsula, Quebec, Canada, ice cover can be expected from late November to April and ice breakup can cause severe ice scouring of exposed surfaces. *N. lapillus* spends from October to early May clustered near the base of boulders. The main foraging only begins in early June. *Semibalanus balanoides* cyprids settle in June and Gosselin & Bourget (1989) found *Nucella* foraging on them in early July when the barnacle recruits were 3–5 mm in diameter. These authors examined the influence of substratum heterogeneity on the performance of *Nucella* in the field. It had higher growth rates on heterogeneous than homogeneous surfaces which agrees with barnacles having a higher quality as prey on the former surfaces. The predator also had better protection from exposure and wave action on a heterogeneous surface.

Nucella melones

Nucella melones is present at a very low density of less than 1 m⁻² on Costa Rican shores according to Ortega (1987). It was not found feeding on barnacles during the investigations of Sutherland & Ortega (1986). This gastropod is restricted to the base of pilings and under stones at the places examined by Villalobos (1980) at Costa Rica together with *Acanthina brevidentata* and *Anachis rugosa*. *Tetraclita stalactifera* is also found on the pilings but no details are given about *Nucella melones* preying on this barnacle except to say that it is

one of the important predators. Barnacles here with a diameter of greater than 25 mm were almost free from predation, probably having reached a size-refuge.

Nucella orbata

According to Phillips & Campbell (1974) *Nucella orbata* (as *Dicathais orbata*) on Australian shores is similar in habit and behaviour to *Nucella haemastoma* in the Northern Hemisphere.

The effect of predation on rocky shores near Sydney, NSW, has been investigated by Underwood & Fairweather (1985) and Fairweather (1986). The distribution and abundance of all predatory species were observed but only two, *Morula marginalba* and *Nucella orbata* were significant. The predation of the former has been dealt with on pp. 182–6. Predation of *Tesseropora rosea* by *Nucella orbata* was also found to be important by Caffey (1985).

Nucella orbata grows larger than *Morula marginalba*, feeds faster and moves more extensively on the shore. It is capable of moving several metres overnight or within a few days. Some *Nucella* moved further than *Morula* over one or two days but a larger proportion of the former than the latter did not move at all (Fairweather 1988d). *Nucella orbata* is found in areas with more wave action than that experienced by *Morula*. *Nucella* is not so dependent on nearby shelter as is *Morula* but it still retreats to shelter in some conditions. In the mid-intertidal zone there was no trend in the abundance of *Nucella* along a gradient of exposure to waves (Moran 1985b, Fairweather 1988a).

Moran (1985c) developed the idea of feeding fronts of predators on a shore. The progression of feeding fronts of *Nucella* is rapid; this predator has a larger foot than *Morula* and is, therefore, more mobile. The rapid movement of *Nucella* allows it to predate on barnacles higher up the shore than does *Morula* and then retreat to shelter lower down on the shore when necessary (Fairweather 1988d). *Nucella* is also able to cover a greater area in search of its preferred prey and this may be the reason for it concentrating on *Tesseropora rosea*. This barnacle forms more than 80% of its diet (Moran 1985c). The distribution and movement of *Nucella orbata* (as *Dicathais aegrota*) of different sizes can vary from place to place in ways that may be due to differing prey distributions. When predation occurs the barnacles may not be drilled, but merely smothered by the foot of the *Nucella* until the valves are dislodged and the proboscis can be inserted (Phillips 1969).

Nucella pansa

On exposed Pacific coasts of Panama *Chthamalus* sp. and *Tetraclita stalactifera panamensis* each form <0.01% of the diet of *Nucella pansa*, a high intertidal neogastropod (Garrity & Levings 1981). In a short-term experiment, settlement of *Chthamalus fissus* was inhibited by the grazing and/or bulldozing of the mobile herbivore *Nerita scabricosta* the principal predator of which is *Nucella pansa* (Garrity & Levings 1981, Levings & Garrity 1983).

Ocenebra species

Luckens (1970b) found that there was some uncertainty about the identification of the *Ocenebra* species found on the Japanese coast near Asamushi. It will, therefore, merely be referred to as *Ocenebra*. In the Asamushi area Luckens (1970b) found that predators were not as common as on northern New Zealand shores and that their level on the shore varied

with the season. In general, she decided that predation was not an important factor affecting intertidal zonation.

The distribution of *Ocenebra* shows definite vertical movement throughout the year. In winter all those on steep shores, where algae are scarce, move down to subtidal levels. Where algae are present a few remain in the low intertidal area. In late April to early May *Ocenebra* re-appears in the low intertidal, but retreats again in the heat of the summer. *Ocenebra* may be found on the lowest barnacles in the spring. At the end of June newly hatched *Ocenebra* were found feeding on newly settled *Chthamalus*. The species eaten by *Ocenebra* during feeding trials included *Megabalanus tintinnabulum rosa*, *Chthamalus challengerii*, *Balanus trigonus* and *B. albicostatus albicostatus*. The barnacles were usually bored either at the junction of the opercular valves, where a long scraped out depression was common, or in the wall plates, where slightly tapering holes were produced (Luckens 1970b). *Ocenebra* appears to prefer larger barnacles to smaller ones with a size range that can be bored and eaten. *Balanus albicostatus albicostatus* was preferred to *Chthamalus challengerii*. She found, however that two very young *Ocenebra* that were able to crawl much more readily than adults, consumed 77 *Chthamalus challengerii* less than three weeks old in eight days. The barnacles had been bored through the wall plates. Other species, such as *Balanus trigonus*, *Megabalanus tintinnabulum rosa* and *Balanus rostratus* are eaten by *Ocenebra* but these prey occur in such small numbers that they only form a small part of the predator's diet.

Urosalpinx species

Urosalpinx cinerea occurs on the Atlantic coast of North America and has been carried by artificial means to other parts of the world. Populations can vary in size, colour, and shell shape. This variation has led to taxonomic separation of the species into *U. cinerea follyensis* and *U. cinerea cinerea* (see Wood 1968) but they are all essentially *U. cinerea* and that will be the name used in this review.

Chemical stimuli guide this predator to its prey. *U. cinerea*, commonly known as the oyster drill, from Narragansett Bay, Rhode Island, is accustomed to feeding on *Semibalanus balanoides* in that area. In choice chamber experiments *Urosalpinx* was strongly attracted by effluents of *Semibalanus balanoides* with a preference of 3.5:1 in summed runs compared with controls. The mean time of response was 15.9 min. *Urosalpinx* was even more attracted to *Balanus eburneus* (Pratt 1974). Newly hatched *Urosalpinx* from Delaware Bay that had not eaten prey and had had no previous experience of prey detection responded to odours of living *Semibalanus balanoides* and *Balanus eburneus* more readily than to odours of other potential prey. The barnacle odours caused 90% of the *Urosalpinx* to move upstream and the attraction persisted even after a 200-fold dilution (Rittschof et al. 1983). Water from *Trypetesa lampas*, a small barnacle which burrows into gastropod shells inhabited by hermit crabs elicited a low but significant response of 15%. The hatching and early stages of life are critical to *Urosalpinx* and Rittschof et al. (1983) suggest that all the senses, including those involved in chemoreception, are probably evolved to direct the young snails to habitats with plenty of prey barnacles and areas that will be free of predators and resistant to desiccation.

Flow rate as well as concentration of attractant affect the responses of *Urosalpinx*. Reactions to either of these alone is negligible. The response of the snail increases with flow rate and concentration of attractant until the response becomes constant (Brown & Rittschof 1984). These authors tested the attractiveness of *Semibalanus balanoides*, *Balanus eburneus*, *B. amphitrite*, *B. subalbidus*, and *B. nubilus*.

As well as the attractant from barnacles, in their natural habitat newly hatched and young *Urosalpinx* are also exposed to attractants from other prey, particularly oysters, *Crassostrea virginica*. Williams et al. (1983) investigated how *Urosalpinx* differentiates between chemical odours from several co-occurring species of prey such as the barnacles, *Semibalanus balanoides* and *Balanus eburneus*, oysters and mussels. Mussel odour inhibited the response of *Urosalpinx* to *Balanus eburneus* but did not itself evoke chemotaxis. Oyster odour was found to inhibit response to high concentrations of barnacle odour but to increase it at low concentrations.

Rittschof et al. (1984) give methods for extracting and desalting attractants originating from living barnacles, *Semibalanus balanoides* and *Balanus eburneus*. They found these attractants to be relatively large, heat-stable and partially proteinaceous molecules (>1000 but <10000 Daltons). Non-specific proteases such as carboxypeptidase and pronase, but not trypsin, destroyed the potency. Kieber & Rittschof (1985) used the bioassay developed by Rittschof et al. (1983) to test the effect of a series of low molecular weight organics on the ability of newly hatched *Urosalpinx* to detect prey odour from *Semibalanus balanoides*. Two series were tested using methanol as a reference compound. In the first series, R-OH, the chain length varied from 1 to 4. In the second, CH₃-R, the chain length was constant but the functional group R was varied. When present in the mM range the response of *Urosalpinx* to barnacle odour was inhibited to varying degrees in the CH₃-R series: sodium acetate>ethyl acetate>acetonitrile>methanol; in the alcohol series inhibition increased with increasing chain length C₁ to C₄.

Because the attractant produced by barnacles has withstood selection pressure over the years, Rittschof et al. (1984) suggest that the attractant itself may be of some use to the barnacle or it is an unavoidable excretory product. Adult *Urosalpinx cinerea* and *Eupleura caudata etterae* showed responses higher than expected to *Semibalanus balanoides* attractants, whereas responses to oysters and mussels were lower than expected (Rittschof & Gruber 1988). The general attractive nature of barnacles to *Urosalpinx* could be the result of energy per unit effort (handling time, see Fairweather & Underwood 1983). *Urosalpinx* can consume barnacles by extending the proboscis between the opercular valves whereas they generally have to bore holes in shells of bivalve prey (Wood 1968).

The accessory boring organism (ABO) is essential to shell penetration in boring gastropods. If it is removed, for example in *Urosalpinx cinerea*, even though the snail recovers it is not able to bore until the ABO has been regenerated (Carriker 1981). After being softened by secretion from the ABO, the abrasive action of the radula removes the shell leaving characteristic holes as illustrated by Carriker (1961). The radula function during shell penetration has been examined by slow motion photography and scanning electron microscopy in several species, such as *U. cinerea follyensis* (Carriker et al. 1974) and *Nucella lapillus* (Runham 1969).

The ABO of *Urosalpinx cinerea* acts to dissolve the shell of a prey item for periods varying from a few minutes to about an hour. Radular rasping alternates with chemical activity. The rate of normal shell penetration is about 0.3–0.5 mm day⁻¹. Secretion from the ABO has been found to contain carbonic anhydrase among other substances. Carbonic anhydrase may be involved in the shell dissolution as the normal rate of penetration in both *U. cinerea* (Carriker & Williams 1978) and *Nucella lapillus* (Chétail & Fournié 1969) is reduced if carbonic anhydrase is inhibited by the addition of sodium acetazolamide to sea water containing the gastropods. Chétail & Fournié (1969) found that boring activity was increased in sea water enriched with carbon dioxide and also by the addition of sodium chloride or potassium chloride. As a result of their experiments they concluded that the activity of carbonic anhydrase must be accompanied by complex ionic exchanges.

Urosalpinx is able to bore into calcareous material by action of its radula and ABO producing a slightly conical hole through which the proboscis can be inserted. When preying on barnacles, however, the proboscis can be inserted between the opercular valves; in this case an attack can be successfully completed in less than one hour. Boring a hole through thickened wall plates of barnacles would take more time and energy than boring the thin valve of an oyster spat. At some places (e.g. Locust Point) *Urosalpinx* apparently bored the opercular valves or wall plates of barnacles even though these “holes” were frequently incomplete (Wood 1968). From direct observations spanning four years on the Atlantic coast of North America from Nobska to Nassau, Wood (1968) found that 58% of attacks by *Urosalpinx* were on barnacles, 16% on mussels, and 26% on oysters. Towards the south of the range, predation on mussels and oysters increased slightly owing to the natural distribution of the prey. At Nobska *Semibalanus balanoides* is dominant; at Ocean City, because of peculiarities in the barnacle zonation, few attacks on barnacles were recorded. Wood (1968) provided experimental evidence of the concept of “ingestive conditioning”.

Franz (1971) found *S. balanoides* to be the main prey of *Urosalpinx cinerea* on the Connecticut coast of North America. The barnacles settle in enormous numbers in the spring—about March—and these are preyed on by snails from the previous year’s settlement, thus reducing a finite food supply. By the time the current year class of *Urosalpinx* appear in July the remaining barnacles have grown sufficiently large to be unsuitable for the very young snails and an alternative prey has to be found. Katz (1985) confirmed *Semibalanus balanoides* as the prey of *Urosalpinx* on the Connecticut coast. He used field manipulations and observations to investigate the interaction between predator and prey (*Semibalanus balanoides* and *Mytilus edulis*). Given the choice it is known that *Urosalpinx* is preferentially attracted to barnacles (see e.g. Wood 1968, Pratt 1974). It is also known that the strength of the attraction depends on the previous feeding history. If accustomed to barnacles then *Urosalpinx* selects barnacles. When previously fed on oysters and then given the choice of barnacles or oysters, *Urosalpinx* will respond equally to the odours from oysters and barnacles (Pratt 1974). Environmental conditioning to barnacles and a preference for them probably contribute to *Urosalpinx* not fully switching its feeding behaviour as barnacles become scarce. The destabilizing predator responses and extinction of the prey suggest that interaction between *Urosalpinx* and *Semibalanus balanoides* is best explained by a non-equilibrium theory.

Further south on the North American coast, as *Semibalanus balanoides* reaches its southern limit of distribution, *Balanus eburneus* becomes the barnacle prey for *Urosalpinx* as on the coast of New Jersey (Peterson 1979).

Mollusca, Nudibranchia

One of the common nudibranchs found on British shores is *Onchidoris bilamellata*. Since Farran (1909) found it in Irish waters associated with objects covered with acorn barnacles papers have been written about it under various names (see p. 154).

According to Thompson & Brown (1984) this is a “boreo-panarctic species reaching a southern limit in Europe on the French coast”. It is locally abundant on British coasts and along the Norwegian coast to the White Sea and Spitzbergen. It is found on the eastern coast of America as far south as New England and on the west coast in Alaska and Puget Sound (see also Potts 1970).

Before the work of Barnes & Powell (1951, 1954) the diet of this species was not known although it was thought that it might have been polyzoans. It is now clear that acorn

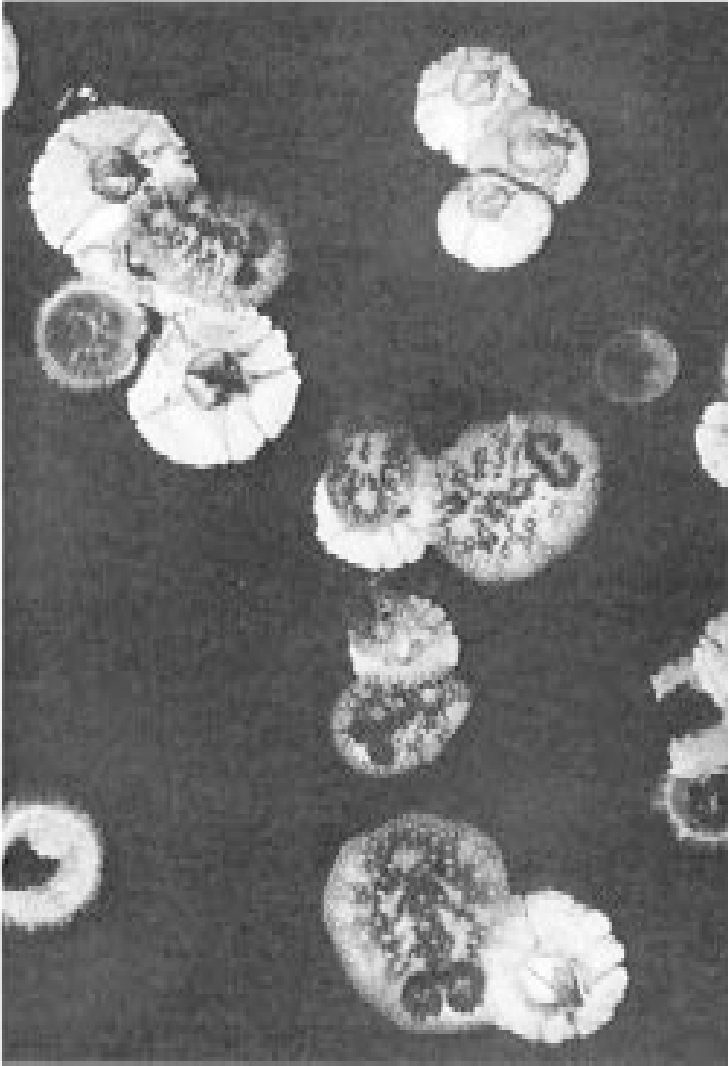


Figure 5 Millport, Scotland; *Onchidoris fusca* feeding on *Balanus crenatus* of various sizes growing on a dark bakelite panel. (With permission of *The Journal of Animal Ecology*, plate published in Vol. 23, 1954).

barnacles are the main food item (Thompson & Brown 1984). The opercular plates of the barnacle are forced apart and the soft parts removed. The cirri and chitinous exoskeleton are left in the dead barnacles (Barnes & Powell 1954, Thompson & Brown 1984).

At Millport, Scotland, *O. bilamellata* was observed on barnacle-covered panels suspended 2 ft below the sea surface (Barnes & Powell 1951, 1954). The barnacles were mixed *Semibalanus balanoides* and *Balanus crenatus* and the nudibranchs spent long periods covering the uppermost parts of the barnacles (Fig. 5). A detailed examination was made in mid-October at a time when ovarian material was present in *Balanus crenatus*. When the nudibranchs were removed the opercular valves of the barnacles were still sticking

to the anterior region of the ventral surface. There were no chitinous remains in the guts of the nudibranchs but the oily appearance could have resulted from ingestion of the ovarian material of the barnacles. The behaviour of the predator was followed in detail in the laboratory. On making contact with a barnacle, *Onchidoris* slowly glides up the side of the shell and comes to lie over the opercular orifice. Small *Onchidoris* tend to reach the orifice at or near the rostral end; if it first contacts the barnacle base at the carinal end then it takes an upward, more or less spiral course towards the rostral end. The *Onchidoris* remains in position over the orifice for several hours (5–20 h, varying with the size of both predator and barnacle). After feeding, the nudibranch moves off the orifice and frequently stays alongside the barnacle presumably while the nudibranch digests the soft parts; later it begins to move away and becomes active again. Examination of a barnacle after predation shows that the scutal valves have been pushed into the mantle cavity, the opercular membrane having been torn away from the calcareous plates in the scutal region. Because the details of this process are obscured by the body of the predator it is impossible to be certain exactly how entry is made. Enzymes may be used or the pressure exerted on the operculum may be sufficient to break it away from the barnacle shell. The downward pressure on the horizontal plane at the scutal end will be greater than at the steeper tergal end. Once the edge is ruptured, the muscles closing the operculum are no longer effective. The barnacles used in these tests were grown on panels under raft conditions and were 8–24 mm carino-rostral length. Forty-eight such barnacles had their soft parts removed by 16 *Onchidoris bilamellata* (15–30 mm long) in 11 days (Barnes & Powell 1954).

According to Thompson (1964) nudibranchs feeding on flattish incrustations such as aggregations of barnacles usually have a broad, flattened foot and are more or less oval in shape (see Fig. 5). Their radula is usually broad and in nature they are well camouflaged. Thompson says that it is the action of the buccal mass that breaks open the opercular plates of a barnacle. He gives *Balanus balanus* (= *B. porcatus*) (Miller 1961) and *Elminius modestus* (Swennen 1961) as prey in addition to *Semibalanus balanoides* and *Balanus crenatus* (Barnes & Powell 1954).

Onchidoris bilamellata may stay in position over a barnacle (*Semibalanus balanoides* or *Balanus crenatus*) for 10 min to 2 h according to Crampton (1977) but only a few seconds (5–15) of this time are spent ingesting the contents. The longest time is taken in getting entry to the barnacle. Crampton (1977) managed to observe the process by cutting away the portion of the mantle overhanging the mouth and small areas of the oral veil. The first phase is a dilatation of the outer lips with the oral veil tightly pressed against the vertical wall of the barnacle shell. The expanded inner lips form a horseshoe-shaped ring, the cavity of which is filled by the buccal lips once the mouth is fully opened. The buccal lips then protract rapidly and separate revealing a pear-shaped aperture with the tapered end ventral. The odontophore can then be seen between the buccal lips. When fully protracted the odontophore contacts the barnacle and executes a rapid anterior and dorsal movement during which the radular teeth open and close in a grabbing action. This eventually ruptures the barnacle mantle. Crampton (1977) describes in detail the anatomy of the buccal apparatus of *Onchidoris bilamellata* as well as the innervation of the buccal apparatus and the feeding cycle. The combination of a piercing, grabbing and suctorial feeding method used by this nudibranch has enabled it to exploit the food source supplied by barnacles.

Semibalanus balanoides and *Balanus balanus* at lower levels, were preyed on by *Onchidoris bilamellata* around the Isle of Man (Miller 1961). The distribution of *O. bilamellata* in the intertidal zone is governed by the distribution of barnacles (Potts 1970). At Sandgate, Kent, *Semibalanus balanoides* was the main prey although *Elminius modestus* was present. Swennen

Table 12 Predation by nine adult *Onchidoris bilamellata* on three species of barnacles in five days. *n*=number available. (After Todd 1979.)

Position on rock	<i>Semibalanus balanoides</i>			<i>Balanus crenatus</i>			<i>Elminius modestus</i>	
	<i>n</i>	No. taken	Mean aperture length (mm)	<i>n</i>	No. taken	Mean carino-rostral length (mm)	<i>n</i>	No. taken
Upper surface	59	57	3.11	0	0	–	3	1
Lateral surface	46	45	3.17	1	1	4.00	8	7
Lower surface	8	7	3.28	852	46	5.53	9	1
Total	113	109	–	853	47	–	20	9

(1961) records the nudibranch feeding on *E. modestus* in the Netherlands but states that *Balanus crenatus* was preferred; only when food was short did *Onchidoris* crawl higher on the shore and feed on *Semibalanus balanoides*. Swennen suggests that smell may be the means of attraction of nudibranchs to barnacles. The time of 2–14 h spent on a barnacle is similar to that of 5–20 h given by Barnes & Powell (1954). Swennen (1961) also found that chitinous parts and eggs remained in the barnacle after predation; that Barnes & Powell (1954) specifically said ovarian tissue was taken (not eggs) agrees with this. Very large nudibranchs may grate off the tops of the wall plates of the barnacle although these are not normally damaged (Swennen 1961).

The ecology of nudibranch molluscs in general has been extensively reviewed by Todd (1981) and the population ecology of *Onchidoris bilamellata* in particular by Todd (1979). *Balanus balanus* (as *B. porcatus*), *B. crenatus*, *Semibalanus balanoides*, *Elminius modestus*, and *Chthamalus* species are all listed as prey of *Onchidoris bilamellata* by Todd (1981). The planktotrophic veliger larvae of *O. bilamellata* will only metamorphose in the presence of live barnacles (Todd 1979, Todd & Doyle 1981). Recruitment, therefore, only occurs in about June at Robin Hood's Bay, England, after *Semibalanus balanoides* has settled. Pediveligers settling too early, before the barnacle spat are available, have a high mortality owing to starvation and those settling too late are also deprived of food because by then the barnacle spat has outgrown the prey size-range of the post-metamorphic nudibranchs. Some rapidly growing nudibranchs may mature precociously in late summer but unless juvenile *Balanus crenatus* or *Elminius modestus* are available at that time the nudibranchs are not likely to survive.

In a laboratory test Todd (1979) compared the number of different species of barnacles preyed on by nine *Onchidoris bilamellata* in five days (Table 12). A single rock on which there were the three species of barnacles was used. *Semibalanus balanoides* was densely crowded and so only the aperture measurement was meaningful. For *Balanus crenatus* the carino-rostral length was given; no size was given for *Elminius modestus*. A total of 165 barnacles was consumed in five days, that is 3.67 barnacles (up to about 8 mm diameter) predator⁻¹ day⁻¹. Barnes & Powell (1954) recorded 0.27 barnacles consumed predator⁻¹ day⁻¹ but this was in October with *Balanus crenatus* of 8–24 mm carino-rostral length. Feeding rate will depend not only on size of predator relative to prey size but on the amount of soft tissue in each barnacle. This varies seasonally with a maximum in mid-October and a minimum in mid-winter. The results in Table 12 indicate a preference for *Semibalanus*

Table 13 Daily rates of predation and sizes and species of barnacle consumed by three individual *Onchidoris bilamellata* (from Todd 1979).

Size of nudibranch (mm)	21.5	23.0	19.0
	Number and mean size of aperture (mm in parentheses) consumed		
Prey	<i>Semibalanus balanoides</i>		<i>Balanus crenatus</i>
Day 0	Experiment started		
1	6 (2.52)	8 (2.43)	6 (2.15)
2	9 (2.27)	6 (2.50)	4 (2.30)
3	4 (2.25)	8 (2.45)	7 (2.03)
4	0 –	8 (2.49)	7 (1.99)
5	5 (2.30)	1 (2.30)	10 (1.95)
6	4 (2.53)	10 (2.37)	9 (2.22)
7	9 (2.37)	8 (2.46)	0 –
8	5 (2.24)	3 (2.47)	4 (1.98)
Total	42	52	47
Mean no. of prey day ⁻¹ ± S.E.	5.25 ± 1.03	6.50 ± 1.07	5.50 ± 1.13

balanoides but this may have been because of the distribution of the barnacles on the rock used. The nudibranchs spent most of the time on the upper rock surface where *Balanus crenatus* was absent.

In another experiment, *B. crenatus* was available on both upper and lower rock surfaces and *Semibalanus balanoides* on the upper surface only. In this case, there was a significant difference in the *Balanus crenatus* taken on the upper and lower surfaces owing to predators taking the larger barnacles. There was no significant difference for *Semibalanus balanoides* although the small increase in aperture size may correspond to a large increase in absolute body size. Because the *S. balanoides* were crowded no comparison in size of *S. balanoides* and *Balanus crenatus* could be made although the former are generally larger. It seemed that the smallest *B. crenatus* available were outside the preferred prey size range for nudibranchs of 19–29 mm length. In this experiment, 189 barnacles were consumed at a rate of 4.20 barnacles predator⁻¹ day⁻¹.

Todd (1979) also investigated the rates of feeding of three *Onchidoris bilamellata* of known size and the size of barnacles taken. Two nudibranchs were given *Semibalanus balanoides* and one was given *Balanus crenatus*. The experiment ran for 8 days and after each 24-h period the barnacles taken were counted, measured and removed (Table 13). Todd's experiments suggest a feeding rate of five to six barnacles of up to 8 mm length nudibranch⁻¹ day⁻¹.

Very occasionally adult *Onchidoris bilamellata* feed on the asymmetrical barnacle, *Verucca stroemia*, but juveniles cannot handle this species. Because the mode of feeding is largely mechanical and involves forcing down the opercular valves of the barnacle, the asymmetrical *Verruca* is well protected from attack by young nudibranchs (Todd 1981). Juvenile *Onchidoris bilamellata* preferentially consume the smallest barnacles; the optimum prey size increases with predator size. A 2-mm nudibranch can consume a 2-mm (carino-rostral length) *Semibalanus balanoides* and an 8-mm nudibranch can consume a 7.5-mm barnacle. The feeding rate of adult *Onchidoris bilamellata* represents the maximum pressure that this adult nudibranch would exert on a barnacle community. In view of the mortality

of the nudibranchs this predation is very small compared with the large numbers of very small barnacles presumed to be destroyed by post-metamorphic nudibranchs.

Todd (1979) found that the faeces of *O. bilamellata*, which had been feeding on *Balanus crenatus* up to 8 mm carino-rostral length, consisted largely of barnacle cirri and exoskeletons. This is contrary to the finding of Barnes & Powell (1954) that only soft material was taken by the nudibranch when feeding on *B. crenatus* of 8–24 mm carino-rostral length. It may be that the nudibranch feeds less efficiently on larger barnacles or is more selective when ovarian as well as body tissue is available.

Whereas Todd (1979) emphasizes that crawling larvae of *Onchidoris bilamellata* must contact adult prey (barnacles) before metamorphosis occurs, Chia & Koss (1988) present evidence that a diffusible chemical from living barnacles is necessary to stimulate settlement of the nudibranch larvae. Thereafter metamorphosis is induced by a chemical or mechano-chemical cue also associated with barnacles. The settlement process is reversible but metamorphosis is irreversible; both processes, however, are influenced by the presence of the adult prey (barnacles). Chia & Koss (1988) worked on *O. bilamellata* collected at Friday Harbor on the west coast of America and at Bamfield on Vancouver Island, Canada. At Friday Harbor this nudibranch preys on barnacles (Connell 1970, Chia & Koss 1988). Sea water alone was not sufficient to induce settlement of competent veligers of *O. bilamellata* but in sea water that contained or had contained living barnacles (*Chthamalus dalli* or *Balanus glandula*) 100% settlement was achieved. Only 8% settlement was attained in sea water conditioned with *Polymerus pollicipes*. A chemical cue derived from subsequent adult prey was necessary for settlement. Metamorphosis, however, involved direct contact with a substratum associated with barnacles. These do not have to be living as dead barnacles or shell fragments and tissue in combination with conditioned sea water was sufficient. A newly metamorphosed *Onchidoris bilamellata* is not only very small but is also very soft and it would not be able to feed on barnacle spat immediately. Hadfield (1963) suggested that the small adults may depend on grazing of algae or sessile ciliates, or even on detritus, until they are old enough to feed on barnacles. Chia & Koss (1988) observed newly metamorphosed juveniles surviving on detritus, and Todd has also seen juvenile nudibranchs feeding on debris associated with established barnacles.

Eliot (1910) records the nudibranch *Fiona marina* as having a pale brown colour when feeding on young barnacles. Thompson (1964) uses the name *F. pinnata* when quoting Eliot (1910). Marcus (1961) mentions *Fiona* feeding on stalked barnacles belonging to the Lepadidae. Todd (1981) also records it as feeding on *Lepas* species. This would agree with the oceanic pelagic habit of this nudibranch.

Mollusca, Cephalopoda

The ability of *Octopus vulgaris* to drill holes in the shells of its prey is well documented (Nixon & Maconnachie 1988, and references given therein). The shape and form of the holes drilled are determined by the composition and structure of the shell being drilled. The drilling is a result of the action of saliva and the organs of the buccal complex of the octopus on the mineral and organic material of calcareous shells of molluscs and crustaceans. Removal of the salivary gland prevents further drilling. The secretions contain several substances that can affect the muscle attachments in the exoskeleton of crustaceans. The calcite plates of a barnacle rapidly dissolved in *in vitro* tests (Nixon & Maconnachie 1988, and the references therein). After drilling the calcareous shell of prey some predators apparently inject a toxin through the hole and so relax or paralyse the prey. *Octopus vulgaris*

Table 14 Dimensions of holes found in barnacles on a *Patella* shell found in an octopus midden in the Ria de Vigo (after Guerra & Nixon 1987).

Maximum diameter on external surface, mm	Maximum diameter on internal surface, mm
0.5 × 0.5	0.1
1.0 × 0.8	0.2
1.5 × 1.0	0.1
1.5 × 1.3	0.3

weakens its prey with a venom (Arnold & Arnold 1969). Nixon & Maconnachie (1988) investigated the drilling by *O. vulgaris* in the Mediterranean. They used scanning electron microscopy to examine the holes drilled by *O. vulgaris* caught in the Bay of Naples.

Molluscs and crustaceans are the main prey of *O. vulgaris*. Barnacles are not regarded as important but occasionally cirripede shells have been found with drill holes. A group of barnacles attached to *Gibbula magus* was found to have been drilled through a wall plate, but Nixon & Maconnachie (1988) assumed that the octopus treated the barnacles as molluscs because in the Mediterranean at that time crabs had not been found to be drilled. The maximum diameter of the hole was 1.55 mm at the shell surface similar to that found in molluscs. The hole was ovoid and had a slight lip on one side, the sides were steep and a small penetration hole had been drilled on the side of the cavity. Scanning electron micrographs showed signs of erosion but the organization of the calcite crystals was not clear.

In the Ria de Vigo, north western Spain, shell middens associated with *Octopus vulgaris* were collected by SCUBA divers and examined. One of these middens contained a *Patella vulgata* shell to which was attached a group of *Semibalanus balanoides* of basal width 5–7 mm. According to Guerra & Nixon (1987) drill holes with the dimensions shown in Table 14 were found in three of the barnacles. The features of these holes were the same as those made in the barnacles at Naples. Plate II in Guerra & Nixon (1987) shows a scanning electron micrograph of the hole in *S. balanoides* from the Ria de Vigo and in the barnacle at Naples. There is, however, no record of how long it took the octopus to devour the contents of the barnacles.

Echinodermata, Asteroidea

The significant role of asteroid predation was first demonstrated experimentally by Paine (1966a) although its potential importance had been suspected by earlier workers. Since the 1960s much has been published on the effect of asteroid predation on community structure.

The feeding biology of asteroids, including chemoreception, has been reviewed by Sloan (1980, see also references therein). He considers that there is probably overall dermal chemosensitivity in asteroids with especially the terminal tube feet aiding in chemoreception.

Castilla & Crisp (1970) studied the olfactory stimuli of *Asterias rubens* and found that this predator could sense water-borne odours of living barnacles. These authors did experiments in a wooden Y-maze, 250 cm long, in which prey and controls were put in separate arms. The prey used was a mixture of *Semibalanus balanoides* and *Elminius modestus* (a total of about 3500 altogether) on pieces of rock. The experiments were done

in spring at Menai Bridge, North Wales. Taking all the results together, 72% of the starfish entered the prey channel representing a highly significant increase above random expectations. Starfish can be induced to change their food preference if fed for three months on a single prey (Castilla 1972). A response to chemical gradient may explain one advantage of the long-armed radial symmetry of the starfish. This shape could maximize the chemical gradient independently of the orientation of the animal if the sense organs are present in the extremities of the arms (Castilla & Crisp 1970, Sloan 1980).

Galstoff & Loosanoff (1939) report on the toxic effect of secretions from the starfish *Asterias forbesi* that paralyses the adductor muscle of its prey. The same was found for *Marthasterias glacialis*; the extracts cause violent reactions in the gastropod *Buccinum undatum* (Feder & Arvidsson 1967). The diet and feeding behaviour varies according to the size of the asteroid, the type of prey encountered, habitat, time of day, and season of the year (Sloan 1980). Asteroids consume prey both extra- and intra-orally (e.g. Sloan 1980, Menge 1983) and may attempt to eat several prey simultaneously (e.g. Mauzey et al. 1968).

Table 15 includes the majority of asteroid predators of barnacles. The majority of these asteroid predators belong to the Order Forcipulatida, two belong to the Spinulosida and one to the Valvatida. *Mediaster aequalis* (Valvatida) in Puget Sound, Washington, and on Gabriola Island, British Columbia, preys on *Balanus crenatus* (Birkeland 1974, Sloan & Robinson 1983). Of 1429 *Mediaster* feeding, 2.3% were taking *Balanus crenatus* (Birkeland 1974). Mauzey et al. (1968) give *Mediaster aequalis* as having a diet that varies with both habitat and season. Examination of the stomach contents of those living on muddy substrata revealed empty tests of diatoms, dinoflagellates and barnacle cyprids. On pier pilings one *Mediaster* had its stomach everted over several *Balanus crenatus* but they did not appear to be damaged (Mauzey et al. 1968). Sloan & Robinson (1983) found 41% of *Mediaster* feeding and of these 4% were taking barnacles.

Crossaster papposus (sometimes cited as *Solaster papposus*) and *S. dawsoni* (Spinulosida) also feed on *Balanus crenatus* in the Puget Sound region (Mauzey et al. 1968, Birkeland 1974). Of 476 feeding *Crossaster papposus* Birkeland (1974) found 1.5% taking *Balanus crenatus*. Mauzey et al. (1968) record one occasion when *B. crenatus* was the prey of *Solaster dawsoni*.

All the remaining asteroids preying on barnacles belong to the Order Forcipulatida and they play an important role in the structure and organization of rocky intertidal communities. Details of their predatory behaviour, particularly on barnacles are somewhat restricted, e.g. to the Pacific and Atlantic shores of North America, European and Australasian shores including a few observations on Japanese shores. *Aphelasterias japonica* and *Asterias amurensis* have been found preying on *Chthamalus challengerii* in the Asamushi region of Japan (Hoshiai 1958, 1959, 1960, Luckens 1970a,b, Menge 1982b). The starfish are commonest in the intertidal zone in late summer and autumn but are not normally found above the lower edge of the *C. challengerii* zone (Luckens 1970b). *Stichaster australis* preys on barnacles on New Zealand shores (Paine 1971, Menge 1982b). At Anawhata in New Zealand Paine (1971) found that the barnacles *Chamaesipho columna* formed 24% of the diet of *Stichaster australis* whereas *Chamaesipho brunnea* and *Tetraclitella purpurascens* each formed less than 1%. Three asteroids occur on the Chilean coast, *Heliaster helianthus*, *Stichaster striatus* and, only in the low zone, *Meyenaster gelatinosus*. All these prey on barnacles (Viviani 1978, Menge 1982b).

On European shores asteroids are largely subtidal but Lewis (1964, 1976) suggests that *Asterias rubens*, like *A. vulgaris* (= *A. rubens*?) and *A. forbesi* in New England, is found in the low intertidal region in winter rather than in summer and can prey on barnacles in that

THE MORTALITY OF INTERTIDAL CIRRIPEDES

Table 15 Asteroids and their barnacle prey. For extensive lists of asteroids and their prey see Sloan (1980).

Order Predator	Prey	Place	Reference
Valvatida			
<i>Mediaster aequalis</i>	<i>Balanus crenatus</i>	Puget Sound	Birkeland 1974
<i>Mediaster aequalis</i>	<i>Balanus</i> sp.	Gabriola Island, BC	Sloan & Robinson 1983
Spinulosida			
<i>Crossaster papposus</i> (often cited as <i>Solaster papposus</i>)	<i>Balanus crenatus</i>	Shore of Washington, USA	Mauzey et al. 1968
<i>Crossaster papposus</i>	<i>Balanus crenatus</i>	Puget Sound	Birkeland 1974
<i>Solaster dawsoni</i>	<i>Balanus crenatus</i>	Southern Puget Sound and San Juan Island	Mauzey et al. 1968
Forcipulatida			
<i>Aphelasterias japonica</i>	<i>Chthamalus challengerii</i>	Asamushi, Japan	Luckens 1970b, Menge 1982b
<i>Asterias amurensis</i>	<i>Chthamalus challengerii</i>	Asamushi, Japan	Hoshiai 1958, 1959, 1960, Luckens 1970b, Menge 1982b
<i>Asterias forbesi</i>	<i>Semibalanus balanoides</i>	Nahant, MA, USA	Sebens 1985
<i>Asterias forbesi</i>	<i>Semibalanus balanoides</i>	East coast, USA	Menge 1982b, 1983
<i>Asterias forbesi</i>	<i>Balanus eburneus</i>	New Jersey, USA	Peterson 1979
<i>Asterias rubens</i>	Barnacles	Plymouth, UK	Vevers 1949
<i>Asterias rubens</i>	<i>Semibalanus balanoides</i>	Menai Strait, Puffin Island, North Wales	Castilla & Crisp 1970, Castilla 1972
<i>Asterias rubens</i>	<i>Semibalanus balanoides</i>	Millport, Scotland	Barnes & Powell 1951
<i>Asterias rubens</i>	Barnacles, <i>Elminius modestus</i>	Oysterbeds, Essex, UK	Hancock 1955, 1958
<i>Asterias vulgaris</i> (= <i>A. rubens</i> ?)	<i>Semibalanus balanoides</i>	East coast, USA	Menge 1982b
<i>Asterias vulgaris</i>	<i>Semibalanus balanoides</i>	Nahant, MA, USA	Sebens 1985
<i>Evasterias troscheli</i>	Barnacles	Gabriola Island, BC	Sloan & Robinson 1983
<i>Evasterias troscheli</i>	<i>Balanus</i> sp., <i>Balanus nubilus</i>	San Juan Archipelago	Mauzey et al. 1968
<i>Evasterias troscheli</i>	<i>Balanus crenatus</i> , <i>Semibalanus cariosus</i>	Lower Puget Sound	Mauzey et al. 1968
<i>Heliaster helianthus</i>	Two <i>Chthamalus</i> spp.	Chile	Menge 1982b
<i>Heliaster kubiniji</i>	Barnacles	Northern Gulf of California	Paine 1966a
<i>Leptasterias hexactis</i>	<i>Balanus</i> spp.	Torch Bay, Alaska	Paine 1980
<i>Leptasterias hexactis</i>	<i>Balanus glandula</i>	Bamfield, Vancouver Island, BC	Palmer et al. 1982
<i>Leptasterias hexactis</i>	<i>Balanus glandula</i> , <i>Balanus</i> spp., <i>Chthamalus dalli</i> , <i>Pollicipes polymerus</i>	Cape Flattery, WA, USA	Paine 1980

Table 15 continued

Order Predator	Prey	Place	Reference
<i>Leptasterias hexactis</i>	<i>Balanus glandula</i> , <i>Semibalanus cariosus</i> , <i>Chthamalus dalli</i>	San Juan Island, WA, USA	Menge 1972a,b
<i>Leptasterias hexactis</i>	Barnacles	San Juan Archipelago, WA, USA	Connell 1970, Menge & Menge 1974, Menge & Sutherland 1976
<i>Leptasterias hexactis</i>	<i>Semibalanus cariosus</i> , <i>Chthamalus dalli</i>	Puget Sound	Mauzey et al. 1968
<i>Leptasterias hexactis</i>	<i>Balanus glandula</i> , <i>Semibalanus cariosus</i> , <i>Chthamalus dalli</i> , <i>Pollicipes polymerus</i> ,	West coast, USA	Menge 1982b
<i>Leptasterias littoralis</i>	Barnacles	Northeast coast, USA	O'Brien 1976
<i>Marthasterias glacialis</i>	Barnacles, <i>Tetraclita</i> sp.	South Africa	Branch 1976, 1978
<i>Meyenaster gelatinosus</i>	Barnacles	North Chile	Viviani 1978
<i>Orthasterias kochleri</i>	<i>Balanus nubilus</i> , <i>Pollicipes polymerus</i>	Puget Sound	Mauzey et al. 1968
<i>Pisaster brevispinus</i>	<i>Balanus</i> sp.	Near Seattle, WA, USA	Mauzey et al. 1968
<i>Pisaster giganteus</i>	<i>Megabalanus</i> <i>tintinnabulum</i>	Santa Catalina Island, CA, USA	Vance 1978
<i>Pisaster giganteus</i>	Barnacles	Monterey Bay, CA, USA	Farmanfarmaian et al. 1958
<i>Pisaster giganteus</i>	<i>Balanus pacificus</i>	California, Baja California	Hurley 1975
<i>Pisaster ochraceus</i>	<i>Balanus pacificus</i>	California, Baja California	Hurley 1975
<i>Pisaster ochraceus</i>	<i>Tetraclita squamosa</i> <i>rubescens</i>	Santa Barbara, CA, USA	Villalobos 1979a,b
<i>Pisaster ochraceus</i>	<i>Balanus glandula</i> , <i>Tetraclita squamosa</i> <i>rubescens</i> , <i>Balanus nubilus</i> , <i>Megabalanus</i> <i>tintinnabulum</i> , <i>Pollicipes polymerus</i>	Moss Landing, Monterey, CA, USA	Feder 1959, 1970
<i>Pisaster ochraceus</i>	<i>Balanus glandula</i> , <i>Pollicipes polymerus</i>	Oregon Coast	Navarrete & Menge 1996
<i>Pisaster ochraceus</i>	<i>Semibalanus cariosus</i>	West coast, USA	Menge 1982b
<i>Pisaster ochraceus</i>	<i>Balanus</i> spp., <i>Balanus glandula</i> , <i>Chthamalus dalli</i> , <i>Pollicipes polymerus</i>	Cape Flattery, WA, USA	Paine 1980
<i>Pisaster ochraceus</i>	Barnacles	Monterey Bay, CA, USA	Farmanfarmaian et al. 1958
<i>Pisaster ochraceus</i>	Barnacles, <i>Pollicipes polymerus</i>	San Juan Island, WA, USA	Menge & Sutherland 1976

Table 15 continued

Order Predator	Prey	Place	Reference
<i>Pisaster ochraceus</i>	<i>Semibalanus cariosus</i> , <i>Balanus glandula</i>	San Juan Island, WA, USA	Mauzey 1966
<i>Pisaster ochraceus</i>	<i>Balanus glandula</i> , <i>Semibalanus cariosus</i> , <i>Chthamalus dalli</i>	San Juan Island, WA, USA	Dayton 1971, Menge 1972a,b
<i>Pisaster ochraceus</i>	<i>Pollicipes polymerus</i>	Vancouver Island, BC	Bernard 1988, Barnes 1996
<i>Pisaster ochraceus</i>	<i>Balanus</i> spp.	Torch Bay, Alaska	Paine 1980
<i>Pycnopodia</i> <i>helianthoides</i>	Barnacles	Gabriola Island, BC	Sloan & Robinson 1983
<i>Pycnopodia</i> <i>helianthoides</i>	<i>Balanus glandula</i>	Barnfield, Vancouver Island, BC	Palmer et al. 1982
<i>Pycnopodia</i> <i>helianthoides</i>	<i>Chthamalus dalli</i>	Cape Flattery, WA, USA	Paine 1980
<i>Pycnopodia</i> <i>helianthoides</i>	<i>Balanus</i> spp.	Torch Bay, Alaska	Paine 1980
<i>Stichaster australis</i>	Barnacles	New Zealand	Paine 1971, Menge 1982b
<i>Stichaster striatus</i>	Barnacles	North Chile	Viviani 1978

region. Connell (1961b) also found that *A. rubens*, which accidentally penetrated one of his exclusion cages, ate most of the barnacles. Hancock (1955, 1958) found *A. rubens* and *Solaster papposus* on oyster beds in Essex, UK. He mentions some of the older work which merely recorded barnacles as part of the diet of *Asterias rubens* including that of Vevers (1949) who found that barnacles were taken by young *Asterias* but the number decreased as the barnacles increased in size. Hancock (1955, 1958) does not mention *Solaster* as preying on barnacles but he did several experiments involving *Asterias rubens* and the barnacles *Elminius modestus* and "*Balanus* sp.". He determined the average number of barnacles eaten by one *Asterias rubens* from four different size groups in 18 days (see Table 16) when presented with a selection of food. Barnacles were certainly the preferred food of the smaller sizes of *Asterias*. Hancock (1958) found that young *A. rubens* (1–8 mm diameter) fed at an average rate of 15.2 barnacles per day (equivalent to 191 per 18 days) in August 1955 which compares with rates given in Table 16.

The method of feeding by *A. rubens* depended on its strength and the size of the barnacle. Group I (Table 16) starfish ate the contents of a barnacle from the base if they were able to detach the barnacle from the substratum. Contents of larger barnacles were removed through the opercular valves. Group II starfish could feed on all sizes of barnacles by detaching them from the substratum and removing the contents through the base. Larger *Asterias* did not appear to take small barnacles until all the larger ones had been eaten (Hancock 1955). *A. rubens* differs from *A. forbesi* in that the former can feed at 2–3°C whereas the latter is inhibited between 0°C and 6°C. Menge (1982b) suggests that low intertidal asteroids may play comparable roles on the temperate shores of Europe and New England.

On the west coast of North America and Canada there are three common intertidal acorn barnacles, *Chthamalus* sp., *Balanus glandula*, and *Semibalanus cariosus*, plus the stalked

Table 16 Number of barnacles eaten by *Asterias rubens* in an 18-day period in May 1954 (after Hancock 1955).

Group	<i>Asterias rubens</i> size (diameter) mm	Number of barnacles eaten per 1 <i>Asterias rubens</i>
I	15–30	260
II	40–70	350
III	70–100	61
IV	100–145	3

barnacle *Pollicipes polymerus*. This contrasts with the New England coast on the east where there is only one abundant intertidal barnacle, *Semibalanus balanoides*, which forms 20–95% of the cover in the high intertidal zone (Menge 1982b). There are, however, three to five asteroid species in the intertidal region of each coast (Menge 1976, Menge & Sutherland 1976).

In New England *Asterias forbesi* and *A. vulgaris* occur from the low intertidal region to 50 m depth. They are found on all types of substratum ranging from rock to mud (Menge 1982b). The predatory activity is highly seasonal in this region (Menge 1978a, 1983). *Nucella* and *Asterias* species are characterized by high levels of movement and feeding on barnacles in the intertidal from May to early October. *Asterias* move to subtidal regions in late October to April and *Nucella* retreat to crevices in the intertidal region.

On the west coast of North America and Canada the two most common asteroids are *Pisaster ochraceus* (mean ww from 150–2450 g) and *Leptasterias hexactis* (mean ww 3–8 g) (Menge 1972a,b). They are the main benthic predators and extend into the midtidal zone. Generally, the most important numerical part of their diet is mussels and barnacles (Feder 1959, 1970, Mauzey 1966, Paine 1966a, Mauzey et al. 1968, Menge 1972a,b, 1982b, Menge & Menge 1974). The ingestion rate of prey per g for *Pisaster ochraceus* and *Leptasterias hexactis* differs by almost an order of magnitude on this coast (Menge & Menge 1974).

Villalobos (1979a,b), in California, found that the age structure of a *Tetraclita rubescens* community was regulated by predation by *Pisaster ochraceus*. Barnacle mortality rates were high in the first year but then decreased as the barnacle size increased. In some places the starfish was quite rare and the older barnacles were, therefore, almost free from predation. This starfish preys on several barnacles on the Californian coast (Feder 1959). He examined the starfish at low tide in the Monterey Bay area by removing them from the substratum and turning them over. If the animals were feeding the prey was lodged in the oral region (see his Fig. 1, Feder 1959). Small prey would be completely covered by the everted stomach of the starfish. Feder's results for starfish feeding on barnacles are given in Table 17 and are the outcome of his examination of about 3450 starfish on 70 different field trips. About 18% of the predators were feeding when examined. Young *P. ochraceus* usually prey on younger barnacles of the same species as the older starfish.

In Monterey Bay, Farmanfarmaian et al. (1958) record *P. ochraceus* feeding on barnacles in the intertidal region, *P. brevispinus* on wharf pilings exposed at lowest tide levels feeding on *Balanus nubilus* and *Pollicipes polymerus*, and *Pisaster giganteus* at a depth of 10 m, and rarely exposed, feeding on *Tetraclita*. *Pisaster brevispinus* in deeper water has also been seen feeding on *Balanus nubilus* (Mauzey et al. 1968).

Table 17 Barnacles taken in the field by 633 *Pisaster ochraceus* of all ages, in January 1953 to January 1955. (From Feder 1959.)

Prey	Number of cases seen	% of feeding starfish
<i>Balanus glandula</i>	191	30.1
<i>Tetraclita squamosa rubescens</i>	162	25.6
<i>Balanus nubilus</i>	8	1.3
<i>Megabalanus tintinnabulum</i>	3	0.5
<i>Pollicipes polymerus</i>	25	3.9

In November on the Oregon coast, Navarrete & Menge (1996) found *Balanus glandula*, *Pollicipes polymerus*, and *Mytilus californianus* were common in the diet of the seastar *Pisaster ochraceus* whereas in January small *Mytilus trossulus* (4–7 mm long) and *Pollicipes* formed the bulk of the diet.

Further north on the west coast much of the information on barnacle predation is from the Puget Sound region. Paine (1980) summarizes the latitudinal variation and variations due to habitat in the primary diet of *Pisaster ochraceus* on the west coast. This starfish, in the rocky intertidal is an important predator of sessile species such as *Balanus* spp. (Paine 1966a, Dayton 1971). It has a seasonal feeding habit in terms of the percentage population feeding at any one time. Less than 5% are feeding in January to February but in July and August it is 60–80%. A large proportion of the summer prey is small barnacles, *Balanus glandula* and young *Semibalanus cariosus* which settled in the spring although some older ones are also eaten (Mauzey 1966). Sloan & Robinson (1983) found that 70.4% of the 73.3% feeding *Pisaster brevispinus* were preying on barnacles as were 80% of the 7.1% feeding *Pycnopodia helianthoides*.

Evasterias troschelii and *Orthasterias kochleri* are also present in Puget Sound but at a lower level in the intertidal region than *Pisaster ochraceus*. In the laboratory *Evasterias* has a preference for *Balanus glandula* over *B. nubilus* but in natural conditions in the San Juan Archipelago in 198 observations of which 35% were feeding eight had taken *B. nubilus* and three *Balanus* spp. together representing 16% of the diet. In Lower Puget Sound 61% of the diet was composed of *B. crenatus* and *Semibalanus cariosus* (Mauzey et al. 1968). *Orthasterias*, occurring at greater depths than *Evasterias*, has a more specialized diet; of 157 feeding only two had taken *Balanus nubilus* and one *Pollicipes polymerus* (Mauzey et al. 1968).

Leptasterias hexactis is considerably smaller than *Pisaster ochraceus* (see above) but the two species compete for food (Menge 1972a, Menge & Menge 1974). The diet of *Leptasterias* is moderately constant, probably related to the small body size of the asteroid. *Balanus glandula*, *Chthamalus dalli*, *Balanus* spp. and occasionally *Pollicipes polymerus* are prey taken at Cape Flattery, Washington; at Torch Bay, Alaska, the prey is merely given as *Balanus* spp. (Paine 1980). Menge (1972b) studied the feeding activity of *Leptasterias hexactis* on rocky intertidal areas on the San Juan Islands. Feeding activity during high tides reaches a maximum in July and August and a minimum in January. Availability of food is reduced in winter compared with summer. Analysis of the diet by number of prey eaten over the whole area and by calories consumed indicate that this asteroid is a good generalist. *Balanus glandula*, numerically the most important prey, represents 35% of all observations in the total diet, but can vary between 3% and 55% at different points on San Juan Island. *Leptasterias* digests its

Table 18 Size selection of *Balanus glandula* by *Leptasterias hexactis* and *Pisaster ochraceus*. *n*=number of observations. (From Menge & Menge 1974.)

Predator	Size of <i>Balanus glandula</i> taken, mean diameter, cm \pm 95% confidence interval	<i>n</i>
<i>Leptasterias</i>	0.31 \pm 0.018	69
Small <i>Pisaster</i>	0.24 \pm 0.011	205
Medium <i>Pisaster</i>	0.32 \pm 0.009	287
Large <i>Pisaster</i>	0.34 \pm 0.008	858
<i>Balanus glandula</i> in the environment	0.31 \pm 0.0058	438

prey, as do many other asteroids, with its cardiac stomach extruded from its mouth. In laboratory experiments it was found that for *Balanus glandula* of diameters <0.9 cm mean consumption time was about 8 h; this increased to 27.5 h for barnacles >0.9 cm diameter. For *Semibalanus cariosus* of < 1.5 cm diameter the time was about 7 h.

Menge & Menge (1974) show that large *Pisaster ochraceus* take significantly larger *Balanus glandula* than do *Leptasterias hexactis* (Table 18). Comparing *Leptasterias* and small *Pisaster* of about the same size shows that the former takes the larger *Balanus glandula*. *Leptasterias* takes barnacles of a similar size to those taken by medium sized *Pisaster*. The barnacles taken by large and small *Pisaster* are significantly larger and smaller, respectively, than the mean size of *Balanus glandula* in the environment, whereas the mean size taken by *Leptasterias* and medium sized *Pisaster* is not different from the mean *Balanus glandula* present. This may mean that small *Pisaster* are only able to pull small barnacles off the substratum. Large *Pisaster* can, however, take the entire range of prey and select larger *Balanus glandula*. The barnacles form 60–80% of the numerical diet of these two asteroids. These results suggest that there is resource partitioning depending on prey size (Menge & Menge 1974).

Echinodermata, Echinoidea

The sea urchin, *Centrostephanus coronatus*, exploits a wide variety of foods as shown by an examination of the gut contents of ten adults. Barnacles formed 1.1% of the diet (Vance 1979). *Arbacia punctulata* denudes areas of barnacles at Beaufort, North Carolina (McDougall 1943).

Fishes

There are three ways in which fishes can act as barnacle predators. Some fishes, particularly young ones, partially depend on the cirripede planktonic stages for food. Other fishes, particularly in the intertidal region, may nip at the barnacle cirri and occasionally will pull out the whole body. Bigger fishes may rasp whole barnacles or groups of barnacles off the rock surface or crush the shells with their teeth.

Table 19 Examples of fishes feeding on cirripede larvae and cyprids.

Species	Reference
<i>Archosargus rhomboidalis</i>	Stepien 1976
<i>Clupea harengus</i>	Blaxter 1968, De Silva 1973
<i>Clupea pallasii</i>	Wailes 1936
<i>Clupea sprattus</i>	De Silva 1973
<i>Dicentrarchus labrax</i>	Ferrari & Chieregato 1981
<i>Diplodus cervinus</i>	Christensen 1978
<i>Diplodus sargus</i>	Christensen 1978
<i>Girella laevisfrons</i>	Varas & Ojeda 1990
<i>Gobius cephalarges</i>	Porumb 1961
<i>Gobius melanostomus</i>	Porumb 1961
<i>Graus nigra</i>	Varas & Ojeda 1990
<i>Lithognathus mormyrus</i>	Kentouri & Divanach 1982
<i>Liza aurata</i>	Ferrari & Chieregato 1981
<i>Liza ramada</i>	Ferrari & Chieregato 1981
<i>Liza saliens</i>	Ferrari & Chieregato 1981
<i>Myoxocephalus aeneus</i>	LaRoche 1982
<i>Myoxocephalus octodecemspinus</i>	LaRoche 1982
<i>Myoxocephalus scorpius</i>	LaRoche 1982
<i>Oncorhynchus gorboscha</i>	Godin 1981
<i>Pomatoschistus</i> (as <i>Gobius</i>) <i>microps</i>	Healey 1972
<i>Pomatoschistus microps</i>	Zander 1979
<i>Pomatoschistus</i> (as <i>Gobius</i>) <i>minutus</i>	Healey 1971
<i>Scartichthys viridis</i>	Varas & Ojeda 1990
<i>Sebastes mystinus</i>	Gaines & Roughgarden 1987
<i>Sparus auratus</i>	Ferrari & Chieregato 1981
<i>Triglops murrayi</i>	LaRoche 1982
<i>Valenciennea strigata</i>	Hiatt & Strasburg 1960
<i>Valenciennea violifera</i>	Hiatt & Strasburg 1960

A variety of fishes feed on the planktonic larvae of cirripedes. There are six nauplius stages and a cyprid and any or all of these may be found in the diets of larval and juvenile fish. Predation on the planktonic stages affects the eventual recruitment of the adult barnacles. A list of some of the fishes involved is given in Table 19; this list is not intended to be exhaustive but merely to indicate some of the fishes examined. In many cases authors do not name the species of cirripede nauplii eaten; this has, therefore only been quoted when given by the author(s) of the original reference.

Barnacle nauplii have been used in the experimental rearing of the larvae of striped sea bream, *Lithognathus mormyrus*. Nauplii of 100–330 µm in length were readily ingested but cyprids of 350–450 µm in length were often found alive in the gut (Kentouri & Divanach 1982). In the laboratory rearing of larvae of all sizes of sea bream, *Archosargus rhomboidalis*, Stepien (1976) found that 5.1% of the gut contents were barnacle nauplii. Larvae up to 9.1–9.5 mm standard length (SL) consumed copepod nauplii (average width 69.6 µm) but barnacle nauplii (average length 246.2 µm) were not taken by the fish larvae of <4.5 mm SL. *A. rhomboidalis* is common in marine sea grass communities and ranges from New Jersey to Rio de Janeiro on the western side of the Atlantic (Stepien 1976).

Juveniles of the sparid fishes *Diplodus sargus* (blacktail) and *D. cervinus* (zebra) are found in the intertidal and near subtidal regions of the southeast coast of Africa but the adults are only found in these zones at high tide (Christensen 1978). Although juvenile *D. sargus* do not consume cirripede nauplii in winter (February to July) they are part of the diet of the fish (size up to 35 mm) from August to December, the majority being taken by sizes between 15 mm and 25 mm. *D. sargus* is found in tidepools throughout the year and presumably takes cirripede nauplii in August to December when these are available. Cirripede nauplii were only taken by juvenile *D. cervinus* in the size range 50–75 mm. *D. cervinus*, however, is only found in October and November when the cirripede nauplii are available.

In British Columbia post-larvae and fry (20–100 mm) of the Pacific herring, *Clupea pallasii*, consume a variety of food with copepod and cirripede larvae being the most important. Differences between localities and seasons suggest that the food taken is that most readily available (Wailes 1936). Herring, *C. harengus*, spawned on the Ballantrae Bank in the Firth of Clyde, Scotland, could be reared successfully in experimental conditions using *Semibalanus balanoides* nauplii while available from about mid-April to mid-May. Later in the season natural plankton, sometimes supplemented with *Anemia* larvae, was used (Blaxter 1968, see also Rosenthal & Hempel 1970). *Clupea harengus* and *C. sprattus* regularly ate *Semibalanus* nauplii and cyprids in Scottish inshore waters during the summer (De Silva 1973). Cyprids were taken by herring from March to June and by sprats from March to October. In both cases, however, they only accounted for a small proportion of the diet.

Pink salmon, *Oncorhynchus gorbuscha*, fry taken in Departure Bay and Hammond Bay near Nanaimo, British Columbia, were found to have cirripede larvae in their stomachs. In Departure Bay, 16.92% of the prey found were cirripede nauplii and in Hammond Bay it was 28.13 % (Godin 1981). The samples were taken in May at a time when nauplii from the local barnacle populations would be a common constituent of the plankton.

In January through to March several species belonging to the family Cottidae feed on barnacle nauplii in the Damariscotta River estuary, Maine, USA (LaRoche 1982). The author refers to *Balanus* nauplii; it is probable that they were what are now called *Semibalanus* nauplii. Nauplii of this barnacle are scarce in January and February but plentiful in March. This is demonstrated by the number of nauplii ingested by the larval fish (Table 20). During March, when the most nauplii are ingested, the frequency of occurrence of a particular stage reflects the changes as the cirripede nauplii develop. Nauplius Stage I is short-lived in the plankton and rapidly moults to Stage II and then Stage III. Stages IV and V would only be present in late March. Stage VI would be rare until early April. The reliance of cottid larvae on barnacle nauplii suggests that the increase in size of the developing barnacle nauplii is no deterrent to the fish larvae (Table 21).

In the brackish lagoons of the Po River delta, Italy, juvenile stages of *Sparus auratus* (gilthead), *Dicentrarchus labrax* (sea bass), and three species of grey mullets (*Liza ramada*, *L. aurata*, and *L. saliens*) were all found to ingest cirripede nauplii (Ferrari & Chiericato 1981). At standard lengths of <30 mm cirripede nauplii formed an appreciable proportion of the stomach contents examined (Table 22). Coefficients of emptiness (ratio of number of empty stomachs to total examined) of <5% were found for *Sparus auratus*, *Dicentrarchus labrax*, *Liza ramada*, and *L. aurata* but were relatively higher in *L. saliens* and tended to increase with fish size. In all species the highest coefficients of emptiness were found from December through to March. No cirripede nauplii would be present in the plankton during these months. In the Po River delta, nauplii would be present in late spring and early summer with another peak in early autumn and this is reflected in the number present in the stomachs of all five species examined (Table 22).

THE MORTALITY OF INTERTIDAL CIRRIPEDES

Table 20 Species, size range of larvae and cirripede nauplii ingested as a percentage of total number of food items taken (after LaRoche 1982).

Species	Month	Size range of fish larvae (mm)	Cirripede nauplii ingested (%)
<i>Myoxocephalus aeneus</i>	Jan.–Feb.	6.5–7.4	0.8
		March	61.8
	March	6.5–7.4	57.5
		7.5–8.4	42.6
		8.5–9.5	54.9
<i>M. octodecemspinosus</i>	Jan.–Feb.	8.5–9.4	1.7
	March	7.5–8.4	39.5
		8.5–9.4	45.3
		9.5–10.4	61.8
		10.5–11.4	76.8
		11.5–12.4	77.8
<i>M. scorpius</i>	Jan.–Feb.	8.5–9.4	0.9
		9.5–10.4	3.1
	March	8.5–9.4	94.3
		9.5–10.4	77.3
		10.5–11.4	90.1
		11.5–12.4	91.6
		12.5–13.4	93.6
<i>Triglops murrayi</i>	Jan.–Feb.	12.5–14.4	2.2
	March	10.5–11.4	43.8
		11.5–12.4	33.8
		12.5–13.4	45.5
		13.5–14.4	42.9
		14.5–15.4	62.0
		15.5–18.1	64.8

Table 21 Frequency of occurrence (%) of the six nauplius stages of cirripedes in fishes examined in early (E) and late (L) March (after LaRoche 1982).

Species	Nauplius stage									
	I		II + III		IV + V		VI		Unidentified	
	E	L	E	L	E	L	E	L	E	L
<i>Myoxocephalus aeneus</i>	7	5	93	52	0	31	0	5	0.6	6
<i>M. octodecemspinosus</i>	12	6	87	41	0	38	0	3	2	11
<i>M. scorpius</i>	6	1	91	45	0.6	41	0	6	2	7
<i>Triglops murrayi</i>	0	3	100	45	0	48	0	2	0	2

Juvenile rockfish, *Sebastes* spp. inhabit kelp forests along the coast of central California. These fishes are planktivorous and feed on invertebrate larvae, particularly those of *Balanus glandula* (Gaines & Roughgarden 1987). When these larvae are abundant (April to August) *B. glandula* cyprids were found (up to 10% of number of items) in >40% of the 30 stomachs

Table 22 Number of cirripede nauplii per stomach (number) in several species of fishes. SL=average standard length of fish (mm); *n*=number of stomachs examined. (After Ferrari & Chieregato 1981.)

Month	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
<i>Sparus auratus</i>											
<i>n</i>	30	30	10	—	—	—	—	—	—	—	—
SL	17.4	17.5	19.3	—	—	—	—	—	—	—	—
Number	2.8	8.3	3.7	—	—	—	—	—	—	—	—
<i>Dicentrarchus labrax</i>											
<i>n</i>	10	6	10	17	20	—	—	—	—	—	—
SL	15.9	17.7	18.0	26.3	37.5	—	—	—	—	—	—
Number	0.2	3.2	0.2	9.5	0.2	—	—	—	—	—	—
<i>Liza ramada</i>											
<i>n</i>	20	20	10	23	3	—	—	—	—	4	—
SL	19.8	19.1	18.7	22.7	38.0	—	—	—	—	17.8	—
Number	3.0	33.5	35.7	25.7	4.7	—	—	—	—	1.3	—
<i>L. aurata</i>											
<i>n</i>	29	20	10	10	10	—	—	—	10	10	—
SL	25.1	26.0	26.5	29.7	55.6	—	—	—	22.6	26.0	—
Number	1.4	38.7	82.5	90.0	8.0	—	—	—	20.3	1.3	—
<i>L. saliens</i> (SL <30 mm)											
<i>n</i>	10	20	—	6	—	5	10	9	10	10	10
SL	24.7	27.3	—	29.2	—	15.2	20.1	12.1	26.8	26.6	22.4
Number	132.0	29.7	—	16.0	—	4.0	34.0	6.7	64.0	11.5	0.5
(SL >30 <50 mm)											
<i>n</i>	20	20	10	20	6	—	—	—	10	—	10
SL	38.5	37.8	41.9	39.1	49.7	—	—	—	35.2	—	34.3
Number	0.1	12.5	74.0	45.5	1.5	—	—	—	39.0	—	1.0
SL >50 mm											
<i>n</i>	10	20	10	—	—	4	10	—	—	—	—
SL	52.5	62.9	57.5	—	—	65.3	90.6	—	—	—	—
Number	434.0	43.8	76.7	—	—	0	148.0	—	—	—	—

of *Sebastes mystinus* examined. This predation reduces the recruitment of barnacle populations on the rocky intertidal zone inshore of the kelp beds to one-fiftieth of the level in the absence of the rockfishes. The recruitment of the low intertidal barnacle, *Megabalanus californianus* is also affected.

Hiatt & Strasburg (1960) found that two species of fishes belonging to the family Eleotridae contained barnacle cyprids in the digestive tract; 11% of *Valenciennea violifera* and 33% of *V. strigata* examined. As near as can be read from figure 5 in Zander (1979) only about 1% of *Pomatoschistus microps* from stony ground on the Isle of Møn in the Baltic contained barnacle cyprids in their gut. In the Ythan estuary, Scotland, Healey (1972) found that *P.* (as *Gobius*) *microps* had cyprids in their gut in April, May, June, and July, the percentage of occurrence being 56, 36, 47, and 18, respectively. Healey (1971) found barnacle larvae in the gut of *P.* (as *Gobius*) *minutus* usually in May in the Ythan estuary. There was an absence of barnacle larvae in the diet from August to the following March. Again this is to be expected as barnacle larvae would not be available during that time. The Black Sea gobies, *Gobius cephalarges* and *G. melanostomus* both feed on larvae of

Table 23 Some fishes feeding on cirri or whole barnacles.

Species	Reference
<i>Abudefduf</i>	Hurley 1975
<i>Acanthoclinus quadridactylus</i>	Jillett 1968
<i>Acipenser transmontanus</i>	McKechnie & Fenner 1971
<i>Archosargus probatocephalus</i>	McDougall 1943
<i>Blennius incognitus</i>	Goldschmid & Kotschal 1981
<i>Blennius incognitus</i> (as <i>zvonimiri</i>)	Gibson 1968
<i>Blennius pavo</i>	Gibson 1968
<i>Blennius pholis</i>	Qasim 1957a, Gibson 1972, Dunne 1977
<i>Blennius sanguinolentus</i>	Gibson 1968
<i>Blennius sphynx</i>	Gibson 1968
<i>Centronotus gunnellus</i>	Qasim 1957b
<i>Clinocottus</i>	Hurley 1975
<i>Clinocottus analis</i>	Yoshiyama 1980
<i>Coryphoblennius galerita</i>	Fives 1980
<i>Coryphoblennius</i> (as <i>Blennius</i>) <i>galerita</i>	Šoljan 1932
<i>Crenilabrus melops</i>	Collins et al. 1991
<i>Damalichthys vacca</i>	Haldorson & Moser 1979
<i>Embiotoca lateralis</i>	Haldorson & Moser 1979
<i>Gobiesox maeandricus</i>	Johnson 1970
<i>Hypsoblennius</i>	Hurley 1975
<i>Lagodon rhomboides</i>	McDougall 1943
<i>Monocanthus hispidus</i>	McDougall 1943
<i>Semicossyphus maculatus</i>	Fuentes 1981
<i>Sicyases sanguineus</i>	Paine & Palmer 1978, Cancino & Castilla 1988
<i>Tautoga onitis</i>	Olla et al. 1974, 1975, Shumway & Stickney 1975
<i>Tautogolabrus adspersus</i>	Shumway & Stickney 1975, Edwards et al. 1982
<i>Thalassoma duperry</i>	Losey et al. 1994
<i>Thunnus alalunga</i>	Dragovich 1969
Cunners	Chao 1973, Edwards et al. 1982
Littoral fish	Gibson 1969, 1982, Zander & Heymer 1977

Balanus sp. in spring and autumn; presumably this is when the larvae are available (Porumb 1961). In summer and winter the local barnacles would not be breeding.

Predation by fishes, particularly by larval and juvenile fishes on plankton containing cirripede larvae and cyprids can affect the eventual recruitment of adult barnacles (e.g. Gaines & Roughgarden 1987). Adult barnacles also suffer from predation by fishes inhabiting the intertidal or nearshore sublittoral zones (Table 23). Here barnacles can be removed by the rasping of fishes. This may not be a direct act of predation by the fish but a side effect of their systematic rasping of algae-covered substrata. Newman (1960) gives several examples on coral reefs where the paucity of cirripedes may be due to such action by rasping fishes.

Table 24 *Sicyases sanguineus*: species and number of cirripedes found in stomachs at several collecting sites. Number and percentage of fish in which cirripedes represent more than 50% of the stomach volume is also given, n =number of fish examined. (After Paine & Palmer 1978.)

Cirripede	Collecting site				
	Islote 1975 $n = 11$	Concon 1976 $n = 8$	Montemar Marine Laboratory $n = 9$	North Montemar $n = 9$	Iquique $n = 11$
<i>Balanus laevis</i>	12	6	3	10	3
<i>Chthamalus cirratus</i>	–	–	2	–	9
<i>Chthamalus scabrosus</i>	–	30	50	–	16
<i>Megabalanus psittacus</i>	2	20	–	3	1
<i>Notobalanus flosculus</i>	32	35	77	121	89
Barnacles	23	–	–	–	9
Fish with cirripedes >50% stomach volume					
Number	0	1	2	3	5
%	0	12.5	22.2	33.3	45.5

Barnacles are heavily browsed by wrasse according to Collins et al. (1991). During the “cleaning” of green turtles, *Chelonia mydas*, by the wrasse, *Thalassoma duperry*, at several sites in Hawaii the barnacle, *Platylepas hexastylus*, is removed (Losey et al. 1994). This barnacle is only found on the skin of sea turtles, manatees, and dugongs. The barnacles are not deeply embedded in the skin and some of this is removed with the barnacles by the wrasse. On three occasions one fish removed two adjacent barnacles with associated tissues in a single bite. The size of barnacles ingested by the wrasse was 2.1–5.0 mm length compared with a length of 1.7–6.2 mm for those living on the turtles. The number of barnacles found on a turtle varied considerably (from 195–490 on three examined). A single wrasse may remove as many as 35 barnacles (Losey et al. 1994).

Northern clingfish, *Gobiesox maeandricus*, is found from southern California to southeastern Alaska and is common in the rocky intertidal zone. In California, fish in the size range 41–82 mm contain *Chthamalus* sp. in their digestive tracts. The frequency of occurrence of the barnacle in 78 fish examined was 5% and the volume was 1% of the food taken (Johnson 1970).

Sicyases sanguineus, an amphibious marine clingfish, collected at Iquique and in the Montemar region of Chile has an extremely varied diet. The fish is known locally as the “pejesapo” (literally frogfish) and is characteristic of the middle and upper rocky intertidal zones on exposed coasts of western South America from Peru to southern Chile. According to Viviani (1975, quoted in Paine & Palmer 1978) these fish prefer barnacles. These are removed by elongate, rodentiform teeth of the fish used in scraping the substratum. One method of feeding is for the fish to anchor itself, preferably to a vertical rocky wall, by its ventral sucker and then to swing its head in a 30° arc while repeatedly raking its teeth in 2–4 cm downward strokes. Several barnacle species have been identified in the stomach contents (Tables 24, 25) by Paine & Palmer (1978) and Cancino & Castilla (1988).

THE MORTALITY OF INTERTIDAL CIRRIPEDES

Table 25 *Sicyases sanguineus*: size and number (in parentheses) of fish examined; species and number of cirripedes in stomachs. (After Cancino & Castilla 1988.)

Cirripede	Size of fish, cm		
	<15	15–23	>23
<i>Balanus laevis</i>	–	5 (1)	–
<i>Chthamalus cirratus</i>	331 (10)	1072 (9)	1298 (4)
<i>Chthamalus scabrosus</i>	13 (2)	75 (2)	154 (2)
<i>Megabalanus psittacus</i>	–	6 (2)	–
<i>Notobalanus flosculus</i>	9 (3)	1081 (20)	683 (8)

Table 26 Percentage cirripedes in contents of cunner and tautog digestive tracts (determined by volume), *n*=number of fish. (After Olla et al. 1975.)

	May–June	July–Aug.	Sept.–Oct.
Cunner			
<i>n</i>	31	21	12
Length (mm)	63–215	108–240	154–223
% cirripedes	0.2	1.6	1.9
Tautog			
<i>n</i>	14	12	13
Length (mm)	105–254	136–260	177–235
% cirripedes	15.3	2.7	7.4

The feeding habit of another littoral fish, *Semicossyphus maculatus*, in northern Chile was examined by Fuentes (1981). The cirripedes found in the diet were the same as quoted in Tables 24 and 25. There was no change in diet with increased size of fish from 34 cm to 72cm.

The cunner, *Tautogolabrus adspersus*, and the tautog, *Tautoga onitis*, are found in the north temperate waters of the western Atlantic along the coast of North America and Canada. They feed during the day (Olla et al. 1975, Shumway & Stickney 1975). The cunner is primarily carnivorous and its feeding habits change during growth. The juveniles feed on planktonic crustaceans but adults favour mussels and barnacles. At Nahant, of the cunners with food in their digestive tracts 40.7% of 100–225 mm length (1–4 years old) and 50% of 230–300 mm length (4–6 years old) contained *Semibalanus balanoides* (Chao 1973). At Cape Ann, Edwards et al. (1982) sampled cunners in the rocky intertidal zone from May to August and found that 53–100% contained barnacles (see comment by Menge 1982a). Further south, in Rhode Island, Shumway & Stickney (1975) found *S. balanoides* in 47.6% of 309 feeding cunners. In cunners above a standard length of 71 mm, barnacles were present in more than 30% of all feeding fish independent of size of fish. The digestive tracts of *Tautoga onitis* (240–460 mm length) contained decapod and cirripede crustaceans in varying amounts (0.6–68.1% of total gut contents) depending on the time of day and size of fish (Olla et al. 1974). Olla et al. (1975) compared the cirripede content of the digestive tracts of cunners and tautogs as a percentage of the total food contents (Table 26).

Table 27 *Balanus* sp. in the diet of *Acipenser transmontanus*; volume is percentage of total food volume of food and frequency is percentage of all stomachs containing food, *n*=number of animals. (After McKechnie & Fenner 1971.)

Season	<i>n</i>	Place				
		San Pablo Bay		Suisan Bay and Carquinez Strait		
		Volume %	Frequency %	<i>n</i>	Volume %	Frequency %
Winter	49	3.4	4.1	15	Trace	6.7
Spring	90	0.9	4.4	59	10.9	13.5
Summer	35	44.1	25.7	27	29.1	21.2
Winter	39	—	—	41	5.4	12.2

The diets of two species of surfperch, *Damalichthys vacca* (pile surfperch) and *Embiotoca lateralis* (striped surfperch) have been examined by Haldorson & Moser (1979) in seven places over much of the range of distribution on the Pacific coast of North America and Canada. South of Santa Barbara to Santo Tomas cirripedes were rarely found in the stomach contents but from Avila northwards to Puget Sound, barnacles were found in both species albeit more so in pile surfperch than in striped surfperch. At Avila and San Francisco the percentage occurrence of barnacles in both species (read off Fig. 2 in Haldorson & Moser 1979) was about 38–40% and about 20–25%, respectively, at both places. The value of 38–40% at Avila was consistent over the first three quarters of the year for striped surfperch but decreased to about 30% in the fourth quarter. In Puget Sound however, the occurrence of barnacles in the pile surfperch was about 75% compared with about 40% in striped surfperch (Haldorson & Moser 1979).

The common predation by intertidal fish on cirripedes involves them nipping at the cirri of the barnacles when these are extended and in some cases even dragging the whole cirripede body from its shell. Yoshiyama (1980) examined 62 intertidal sculpins, *Clinocottus analis*, from California and found that cirripede appendages only occurred in the 41–50 mm size class and then only formed 1% of the total identifiable diet. The proportion of total individuals with food in their stomachs containing cirri was only 0.02. The percentage frequency and percentage volume of *Balanus* sp. in the stomach contents of the white sturgeon, *Acipenser transmontanus*, from California are given in Table 27. It is not clear whether *Balanus* sp. refers to whole barnacles, to the cirri or to the planktonic stages. Cirripedes do not apparently occur in the diet in winter in San Pablo Bay (McKechnie & Fenner 1971). In the area where these samples were taken cirripedes would be available for most of the year but most plentiful in summer.

The biology and behaviour of littoral fish has been comprehensively reviewed by Gibson (1969, 1982). In dealing with food and feeding he comments on the variety of food available in the littoral zone and the large number of feeding types found among the fish as a consequence of this. A “pouncing” action is employed by many carnivorous blennies when feeding on barnacles as the aim is to nip off the extended cirri before they are able to retract into the shell. This action is used by *Coryphoblennius* (as *Blennius*) *galerita* on the Adriatic coast of Yugoslavia. It rides up rock faces with the waves and pulls off the extended cirri of *Chthamalus stellatus* before they can be retracted (Šoljan 1932). Zander & Heymer (1977) compared the barnacles (quoted merely as *Balanidae*) in the diet of four littoral fishes at different places in the Mediterranean (Table 28). Whole barnacles were found by

Table 28 Percentage of Balanidae in food of different fish populations (after Zander & Heymer 1977).

Species and place	Number of fish, <i>n</i>	Balanidae, %
<i>Blennius nigriceps</i>		
Grotto of Banjole, Rovinj	28	14.5
Red Island	6	13.4
<i>Blennius incognitus</i> (as <i>zvonimiri</i>)		
Grotto of Banjole, Rovinj	5	9.2
<i>Tripterygion melanurus</i>		
Grotto of Banjole, Rovinj	33	1.6
Banyuls-sur-Mer	17	0.7
<i>Tripterygion xanthosoma</i>		
Grotto of Banjole, Rovinj	9	1.6

Table 29 Cirripedes found in fishes at Roscoff; percentage occurrence of food in stomachs, *n*=number of fishes examined. (From Gibson 1972.)

Species	<i>n</i>	Occurrence, %
<i>Blennius pholis</i>		
Exposed shore	60	93
Sheltered shore	76	54
<i>Coryphoblennius galerita</i>	12	75
<i>Gobius paganellus</i>	170	1
<i>Crenilabrus melops</i>	10	10

Goldschmid & Kotschal (1981) in the intestines of *Blennius incognitus* from the vicinity of Rovinj.

Gibson (1968), working in the region of Banyuls-sur-Mer, found barnacle cirri in the stomachs of *Coryphoblennius* (as *Blennius*) *galerita* confirming the observations of Šoljan (1932). *Blennius sphynx*, *B. pavo* and *B. incognitus* (as *B. zvonimiri*) were also found to take barnacle cirri. The occurrence of cirri (expressed as the percentage of fish in the sample containing them) was 18, 17, and 12, respectively. The mouths of these blennies have a row of sharp cutting teeth on both jaws and these are well-adapted for biting off cirri. *B. sanguinolentus* has fine flexible teeth and is almost completely herbivorous; barnacle cirri were only found in one of the 27 fish examined and these appeared to be a moult rather than part of a living barnacle.

At Roscoff on the Atlantic coast of France, Gibson (1972), while diving over his study areas, observed the "vertical migration" of *B. pholis* and *Coryphoblennius galerita* on a rising tide. These two species were seen feeding on barnacles on the tops and sides of boulders that would not have been accessible at low tide. The percentage occurrence of Cirripedia in these and two other species are given in Table 29. Barnacles are the staple diet of adult *Blennius pholis* and *Coryphoblennius galerita* but some competition for food seems to be evident in the younger stages. A comparison was, therefore, made between juveniles of the former (<60 mm length) and *C. galerita* collected on an exposed shore where the latter species was the more common. The most important food of *C. galerita*

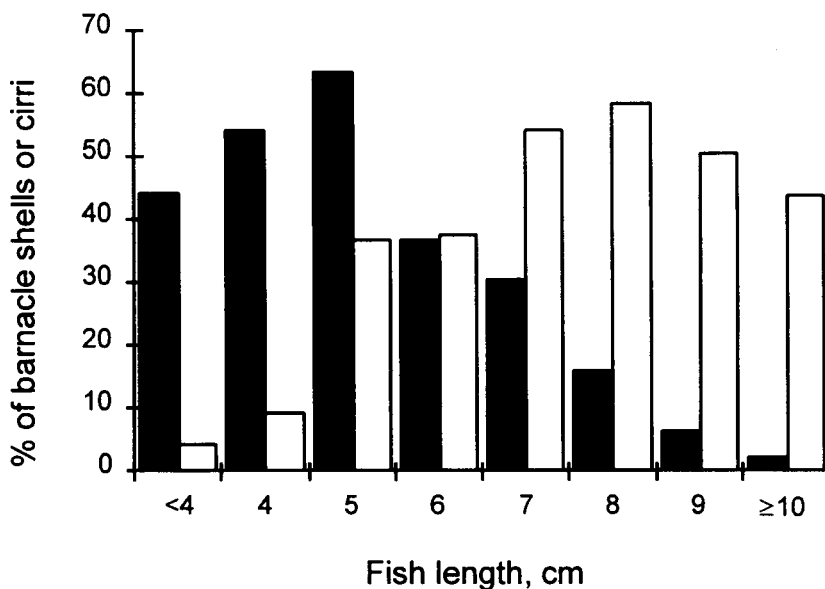


Figure 6 Occurrence (%) of barnacle cirri (black) or shells (white) in *Blennius pholis*. (Data from Dunne 1977).

proved to be barnacle cirri but not the whole animal. Other food items occurred in less than a third of the stomachs examined. In juvenile *Blennius pholis*, however, whole shells or fragments of barnacles were found as well as cirri. Molluscs and other food items were also found in stomachs of these juveniles suggesting that this species is less discriminating in its feeding habits than *Coryphoblennius galerita* of the same size. As *Blennius pholis* grows, barnacles continue to be a major part of its food; whole animals—as many as 40 complete shells—were found in one stomach. Qasim (1957a) made a study of this species at Menai Bridge, Wales and mentions older works dating from 1880 onwards that refer to barnacles being a food of this blenny. Qasim (1957a) found barnacles every month in the guts of adolescent and adults. Their occurrence in the total number of guts containing food throughout the year was 67%. Several individuals during autumn contained nothing but barnacles and in December a single fish contained 24 barnacle remains. The presence of finely crushed barnacle shells indicates a browsing or chewing habit. Eggs and embryos were found in November and cyprids and spat in April and May. Mainly barnacle cirri occurred in 84% of 0-group fish indicating that these young fish must nip at the cirri when these are extended during beating.

Dunne (1977) found similar results (56.9% compared with 67% at Menai Bridge) for *B. pholis* at Carna in Ireland. Barnacles were present in both sexes throughout the year. The change of feeding on cirri to whole barnacles during growth is shown in Figure 6. This dependence on barnacles is evident from the number of blennies found on barnacle-covered shores and their absence on similar shores in the absence of barnacles.

Cirripedes also formed a major food item (68.6% occurrence) for *Coryphoblennius galerita* on the Connemara Coast, Ireland (Fives 1980). Barnacle cirri are found in the guts of all sizes of fish but the percentage occurrence varies with the size of fish; all six pairs of cirri and the penis may be found in fish of =4.0 cm length. In one individual of 2.6 cm length, cirri formed 100% of the food, whereas in one of 6.5 cm cirri formed only 30%. Fragments of barnacle shell were only occasionally found; a complete barnacle of

Table 30 Occurrence (%) of cirripedes in *Centronotus gunnellus*. *n*=number of fish. (After Qasim 1957b.)

Months	Jan.–Mar.	Apr.–June	July–Sept.	Oct.–Nov.
<i>n</i>	85	130	31	15
No food in stomachs	31	10	1	3
% occurrence of cirripedes	16.4	32.3	19.4	53.1

3.25 mm basal diameter was taken from a fish of 5.0 cm length. O'Farrell & Fives (quoted in Fives 1980) recorded a single *C. galerita* with 127 barnacle penes in its stomach; 291 cyprids have also been found in a single gut. Barnacle cirri were found in 13% of *Lophogobius cyprinoides* but as no pieces of shell were found the cirri must have been nipped off while extended. The cirri were from 3.2–5.0 mm long (Darcy 1981). The predatory effect of these small fishes on a rocky shore population of barnacles cannot be neglected.

Centronotus gunnellus occurs low on the shore usually among *Laminaria* (Qasim 1957b). Cirripedes form part of its diet at all times of the year, the percentage occurrences are in Table 30. In New Zealand, Jillett (1968) found barnacles (*Elminius modestus*) as part of the diet of *Acanthoclinus quadridactylus*. The guts of 709 adolescent and adult fish were examined and 13% of these contained barnacles. In juveniles (0+ age group) this dropped to 9%.

Gibson et al. (1998) found bits of barnacle cirri in the stomachs of young plaice in Swedish waters over sandy bottoms. Mussels carrying barnacles were common in the vicinity and the cirri may have been merely taken in plankton as moults from this cirripede population but direct predation is a possibility.

Dragovich (1969) examined the stomach contents of seven species of Atlantic tuna. In one species only, *Thunnus alalunga*, he found the stalked barnacle *Lepas anatifera*.

Birds

Birds are frequently seen foraging and feeding on rocky shores in many parts of the world. Such habitats support high densities of prey but this is not always available to the birds. Several factors such as exposure, the state of the tide, and of the weather as well as the topography of a shore can restrict the ability of the birds to forage successfully (Feare & Summers 1985). In winter, ice on a shore can be a problem for some birds which for preference feed on mobile prey (Feare & Summers 1985). In the boreo-arctic regions non-mobile prey such as barnacles may be covered with a glaze of ice in the intertidal region in severe weather conditions.

During the winter, purple sandpipers, *Calidris maritima*, at Robin Hood's Bay feed in the barnacle zone (Feare 1966) but usually on the small littorinids that find shelter there. In Nova Scotia, where ice covers sheltered shorelines, purple sandpipers seek areas where wind and waves keep the shore free of ice and here *Balanus* sp. have been recorded in the diet (Feare & Summers 1985).

The region foraged by the turnstone, *Arenaria interpres*, on Anglesey, North Wales in winter depended on the state of the tide. As the tide receded so the birds tended to move down the beach. At mid- and low-tide levels there was a reasonable correlation between

Table 31 Ruddy turnstones feeding on barnacle-covered rocky shores: foraging rates, success rates, and frequencies of success, t=time in seconds; results \pm S.D.; n=number of animals. (After Groves 1978.)

	Juveniles ($n = 78$)	Adults ($n = 108$)
Foraging rate, $(P + F)t^{-1}$	$0.188 \pm 0.069.s^{-1}$	$0.222 \pm 0.070.s^{-1}$
Success rate, Pt^{-1}	$0.156 \pm 0.069.s^{-1}$	$0.185 \pm 0.069.s^{-1}$
Frequency of success, $P(P + F)^{-1}$	0.812 ± 0.196	0.814 ± 0.137

birds and barnacles, suggesting that the birds could be preying on the barnacles. Indeed “barnacle plates” according to Harris (1979) formed almost 60% of the faecal pellets collected from turnstones. Presumably the birds attacked the barnacles through the opercular valves and these are the plates to which Harris refers. This was confirmed by Groves (1978) working on ruddy turnstones on the Massachusetts coastline of North America. Rocky shores with dense barnacle cover were common feeding grounds for the turnstones. Groves found that a foraging bird with its mandibles tightly closed delivers a few sharp blows to the tergal and scutal valves of the barnacle. This opens the barnacle and the flesh is then removed by frequent pecks by the bird. By tilting its head in different directions the bird is able to remove most of the soft parts of the barnacle. Occasionally broken pieces of the valves are also removed by the bird. A group of barnacles (about 50 cm \times 50 cm) may be consumed by the same turnstone which remains in the area for 20 min or more. A turnstone will peck among the wall plates of dead barnacles and sometimes it will displace another turnstone already feeding and will feed on the barnacle opened by the displaced bird. Groves (1978) compared foraging rate, success rate, and frequency of success for juvenile and adult turnstones when foraging on barnacles. Foraging movements involved contact of the bird’s beak with the substratum or manipulation of the substratum in the search for prey. As it was difficult to distinguish between searching activities and unsuccessful attempts to capture prey they were considered together as directed foraging movements (F). A successful single foraging movement resulting in ingestion of the prey was regarded as a prey capture (P). The results are shown in Table 31. The time available for foraging was limited by the tides; adults and juveniles foraged continuously during the time available (Groves 1978). The efficiency of foraging improved with age of the birds. Very young birds were hesitant and somewhat inefficient but within a few days their hesitancy was overcome and foraging efficiency improved as they matured.

Most species of oystercatchers feed in the intertidal area of rocky shores but appear to ignore barnacles which are abundant in such regions. Randall & Randall (1982) suggest that this may be because the birds are unable to break open the shells or have difficulty in pecking out the contents through the narrow aperture.

In the work carried out by both Groves (1978) and Harris (1979) the barnacles being preyed upon were *Semibalanus balanoides*, the common intertidal barnacle in the areas where they worked. Hadley & Castle (1940) found that the metacercarial stage of *Maritrema arenaria* occurs in *Semibalanus balanoides* and that these cysts are found in many barnacles on the shores frequented by ruddy turnstones in Maine and the Woods Hole region on the east coast of North America. It is apparent that these metacercariae are part of the life cycle of adult *Maritrema arenaria* found in the guts of the ruddy turnstone. The gut of one bird that was examined contained bits of barnacle shell with partially digested barnacles.

In addition, there were partially and freshly excysted metacercariae and over 10000 adult *M. arenaria*. This was not uncommon and Hadley & Castle (1940) had difficulty in finding uninfected birds. These metacercariae could be an attraction to foraging rurnstones.

The intertidal pedunculate barnacle *Pollicipes polymerus* is widely distributed on the Pacific coast of North America (Barnes 1996). Morphological and physical factors (Barnes & Reese 1960) and interspecific competition for space (Paine 1974) may affect distribution and abundance patterns. In addition, predation by birds should be considered. Marsh (1986) found *Pollicipes* in pellets regurgitated by gulls. As this work was done on the coast of Oregon, USA it is assumed that this was *P. polymerus*. Flocks of birds are common on these shores in autumn and winter. Surfbirds, *Aphriza virgata* and gulls, principally *Larus occidentalis* and *L. glaucescens*, feed on mussels and *Pollicipes* during these months. At other times they normally feed offshore. Thus, predation by *Larus glaucescens*, can alter the cover of *Pollicipes polymerus* and *Mytilus californianus* (Wootton 1992). By feeding on *Pollicipes polymerus* itself gulls can cause increases in *Mytilus californianus* (by allowing late recruitment to be successful) especially where *Pollicipes* gains an initial size advantage (Wootton 1993). If predation by birds is prevented *P. polymerus* increases (Wootton 1993, 1994).

Meese (1993) made a detailed and experimental investigation of the effect of predation by birds on *P. polymerus* communities. He found that the abundance of *Pollicipes* was significantly reduced in plots accessible to birds compared with control plots from which birds were excluded. *Pollicipes* often grow together as clumps forming a "rosette" pattern on the shore. Barnes & Reese (1960) described these rosettes and suggested that the tight packing provided protection from predation, but did not specify which predators. Meese (1993) speculated that a tight rosette formation was the result of the "shadow reflex" (Gwilliam 1963, Ozawa et al. 1977) exhibited by stalked and acorn barnacles. A gull may attack several tight rosettes before it manages to remove an individual barnacle but once this happens the tightness of the rosette is destroyed and further predation by the same or other gulls follows. In this way whole rosettes may be consumed leaving clear spaces and causing patchiness in the distribution pattern of *P. pollicipes* (Meese 1993, Barnes 1996).

Man

Marine habitats have been subjected to human interference for many hundreds of years and recently this has increased. On rocky shores animals may be collected for food or bait and in this search boulders may be overturned and microhabitats disturbed. Animals may be dislodged by people as in the case of *Elminius plicatus* in New Zealand (Luckens 1976).

The effect of trampling by man on intertidal rocky shores can have a detrimental effect on the cirripede populations. This has been demonstrated by Povey & Keough (1991) on the Bass Strait coast, Victoria, Australia and by Brosnan & Crumrine (1994) on the Oregon coast of the Pacific northwestern USA. On the shores investigated by Povey & Keough (1991) the common cirripede was *Chthamalus antennatus*. The damage caused by a single footstep in 15 random quadrats was recorded. Barnacles were damaged in five of the nine quadrats in which they were found. This represented a total of 10 (17.5%) crushed animals out of 57 found.

Brosnan & Crumrine (1994) tested the effect of human trampling on two exposed rocky intertidal communities, Fogarty Creek and Little Whale Cove. In an upper shore barnacle-algal assemblage, *Balanus glandula* and *Chthamalus dalli* were present. In a second community, mussels occupied about 95% of the primary spaces with *Pollicipes polymerus* covering the remaining 5%. *Balanus glandula* and *Chthamalus dalli* were present as

Table 32 Effect of trampling on two sites, Oregon coast, North America. (After Brosnan & Crumrine 1994.)

	Barnacle cover, %	
	Fogarty Creek	Little Whale Cove
Trampled (initial)	66.6	21.3
Control	71.0	15.0
Trampled	7.2 (after 4 months)	5.3 (after 6 months)

epibionts on the mussel shells. Brosnan & Crumrine “trampled” experimental plots on the barnacle-algal shore with 250 steps on one day every month for 12 months from March 1990 to March 1991. Recovery was monitored in July 1991, September 1991 (6 months after trampling stopped) and April 1992 (one year after). The initial barnacle cover differed between the two sites so the sites were treated separately. The results are shown in Table 32. There was no initial difference at either site in the barnacle cover between control and trampled plots. After trampling barnacle cover at both sites was significantly reduced. Barnacle cover remained significantly lower on the trampled plots until March 1991 when barnacle recruitment increased in the trampled plots. The barnacle density did not increase as much in the control plots because less space was available. Trampling in the mussel community had a pronounced effect on the mussel population and as a consequence on the cirripede epibionts. At Fogarty Creek after four months trampling the percentage cover of barnacle epibionts per mussel dropped from about 58% to 17.8%. The net effect of trampling depends on when the disturbance takes place; if barnacles are crushed before they are sexually mature then the population will suffer a steady decline.

In central Chile, man is an important intertidal predator and Durán & Castilla (1989) report that harvested areas of the mid-intertidal rocky shore are dominated by mussels *Perumytilus purpuratus*. When man is excluded from such areas, barnacles, *Jehlius cirratus* and *Chthamalus scabrosus* become dominate.

The soft parts of several species of cirripedes have been a source of food for local inhabitants in many regions for generations (Moreno et al. 1986). It is usually the ovary or egg lamellae that are cooked and eaten but in some places, where very large genera are available, the muscles of the prosoma may also be eaten. In Chile the large barnacle, *Megabalanus psittacus*, is collected and sold for food in the markets. The same is true for the pedunculate barnacles of the genus *Pollicipes* (Barnes 1996). There is a small fishery for *P. elegans* in Costa Rica, and in Pacific coastal areas of North America *P. polymerus* may be eaten. The European species, *P. pollicipes*, is sold in the markets of Spain and Portugal where the stalk is regarded as a delicacy. Long overfishing of the natural populations has been detrimental to the supply and efforts are now being made to cultivate *Pollicipes* for commercial purposes (Barnes 1996 and references therein).

In spite of intensive collecting for research purposes, particularly in the summer, in the Woods Hole region, Massachusetts, USA, the number of animals, according to Allee (1923) was not noticeably affected. This applies to populations of *Semibalanus balanoides*, *Balanus eburneus* and *Lepas anatifera*. Whether the same is true now over 75 years later is not known. As these cirripedes all have a planktonic phase, renewal from nearby populations is always possible.

Wagh & Bal (1970b) record a case where an indirect action of man caused the deterioration of one barnacle population, displacement of a second, and enhancement of a third. Increased suspended matter in the water caused by dredging at the site of a new jetty in the Maharashtra region on the west coast of India provided abundant food for *Balanus amphitrite*. Prior to dredging the *B. amphitrite* was only of a moderate size compared with animals of large size afterwards. Whereas such conditions favoured *B. amphitrite*, on an exposed point near the dredging a *Megabalanus tintinnabulum* population was eradicated and a *Chthamalus malayensis* population was diminished and was only present on landward-facing rocks.

Conclusion

Predation is often considered important in the organization of the structure and diversity of marine communities but only comparatively recently has it become a major topic of research. Studies such as those of Connell (1961a,b) and Paine (1966a) have demonstrated that predators can influence both the distribution and abundance of prey. There are numerous papers dealing with models that can be applied to various aspects of predation but it has not been the purpose of this review to consider these in detail.

The first experimental approach to the optimal foraging theory was probably that of Emlen (1966, see also Hughes 1980, 1985, Hughes & Dunkin 1984a). The role of learning (Pratt 1974), handling time (Morgan 1972), biases due to handling time (Murdoch 1969, 1971), and the apparent diet of predators (Fairweather & Underwood 1983) have all been considered in detail elsewhere. A great deal of work has been done by a group of marine biologists at the University of Sydney, Australia, under the direction of Dr (now Professor) A.J. Underwood on predation as applied to the rocky shores of New South Wales (for example, Fairweather et al. 1984, Moran et al. 1984, Caffey 1985, Fairweather 1985, 1986, 1987, 1988a,b,c,d,e, Moran 1985a,b).

Predation can create "haloes of bare space" among prey on rocky shores (Fairweather 1988a) that can be used by other organisms (Dayton 1971). Such space is essential for organisms that occur spasmodically and for which space is scarce (Underwood et al. 1983). Predation in "benign" habitats has been considered by Connell (1975, 1985b) and Menge & Sutherland (1976). According to Fairweather et al. (1984), the effect of intertidal predators may be direct, such as reducing the vertical distribution of prey (Connell 1970, Paine 1974). It may also act indirectly by reducing the intensity of competitive interactions or modifying other interactions among prey species (Paine 1966a, 1974, 1980, Garrity & Levings 1981, Underwood et al. 1983).

The part played by predation versus competition in the structure of rocky intertidal communities has not been the object of this review and those interested in the on-going controversy should begin by referring to Menge & Sutherland (1976), Stanley & Newman (1980), Newman & Stanley (1981), Paine (1981) and the references contained in these papers. Co-existence among competitors may be enhanced if predators sufficiently depress the densities of superior competitors without eradicating them (Paine 1966a).

On the rocky shores of the northern Pacific coast of North America (about 49°N latitude) there is a constant association of mussels, barnacles, the starfish *Pisaster ochraceus* and the gastropod *Nucella emarginata*. This food web depends on barnacles; both major predators consume them in quantity (Paine 1966a). On a nutritional basis, however, barnacles are only about one-third as important to the starfish as, for example, are the mussels. In the northern Gulf of California (about 31°N latitude) a similar food web exists with the starfish *Heliaster kubiniji* and the gastropod *Muricanthus nigritus* as the top-ranking carnivores. Numerically,

the major food item is again barnacles but other members of the community provide most of the nutritional value. *Pisaster* and *Heliaster* consume masses of barnacles and by keeping space open they enhance the ability of other species to settle there. Carnivorous gastropods can only penetrate one barnacle at a time and they consume a few during a tidal interval, but the empty barnacle shells remain on the substratum. A starfish, however, may entirely remove 20–60 barnacles simultaneously and leave the surface completely clean and available for other organisms. If the barnacles are not removed from these shores, they potentially dominate the space and diversity is reduced. Examples of this are seen on the shores of Washington State mentioned above, on Scottish shores (Connell 1961a,b) and the rocky intertidal shores of northern Japan (Hoshiai 1960). Local diversity on intertidal rocky shores appears to be directly related to the intensity of predation but other factors may be involved to modify this simplistic conclusion (Paine 1966a, Menge & Sutherland 1976).

A possible consequence of a predator switching between two potentially competing prey species is that both prey species may be able to co-exist indefinitely owing to predation on whichever species is winning the competition. Within wide limits increase in prey species diversity, both in numbers and their relative abundance, may be caused by increased predation (Murdoch 1969).

Underwood & Fairweather (1985) stress that comparison of tropical with temperate communities should be made with a knowledge of the roles of the individual species, not just a group of species. Interactions among several common species in New South Wales are more complex than has been found on the west coast of America. Care should be taken to ensure that the aims, hypotheses, and approaches used in studies that are to be compared are truly comparable, for example, when considering communities in other continents with those in Australia.

Predators are absent in protected areas near Beaufort, North Carolina (Ortega 1981) although they are common in protected areas further north on this coast (Menge 1976, Peterson 1979). Environmental stress appears to be the cause of this contradiction. Predators in protected sites suffer from desiccation compared with those in exposed sites receiving splashing waves. Also protection from an algal canopy is absent on protected shores at Beaufort but is effective further north. Underwood et al. (1983) concluded that co-evolved community relationships are probably not important in communities where most of the species have widely dispersed pelagic young and interact in different and complex ways at different densities. The importance of physical factors as modifying influences on patterns and processes on seashores has been emphasized by Underwood (1985). Many studies indicate that there are several possible models for patterns of distribution and abundance of individual species. The influence of physical environmental factors should not be assumed without direct evidence to support hypotheses based on models involving physical factors. According to Paine (1980) "Food webs along with their associated cross-links provide a realistic framework for understanding complex, highly interactive multispecies relationships".

Acknowledgements

I am grateful to friends and colleagues with whom I have been able to discuss this review during its preparation, particularly those who read various sections of it. As always, Miss E. Walton has been most efficient and helpful in tracing and obtaining obscure literature. Mrs L. Robb kindly drew Figure 6. I appreciate the expertise with which Mrs Margaret Batty typed the original manuscript and corrected subsequent revisions.

References

- Allee, W.C. 1923. Studies in marine ecology. I. The distribution of common littoral invertebrates of the Woods Hole Region. *Biological Bulletin* **44**, 167–91.
- Arnold, J.M. & Arnold, K.O. 1969. Some aspects of hole-boring predation by *Octopus vulgaris*. *American Zoologist* **9**, 991–6.
- Arvy, L. & Nigrelli, R.F. 1969. Studies in the biology of barnacles: parasites of *Balanus eburneus* and *B. balanoides* from New York Harbor and a review of the parasites and diseases of other Cirrhipedia. *Zoologica* **54**(3), 95–102.
- Bahls, H. 1903. *Über Struktur und Wachstum der Schale von Balanus improvisus*. Inaugural Dissertation, Greifswald.
- Barnes, H. & Powell, H.T. 1950. The development, general morphology and subsequent elimination of barnacle populations, *Balanus crenatus* and *B. balanoides*, after a heavy initial settlement. *Journal of Animal Ecology* **19**, 175–9.
- Barnes, H. & Powell, H.T. 1951. The growth-rate of juvenile *Asterias rubens* L. *Journal of the Marine Biological Association of the United Kingdom* **30**, 381–5.
- Barnes, H. & Powell, H.T. 1954. *Onchidoris fusca* (Müller); a predator of barnacles. *Journal of Animal Ecology* **23**, 361–3.
- Barnes, H., Read, R. & Topinka, J.A. 1970. The behaviour on impaction by solids of some common cirripedes and relation to their normal habitat. *Journal of Experimental Marine Biology and Ecology* **5**, 70–87.
- Barnes, H. & Reese, E.S. 1960. The behaviour of the stalked intertidal barnacle *Pollicipes polymerus* J.[sic] B. Sowerby, with special reference to its ecology and distribution. *Journal of Animal Ecology* **29**, 169–85.
- Barnes, M. 1996. Pedunculate cirripedes of the genus *Pollicipes*. *Oceanography and Marine Biology: an Annual Review* **34**, 303–94.
- Barnett, B.E. 1979. A laboratory study of predation by the dog-whelk *Nucella lapillus* on the barnacles *Elminius modestus* and *Balanus balanoides*. *Journal of the Marine Biological Association of the United Kingdom* **59**, 299–306.
- Bayliss, D.E. 1982. Switching by *Lepsiella vinosa* (Gastropoda) in South Australian mangroves. *Oecologia (Berlin)* **54**, 212–26.
- Bayliss, D.E. 1993. Spatial distribution of *Balanus amphitrite* and *Elminius adalaidae* on mangrove pneumatophores. *Marine Biology* **116**, 251–6.
- Bayne, B.L. & Scullard, C. 1978. Rates of feeding by *Thais (Nucella) lapillus* (L.). *Journal of Experimental Marine Biology and Ecology* **32**, 113–29.
- Bender, J.A., DeRiemer, K., Roberts, T.E., Rushton, R., Boothe, P., Mosher, H.S. & Fuhrman, F.A. 1974. Choline esters in marine gastropods *Nucella emarginata* and *Acanthina spirata*. A new choline ester, tentatively identified as N-methylmurexine. *Comparative and General Pharmacology* **5**, 191–8.
- Bergeron, P. & Bourget, E. 1986. Shore topography and spatial partitioning of crevice refuges by sessile epibenthos in an ice disturbed environment. *Marine Ecology Progress Series* **28**, 129–45.
- Bernard, F.R. 1988. Potential fishery for the gooseneck barnacle *Pollicipes polymerus* (Sowerby 1833) in British Columbia. *Fisheries Research* **6**, 287–98.
- Bertness, M.D. 1977. Behavioral and ecological aspects of shore-level size gradients in *Thais lamellosa* and *Thais emarginata*. *Ecology* **58**, 86–97.
- Bertness, M.D. 1989. Intraspecific competition and facilitation in a northern acorn barnacle population. *Ecology* **70**, 257–68.
- Bertness, M.D., Gaines, S.D., Bermudez, D. & Sanford, E. 1991. Extreme spatial variation in the growth and reproductive output of the acorn barnacle *Semibalanus balanoides*. *Marine Ecology Progress Series* **75**, 91–100.
- Birkeland, C. 1974. Interactions between a sea pen and seven of its predators. *Ecological Monographs* **44**, 211–32.
- Blaxter, J.H.S. 1968. Rearing herring larvae to metamorphosis and beyond. *Journal of the Marine Biological Association of the United Kingdom* **48**, 17–28.
- Blower, J.G. 1957. Feeding habits of a marine centipede. *Nature* **180**, 560 only.
- Bokenham, N.A.H. 1938. The colonization of denuded rock surfaces in the intertidal region of Cape Peninsula. With a general comment on the results by T.A. Stephenson. *Annals of the Natal Museum* **9**, 47–81.

- Bosch, M. & Moreno, I. 1986. Spatial distribution of *Littorina neritoides* (L. 1758) (Mollusca, Gastropoda) in the supralittoral zone in the Balearic Islands. *Cahiers de Biologie Marine* **27**, 53–62.
- Bourget, E. 1987. Barnacle shells: composition, structure and growth. In *Crustacean issues. 5. Barnacle biology*, A.J. Southward (ed.). Rotterdam: A.A. Balkema, 267–85.
- Branch, G.M. 1975. Intraspecific competition in *Patella cochlear* Born. *Journal of Animal Ecology* **44**, 263–82.
- Branch, G.M. 1976. Interspecific competition experienced by South African *Patella* species. *Journal of Animal Ecology* **45**, 507–29.
- Branch, G.M. 1978. The responses of South African patellid limpets to invertebrate predators. *Zoologica Africana* **13**, 221–32.
- Branch, G.M. 1984. Competition between marine organisms: ecological and evolutionary implications. *Oceanography and Marine Biology: an Annual Review* **22**, 429–593.
- Branscomb, E.S. 1976. Proximate causes of mortality determining the distribution and abundance of the barnacle *Balanus improvisus* Darwin in Chesapeake Bay. *Chesapeake Science* **17**, 281–8.
- Brosnan, D.M. & Crumrine, L.L. 1994. Effects of human trampling on marine rocky shore communities. *Journal of Experimental Marine Biology and Ecology* **177**, 79–97.
- Brown, B. & Rittschof, D. 1984. Effects of flow and concentration of attractant on newly hatched oyster drills, *Urosalpinx cinerea* (Say). *Marine Behaviour and Physiology* **11**, 75–93.
- Burger, J.F., Anderson, J.R. & Knudsen, M.F. 1980. The habits of life history of *Oedoparena glauca* (Diptera: Dryomyzidae), a predator of barnacles. *Proceedings of the Entomological Society of Washington* **82**, 360–77.
- Burrell Jr, V.G. & Van Engel, W.A. 1976. Predation by and distribution of a ctenophore, *Mnemiopsis leidyi* A. Agassiz, in the York River estuary. *Estuarine and Coastal Marine Science* **4**, 235–42.
- Burrows, M.T. 1985. Predation by *Nucella lapillus* on barnacles. *Porcupine Newsletter* **3**, 64–6.
- Burrows, M.T. & Hughes, R.N. 1991. Variation in foraging behaviour among individuals and populations of dog-whelks, *Nucella lapillus*: natural constraints on energy uptake. *Journal of Animal Ecology* **60**, 497–514.
- Butler, A.J. 1979. Relationships between height on the shore and size distributions of *Thais* spp. (Gastropoda: Muricidae). *Journal of Experimental Marine Biology and Ecology* **41**, 163–94.
- Caffey, H.M. 1985. Spatial and temporal variation in settlement and recruitment of intertidal barnacles. *Ecological Monographs* **55**, 313–32.
- Cake Jr, E.W. 1983. Symbiotic associations involving the southern oyster drill *Thais haemastoma floridana* (Conrad) and macrocrustaceans in Mississippi waters. *Journal of Shellfish Research* **3**, 117–28.
- Cancino, J.M. & Castilla, J.C. 1988. Emersion behaviour and foraging ecology of the common Chilean clingfish *Sicyases sanguineus* (Pisces: Gobiesocidae). *Journal of Natural History* **22**, 249–61.
- Carriker, M.R. 1961. Comparative functional morphology of boring mechanisms in gastropods. *American Zoologist* **1**, 263–6.
- Carriker, M.R. 1981. Shell penetration and feeding by naticacean and muricacean predatory gastropods: a synthesis. *Malacologia* **20**, 403–22.
- Carriker, M.R., Schaadt, J.G. & Peters, V. 1974. Analysis by slow-motion picture photography and scanning electron microscopy of radula function in *Urosalpinx cinerea follyensis* (Muricidae, Gastropoda) during shell penetration. *Marine Biology* **25**, 63–76.
- Carriker, M.R. & Williams, L.G. 1978. The chemical mechanism of shell dissolution by predatory boring gastropods: a review and an hypothesis. *Malacologia* **17**, 143–56.
- Castilla, J.C. 1972. Responses of *Asterias rubens* to bivalve prey in a Y-maze. *Marine Biology* **12**, 222–8.
- Castilla, J.C. & Crisp, D.J. 1970. Responses of *Asterias rubens* to olfactory stimuli. *Journal of the Marine Biological Association of the United Kingdom* **50**, 829–47.
- Chao, L.N. 1973. Digestive system and feeding habits of the cunner, *Tautoglabrus adspersus*, a stomachless fish. *United States National Marine Fisheries Service, Fishery Bulletin* **71**, 565–86.
- Chétail, M. & Fournié, J. 1969. Shell-boring mechanism of the gastropod *Purpura (Thais) lapillus*: a physiological demonstration of the role of carbonic anhydrase in the dissolution of CaCO₃. *American Zoologist* **9**, 983–90.
- Chia, F.-S. & Koss, R. 1988. Induction of settlement and metamorphosis of the veliger larvae of the nudibranch, *Onchidoris bilamellata*. *International Journal of Invertebrate Reproduction and Development* **14**, 53–69.

- Choat, J.H. 1977. The influence of sessile organisms on the population biology of three species of acmaeid limpets. *Journal of Experimental Marine Biology and Ecology* **26**, 1–26.
- Christensen, D.J. 1973. Prey preference of *Stylochus ellipticus* in Chesapeake Bay. *Proceedings of the National Shellfisheries Association* **63**, 35–8.
- Christensen, M.S. 1978. Trophic relationships in juveniles of three species of sparid fishes in the South African marine littoral. *United States National Marine Fisheries Service, Fishery Bulletin* **76**, 389–401.
- Christie, A.O. & Dalley, R. 1987. Barnacle fouling and its prevention. In *Crustacean issues. 5. Barnacle biology*, A.J.Southward (ed.). Rotterdam: A.A.Balkema, 419–33.
- Collins, K.J., Jensen, A.C. & Turnpenny, A.W.H. 1991. The artificial reef project, Poole Bay: a fishery enhancement experiment. In *Aquaculture and the environment*, compiled by N.DePauw & J.Joyce, *Special Publication of the European Aquaculture Society* No. 14, 76 only.
- Connell, J.H. 1959a. An experimental analysis of interspecific competition in natural populations of intertidal barnacles. *Proceedings XVth International Congress of Zoology, London*, H.R.Hewer & N.D.Riley (eds). London: Congress of Zoology, 290–92.
- Connell, J.H. 1959b. Studies of some factors affecting the recruitment and mortality of natural populations of intertidal barnacles. In *Marine boring and fouling organisms*, D.L.Ray (ed.). Seattle: University of Washington Press, 226–33.
- Connell, J.H. 1961a. Effects of competition, predation by *Thais lapillus*, and other factors on natural populations of the barnacle *Balanus balanoides*. *Ecological Monographs* **31**, 61–104.
- Connell, J.H., 1961b. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology* **42**, 710–23.
- Connell, J.H. 1970. A predator-prey system in the marine intertidal region. I. *Balanus glandula* and several predatory species of *Thais*. *Ecological Monographs* **40**, 49–78.
- Connell, J.H. 1972. Community interactions on marine rocky intertidal shores. *Annual Review of Ecology and Systematics* **3**, 169–92.
- Connell, J.H. 1975. Some mechanisms producing structure in natural communities: a model and evidence from field experiments. In *Ecology and evolution of communities*, M.L.Cody & J.M. Diamond (eds). Bainbridge, MA, USA: Belknap Press, 460–90.
- Connell, J.H. 1985a. Variation and persistence of rocky shore populations. In *The ecology of rocky coasts: essays presented to J.R.Lewis D.Sc.*, P.G.Moore & R.Seed (eds). London: Hodder & Stoughton, 57–69.
- Connell, J.H. 1985b. The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities. *Journal of Experimental Marine Biology and Ecology* **93**, 11–45.
- Conover, J.T. & Sieburth, J.M. 1966. Effect of tannins excreted from Phaeophyta on planktonic animal survival in tide pools. In *Proceedings of the Fifth International Seaweed Symposium*, E.G. Young & J.L.McLachlan (eds). Oxford: Pergamon Press, 99–100.
- Cory, R.L. 1967. Epifauna of the Patuxent River Estuary, Maryland, for 1963 and 1964. *Chesapeake Science* **8**, 71–89.
- Cowden, C., Young, C.M. & Chia, F.S. 1984. Differential predation on marine invertebrate larvae by two benthic predators. *Marine Ecology Progress Series* **14**, 145–9.
- Crampton, D.M. 1977. Functional anatomy of the buccal apparatus of *Onchidoris bilamellata* (Mollusca: Opisthobranchia). *Transactions of the Zoological Society of London* **34**, 45–86.
- Cranwell, L.M. & Moore, L.B. 1938. Intertidal communities of the Poor Knights Islands, New Zealand. *Transactions of the Royal Society of New Zealand* **67**, 375–406.
- Creese, R.G. 1982. Distribution and abundance of the acmaeid limpet *Patelloida latistrigata*, and its interaction with barnacles. *Oecologia (Berlin)* **52**, 85–96.
- Crisp, D.J. 1958. The spread of *Elminius modestus* Darwin in north-west Europe. *Journal of the Marine Biological Association of the United Kingdom* **37**, 483–520.
- Crisp, D.J. 1960. Mobility of barnacles. *Nature* **188**, 1208–9.
- Daly, M.A. & Mathieson, A.C. 1977. The effect of sand movement on intertidal seaweeds and selected invertebrates at Bound Rock, New Hampshire, USA. *Marine Biology* **43**, 45–55.
- Darcy, G.H. 1981. Food habits of the crested goby, *Lophogobius cyprinoides*, in two Dade County, Florida, waterways. *Bulletin of Marine Science* **31**, 928–32.
- Darwin, C. 1851. *A monograph of the sub-class Cirripedia, with figures of all the species. The Lepadidae; or, pedunculated cirripedes*. London: The Ray Society.

- Darwin, C. 1854. *A monograph of the sub-class Cirripedia, with figures of all the species. The Balanidae, (or sessile cirripedes); The Verrucidae, etc. etc.* London: The Ray Society.
- Dayton, P.K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecological Monographs* **41**, 351–89.
- Dean, T.A. 1981. Structural aspects of sessile invertebrates as organizing forces in an estuarine fouling community. *Journal of Experimental Marine Biology and Ecology* **53**, 163–80.
- Dean, T.A. & Hurd, L.E. 1980. Development in an estuarine fouling community: the influence of early colonists on later arrivals. *Oecologia (Berlin)* **46**, 295–301.
- Denley, E.J. & Underwood, A.J. 1979. Experiments on factors influencing settlement, survival, and growth of two species of barnacles in New South Wales. *Journal of Experimental Marine Biology and Ecology* **36**, 269–93.
- Denny, M.W. 1982. Forces on intertidal organisms due to breaking ocean waves: design and application of a telemetry system. *Limnology and Oceanography* **27**, 178–83.
- Denny, M.W. 1985. Wave forces on intertidal organisms: a case study. *Limnology and Oceanography* **30**, 1171–87.
- Denny, M.W., Daniel, T.L. & Koehl, M.A.R. 1985. Mechanical limits to size of wave-swept organisms. *Ecological Monographs* **55**, 69–102.
- De Silva, S.S. 1973. Food and feeding habits of the herring *Clupea harengus* and the sprat *C. sprattus* in inshore waters of the west coast of Scotland. *Marine Biology* **20**, 282–90.
- Dexter, R.W. 1947. The marine communities of a tidal inlet at Cape Ann, Massachusetts: a study in bio-ecology. *Ecological Monographs* **17**, 261–94.
- Dexter, R.W.D. 1943. Observations on the local movements of *Littorina litorea* [sic](L.) and *Thais lapillus* (L.). *Nautilus* **57**, 6–8.
- Dougherty, W.J. 1990. Barnacle adhesion: reattachment of the adult barnacle *Chthamalus fragilis* Darwin to polystyrene surfaces followed by centrifugational shearing. *Journal of Crustacean Biology* **10**, 469–78.
- Dragovich, A. 1969. *Review of studies of tuna food in the Atlantic Ocean*. United States Fish and Wildlife Service, Special Scientific Report Fisheries No. 593, 21pp.
- Dungan, M.L. 1985. Competition and the morphology, ecology, and evolution of acorn barnacles: an experimental test. *Paleobiology* **11**, 165–73.
- Dungan, M.L. 1986. Three-way interactions: barnacles, limpets, and algae in a Sonoran Desert rocky intertidal zone. *The American Naturalist* **127**, 292–316.
- Dungan, M.L. 1987. Indirect mutualism: complementary effects of grazing and predation in a rocky intertidal community. In *Predation, direct and indirect impacts on aquatic communities*, W.C. Kerfoot & A.Sih (eds). London, New England: University Press of New England, 188–200.
- Dunkin, S.de B. & Hughes, R.N. 1984. Behavioural components of prey-selection by dogwhelks, *Nucella lapillus* (L.), feeding on barnacles, *Semibalanus balanoides* (L.), in the laboratory. *Journal of Experimental Marine Biology and Ecology* **79**, 91–103.
- Dunne, J. 1977. Littoral and benthic investigations on the west coast of Ireland. VII. (Section A: faunistic and ecological studies). The biology of the shanny, *Blennius pholis* L. (Pisces) at Carna, Connemara. *Proceedings of the Irish Academy, Section B* **77**, 207–26.
- Durán, L.R. & Castilla, J.C. 1989. Variation and persistence of the middle rocky intertidal community of central Chile, with and without human harvesting. *Marine Biology* **103**, 555–62.
- Dye, A.H. 1988. Rocky shore surveillance on the Transkei coast, southern Africa: temporal and spatial variability in the balanoid zone at Dwesa. *South African Journal of Marine Science* **7**, 87–99.
- Edwards, D.C., Conover, D.O. & Sutter III, F. 1982. Mobile predators and the structure of marine intertidal communities. *Ecology* **63**, 1175–80.
- Eliot, C. 1910. *A monograph of the British nudibranchiata Mollusca: with figures of the species. Part VIII Supplementary*. London: The Ray Society.
- Ellehaug, J.O. 1978. On the ecology of *Edwardsia longicornis* and *E. danica* (Anthozoa, Actinaria). *Biokon Report* **7**, 13–40.
- Ellis, D.V. 1955. Some observations on the shore fauna of Baffin Island. "Arctic", *Journal of the Arctic Institute of North America* **8**, 224–36.
- Ellis, D.V. & Wilce, R.T. 1961. Arctic and subarctic examples of intertidal zonation. "Arctic", *Journal of the Arctic Institute of North America* **14**, 224–35.
- Emlen, J.M. 1966. The role of time and energy in food preference. *The American Naturalist* **100**, 611–17.

- Endean, R., Duchemin, C., McColm, D. & Fraser, E.H. 1969. A study of the biological activity of toxic material derived from nematocysts of the cubomedusan *Cironex fleckeri*. *Toxicon* **6**, 179–204.
- Endean, R., Gyr, P. & Parish, G. 1974a. Pharmacology of the venom of the gastropod *Conus magus*. *Toxicon* **12**, 117–29.
- Endean, R. & Henderson, L. 1969. Further studies of toxic material from nematocysts of the cubomedusan *Chironex fleckeri* Southcott. *Toxicon* **7**, 303–14.
- Endean, R., Kenny, R. & Stephenson, W. 1956. The ecology and distribution of intertidal organisms on the rocky shores of the Queensland mainland. *Australian Journal of Marine and Freshwater Research* **7**, 88–146.
- Endean, R., Parish G. & Gyr, P. 1974b. Pharmacology of the venom of *Conus geographus*. *Toxicon* **12**, 131–8.
- Endean, R. & Rifkin, J. 1975. Isolation of different types of nematocyst from the cubomedusan *Chironex fleckeri*. *Toxicon* **13**, 375–6.
- Etter, R.J. 1996. The effect of wave action, prey type, and foraging time in growth of the predatory snail *Nucella lapillus* (L.). *Journal of Experimental Marine Biology and Ecology* **196**, 341–56.
- Fairweather, P.G. 1985. Differential predation on alternative prey, and the survival of rocky intertidal organisms in New South Wales. *Journal of Experimental Marine Biology and Ecology* **89**, 135–56.
- Fairweather, P.G. 1986. Interaction between predators and prey, and the structure of rocky intertidal communities. *Australian Journal of Ecology* **11**, 321–2.
- Fairweather, P.G. 1987. Experiments on the interaction between predation and the availability of different prey on rocky seashores. *Journal of Experimental Marine Biology and Ecology* **114**, 261–73.
- Fairweather, P.G. 1988a. Predation creates haloes of bare space among prey on rocky seashores in New South Wales. *Australian Journal of Ecology* **13**, 401–9.
- Fairweather, P.G. 1988b. Correlations of predatory whelks with intertidal prey at several scales of space and time. *Marine Ecology Progress Series* **45**, 237–43.
- Fairweather, P.G. 1988c. Consequences of supply-side ecology: manipulating the recruitment of intertidal barnacles affects the intensity of predation upon them. *Biological Bulletin* **175**, 349–54.
- Fairweather, P.G. 1988d. Movements of intertidal whelks (*Morula marginalba* and *Thais orbitid*) in relation to availability of prey and shelter. *Marine Biology* **100**, 63–8.
- Fairweather, P.G. 1988e. Predation can increase variability in the abundance of prey on seashores. *Oikos* **53**, 87–92.
- Fairweather, P.G. & Underwood, A.J. 1983. The apparent diet of predators and biases due to different handling times of their prey. *Oecologia (Berlin)* **56**, 169–79.
- Fairweather, P.G., Underwood, A.J. & Moran, M.J. 1984. Preliminary investigations of predation by the whelk *Morula marginalba*. *Marine Ecology Progress Series* **17**, 143–56.
- Farmanfarmaian, A., Giese, A.C., Boolootian, R.A. & Bennett, J. 1958. Annual reproductive cycles in four species of west coast starfishes. *Journal of Experimental Zoology* **138**, 355–67.
- Farran, G.P. 1909. Nudibranchiate Mollusca of the trawling grounds off the east and south coasts of Ireland. *Scientific Investigations Fisheries Board of Ireland for 1907*, No. VI, 1–18.
- Farrell, T.M. 1988. Community stability: effects of limpet removal and reintroduction in a rocky intertidal community. *Oecologia (Berlin)* **75**, 190–7.
- Farrell, T.M. 1989. Succession in a rocky intertidal community: the importance of disturbance size and position within a disturbed patch. *Journal of Experimental Marine Biology and Ecology* **128**, 57–73.
- Feare, C.J. 1966. The winter feeding of the purple sandpiper. *British Birds* **59**, 165–79.
- Feare, C.J. 1971. The adaptive significance of aggregation behaviour in the dogwhelk *Nucella lapillus* (L.). *Oecologia (Berlin)* **7**, 117–26.
- Feare, C.J. & Summers, R.W. 1985. Birds as predators on rocky shores. In *The ecology of rocky coasts: essays presented to J.R.Lewis, D.Sc.*, P.G.Moore & R.Seed (eds). London: Hodder & Stoughton, 249–64.
- Feder, H.M. 1959. The food of the starfish, *Pisaster ochraceus*, along the California coast. *Ecology* **40**, 721–4.
- Feder, H.M. 1970. Growth and predation by the ochre sea star, *Pisaster ochraceus* (Brandt), in Monterey Bay, California. *Ophelia* **8**, 161–85.
- Feder, H.M. & Arvidsson, J. 1967. Studies on a sea-star (*Marthasterias glacialis*) extract responsible for avoidance reactions in a gastropod *Buccinum undatum*. *Arkiv för Zoologi* **19**, 369–79.

- Feder, H.M. & Paul, A.J. 1980. Food of the king crab, *Paralithodes camischatica* and the Dungeness crab, *Cancer magister* in Cook Inlet, Alaska. *Proceedings of the National Shellfish Association* **70**, 240–6.
- Ferrari, I. & Chierigato, A.R. 1981. Feeding habits of juvenile stages of *Sparus auratus* L., *Dicentrarchus labrax* L. and Mugilidae in a brackish embayment of the Po River Delta. *Aquaculture* **25**, 243–57.
- Fischer-Piette, E. 1934. Sur l'équilibre des faunes: interaction des moules, des pourpres et des cirripèdes. *Compte rendu sommaire des Séances de la Société de Biogéographie* No. 92, 47–8.
- Fives, J.M. 1980. Littoral and benthic investigations on the west coast of Ireland—XI. The biology of Montagu's blenny, *Coryphoblennius galerita* L. (Pisces), on the Connemara coast. *Proceedings of the Royal Irish Academy* **80B**, 61–77.
- Foster, B.A. 1987. Barnacle ecology and adaptation. In *Crustacean issues. 5. Barnacle biology*, A.J. Southward (ed.). Rotterdam: A.A.Balkema, 113–33.
- Franz, D. 1971. Population age structure, growth and longevity of the marine gastropod *Urosalpinx cinerea* Say. *Biological Bulletin* **140**, 63–72.
- Fretter, V. & Graham, A. 1962. *British prosobranch Mollusca: their functional anatomy and ecology*. London: The Ray Society.
- Fuentes, H.R. 1981. Feeding habit of *Semicossyphus maculatus* (Labridae) in coastal waters of Iquique in northern Chile. *Japanese Journal of Ichthyology* **27**, 309–15.
- Gaines, S.D. & Roughgarden, J. 1987. Fish in offshore kelp forests affect recruitment to intertidal barnacle populations. *Science* **235**, 479–81.
- Galtsoff, P.S. & Loosanoff, V.L. 1939. Natural history and method of controlling the starfish (*Asterias forbesi*). *Bulletin of the Bureau of Fisheries* 49, No. 31, 73–132.
- Garrity, S.D. & Levings, S.C. 1981. A predator-prey interaction between two physically and biologically constrained tropical rocky shore gastropods: direct, indirect and community effects. *Ecological Monographs* **51**, 267–86.
- Gerhart, D.J., Rittschof, D. & Mayo, S.W. 1988. Chemical ecology and the search of marine antifoulants. *Journal of Chemical Ecology* **14**, 1905–17.
- Gibson, R.N. 1968. The food and feeding relationships of littoral fish in the Banyuls region. *Vie et Milieu Série A* **19**, 447–56.
- Gibson, R.N. 1969. The biology and behaviour of littoral fish. *Oceanography and Marine Biology: an Annual Review* **7**, 367–410.
- Gibson, R.N. 1972. The vertical distribution and feeding relationships of intertidal fish on the Atlantic coast of France. *Journal of Animal Ecology* **41**, 189–207.
- Gibson, R.N. 1982. Recent studies on the biology of intertidal fishes. *Oceanography and Marine Biology: an Annual Review* **20**, 363–414.
- Gibson, R.N., Pihl, L., Burrows, M.T., Modin, J., Wennhage, H. & Nickell, L.A. 1998. Diel movements of juvenile plaice *Pleuronectes platessa* in relation to predators, competitors, food availability and abiotic factors on a microtidal nursery ground. *Marine Ecology Progress Series* **165**, 145–59.
- Godin, J.-G.J. 1981. Daily patterns of feeding behavior, daily rations, and diets of juvenile pink salmon (*Oncorhynchus gorbuscha*) in two marine bays of British Columbia. *Canadian Journal of Fisheries and Aquatic Science* **38**, 10–15.
- Goldschmid, A. & Kotschal, K. 1981. Feeding ecology of three populations of *Blennius incognitus* Bath 1968 (Pisces: Teleostei: Blenniidae) during the reproductive period and under human influence. *P.S.Z.N.I.: Marine Ecology* **2**, 1–14.
- Gosselin, L.A. & Bourget, E. 1989. The performance of an intertidal predator *Thais lapillus* in relation to structural heterogeneity. *Journal of Animal Ecology* **58**, 287–303.
- Grant, W.S. 1977. High intertidal community organization on a rocky headland in Maine, USA. *Marine Biology* **44**, 15–25.
- Groves, S. 1978. Age-related differences in ruddy turnstone foraging and aggressive behavior. *Auk* **95**, 95–103.
- Gubbay, S. 1983. Compressive and adhesive strengths of a variety of British barnacles. *Journal of the Marine Biological Association of the United Kingdom* **63**, 541–55.
- Guerra, A. & Nixon, M. 1987. Crab and mollusc shell drilling by *Octopus vulgaris* (Mollusca: Cephalopoda) in the Ria de Vigo (north-west Spain). *Journal of Zoology* **211**, 515–23.

- Guisado, C. & Castilla, J.C. 1983. Aspects of the ecology and growth of an intertidal juvenile population of *Concholepas concholepas* (Mollusca: Gastropoda: Muricidae) at Las Cruces, Chile. *Marine Biology* **78**, 99–103.
- Gul'bin, V.V. & Shadrin, N.V. 1991. Feeding ecology of the predatory gastropod *Nucella heyseana* in Peter the Great Bay, Sea of Japan. *Asian Marine Biology* **8**, 95–102.
- Gwilliam, G.F. 1962. Electrophysiological concomitants of the shadow reflex in certain barnacles. *Biological Bulletin* **123**, 498 only.
- Gwilliam, G.F. 1963. The mechanism of the shadow reflex in Cirripedia. I. Electrical activity in the supraesophageal ganglion and ocellar nerve. *Biological Bulletin* **125**, 470–85.
- Hadfield, M.G. 1963. The biology of nudibranch larvae. *Oikos* **14**, 85–95.
- Hadley, C.D. & Castle, R.M. 1940. Description of a new species of *Maritrema* Nicoll 1907, *Maritrema arenaria*, with studies of the life history. *Biological Bulletin* **78**, 338–48.
- Haldorson, L. & Moser, M. 1979. Geographic patterns of prey utilization in two species of surfperch (Embiotocidae). *Copeia* **1979**, No. 4, 567–72.
- Hancock, D.A. 1955. The feeding behaviour of starfish on Essex oyster beds. *Journal of the Marine Biological Association of the United Kingdom* **34**, 313–31.
- Hancock, D.A. 1958. Notes on starfish on an Essex oyster bed. *Journal of the Marine Biological Association of the United Kingdom* **37**, 565–89.
- Harms, J. & Anger, K. 1983. Seasonal, annual, and spatial variation in the development of hard bottom communities. *Helgoländer Meeresuntersuchungen* **36**, 137–50.
- Harris, P.R. 1979. The winter feeding of the turnstone in North Wales. *Bird Study* **26**, 259–66.
- Hart, M.W. & Palmer, A.R. 1987. Stereotype, ontogeny, and heritability of drill site selection in thaidid gastropods. *Journal of Experimental Marine Biology and Ecology* **107**, 101–20.
- Hartnoll, R.G. & Hawkins, S.J. 1985. Patchiness and fluctuations on moderately exposed rocky shores. *Ophelia* **24**, 53–63.
- Hawkins, S.J. 1981. The influence of *Patella* grazing on the fucoid/barnacle mosaic on moderately exposed rocky shores. *Kieler Meeresforschungen Sonderheft* **5**, 537–43.
- Hawkins, S.J. 1983. Interactions of *Patella* and macroalgae with settling *Semibalanus balanoides* (L.). *Journal of Experimental Marine Biology and Ecology* **71**, 55–72.
- Hawkins, S.J. & Hartnoll, R.G. 1982. Settlement patterns of *Semibalanus balanoides* (L.) in the Isle of Man (1977–1981). *Journal of Experimental Marine Biology and Ecology* **62**, 271–83.
- Hayes, F.R. 1929. Contributions to the study of marine gastropods. III. Development, growth and behaviour of *Littorina*. *Contributions to Canadian Biology and Fisheries, New Series* **4**, No. 26, 413–30.
- Healey, M.C. 1971. The distribution and abundance of sand gobies, *Gobius minutus*, in the Ythan estuary. *Journal of Zoology* **163**, 177–229.
- Healey, M.C. 1972. On the population ecology of the common goby in the Ythan estuary. *Journal of Natural History* **6**, 133–45.
- Hiatt, R.W. & Strasburg, D.W. 1960. Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. *Ecological Monographs* **30**, 65–127.
- Hoffman, D.L. 1989. Settlement and recruitment patterns of a pedunculate barnacle, *Pollicipes polymerus* Sowerby, off La Jolla, California. *Journal of Experimental Marine Biology and Ecology* **125**, 83–98.
- Høpner Petersen, G. 1962. The distribution of *Balanus balanoides* (L.) and *Littorina saxatilis*, Olivi, var. *groenlandica*, Mencke in northern West Greenland. *Meddelelser om Grønland* **159**, Nr. 9, 42 pp.
- Hoshiai, T. 1958. Synecological study on intertidal communities. I. The zonation of intertidal animal community with special reference to the interspecific relation. *Bulletin of the Marine Biological Station of Asamushi* **9**, 27–33.
- Hoshiai, T. 1959. Ecological study of the interspecific relation among littoral sessile animals on the artificially denuded rock. *Bulletin of the Marine Biological Station of Asamushi* **9**, 197–9.
- Hoshiai, T. 1960. Synecological study on intertidal communities. III. An analysis of interrelation among sedentary organisms on the artificially denuded rock surface. *Bulletin of the Marine Biological Station of Asamushi* **10**, 49–56.
- Hoshiai, T. 1965. Synecological study on intertidal communities. VI. A Synecological study of the intertidal zonation of the Asamushi coastal area with special reference to its re-formation. *Bulletin of the Marine Biological Station of Asamushi* **12**, 93–126.

- Huang, C.L. & Mir, G.N. 1971. Pharmacological properties of hypobranchial gland of *Thais haemastoma* (Clench). *Journal of Pharmaceutical Sciences* **60**, 1842–6.
- Huang, C.L. & Mir, G.N. 1972. Pharmacological investigations of salivary gland of *Thais haemastoma* (Clench). *Toxicon* **10**, 111–17.
- Hughes, R.N. 1980. Optimal foraging theory in the marine context. *Oceanography and Marine Biology: an Annual Review* **18**, 423–81.
- Hughes, R.N. 1985. Rocky shore communities: catalysts to understanding predation. In *The ecology of rocky coasts: essays presented to J.R.Lewis, D.Sc., P.G.Moore & R.Seed* (eds). London: Hodder & Stoughton, 223–33.
- Hughes, R.N. & Burrows, M.T. 1990. Energy maximisation in the natural foraging behaviour of the dogwhelk, *Nucella lapillus*. In *Trophic relationships in the marine environment. Proceedings of the 24th European Marine Biology Symposium*, M.Barnes & R.N.Gibson (eds). Aberdeen: Aberdeen University Press, 517–27.
- Hughes, R.N. & Drewett, D. 1985. A comparison of the foraging behaviour of dogwhelks, *Nucella lapillus* (L.), feeding on barnacles or mussels on the shore. *Journal of Molluscan Studies* **51**, 73–7.
- Hughes, R.N. & Dunkin, S.de B. 1984a. Behavioural components of prey selection by dogwhelks, *Nucella lapillus* (L.), feeding on mussels, *Mytilus edulis* L., in the laboratory. *Journal of Experimental Marine Biology and Ecology* **77**, 45–68.
- Hughes, R.N. & Dunkin, S.de B. 1984b. Effect of dietary history on selection of prey, and foraging behaviour among patches of prey by the dogwhelk, *Nucella lapillus* (L.). *Journal of Experimental Marine Biology and Ecology* **79**, 159–72.
- Hui, E. 1983. *Studies on intertidal Lepadomorpha and Balanomorpha (Cirripedia: Thoracica)*. PhD thesis, University of Wales, Swansea, 182 pp.
- Hurley, A.C. 1975. The establishment of populations of *Balanus pacificus* Pilsbry (Cirripedia) and their elimination by predatory *Turbellaria*. *Journal of Animal Ecology* **44**, 521–32.
- Hurley, A.C. 1976. The polyclad flatworm *Stylochus tripartitus* Hyman as a barnacle predator. *Crustaceana* **31**, 110–11.
- Jensen, A.S. 1951. Do the Naticidae (Gastropoda Prosobranchia) drill by chemical or by mechanical means? *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening i København* **113**, 251–61.
- Jernakoff, P. 1983. Factors affecting the recruitment of algae in a midshore region dominated by barnacles. *Journal of Experimental Marine Biology and Ecology* **67**, 17–31.
- Jernakoff, P. 1985a. An experimental evaluation of the influence of barnacles, crevices and seasonal patterns of grazing on algal diversity and cover in an intertidal barnacle zone. *Journal of Experimental Marine Biology and Ecology* **88**, 287–302.
- Jernakoff, P. 1985b. The effect of overgrowth by algae on the survival of the intertidal barnacle *Tesseropora rosea* Krauss. *Journal of Experimental Marine Biology and Ecology* **94**, 89–97.
- Jernakoff, P. 1986. Experimental investigation of interactions between the perennial red alga *Gelidium pusillum* and barnacles on a New South Wales rocky shore. *Marine Ecology Progress Series* **28**, 259–63.
- Jernakoff, P. & Fairweather, P.G. 1985. An experimental analysis of interactions among several intertidal organisms. *Journal of Experimental Marine Biology and Ecology* **94**, 71–88.
- Jewett, S.C. & Feder, H.M. 1982. Food and feeding habits of the king crab *Paralithodes camtschatica* near Kodiak Island, Alaska. *Marine Biology* **66**, 243–50.
- Jillett, J.B. 1968. The biology of *Acanthoclinus quadridactylus* (Bloch and Schneider) (Teleostei-Blennoidea). I. Age, growth, and food. *Australian Journal of Marine and Freshwater Research* **19**, 1–8.
- Jillson, D.A. 1981. A niche analysis of coexisting *Thais lapillus* and *Urosalpinx cinereus* populations. *The Veliger* **23**, 277–81.
- Johnson, C.R. 1970. Notes on the intertidal life history of the northern clingfish, *Gobiesox maeandricus* (Girard). *American Midland Naturalist* **83**, 625–7.
- Johnson, L.E. & Strathmann, R.R. 1989. Settling barnacle larvae avoid substrata previously occupied by a mobile predator. *Journal of Experimental Marine Biology and Ecology* **128**, 87–103.
- Karande, A.A. & Udhayakumar, M. 1989. Shell structure and shell strength in cirripedes. *Proceedings of the Indian Academy of Sciences, Animal Sciences* **98**, 223–31.
- Katz, C.H. 1985. A nonequilibrium marine predator-prey interaction. *Ecology* **66**, 1426–38.
- Keifer, P.A., Rinehart Jr, K.L. & Hooper, J.R. 1986. Renilla-foulins, antifouling diterpenes from the sea pansy *Renilla reniformis* (Octocorallia). *Journal of Organic Chemistry* **51**, 4450–54.

- Kentouri, M. & Divanach, P. 1982. Comportement et régime alimentaire des larves de marbré *Lithognathus mormyrus* (Poisson, Téléost, Sparidae) élevées dans des conditions de choix trophique polyspécifique et pluridimensionnel. *Comptes Rendus de l'Académie des Sciences, Paris, Série III* **294**, 859–61.
- Kieber, D.J. & Rittschof, D. 1985. Inhibition of oyster drill chemotaxis. *Chemical Senses* **10**, 507–16.
- Kohn, A.J. 1961. Chemoreception in gastropod molluscs. *American Zoologist* **1**, 291–308.
- Kohn, A.J. 1978. Gastropods as predators and prey at Easter Island. *Pacific Science* **32**, 35–7.
- Landers, W.S. & Rhodes Jr, E.W. 1970. Some factors influencing predation by the flatworm, *Stylochus ellipticus* (Girard) on oysters. *Chesapeake Science* **11**, 55–60.
- Largen, M.J. 1967a. The influence of water temperature upon the life of the dog-whelk *Thais lapillus* (Gastropoda: Prosobranchia). *Journal of Animal Ecology* **36**, 207–14.
- Largen, M.J. 1967b. The diet of the dog-whelk, *Nucella lapillus* (Gastropoda Prosobranchia). *Journal of Zoology* **151**, 123–7.
- LaRoche, J.L. 1982. Trophic patterns among larvae of five species of sculpins (Family: Cottidae) in a Maine estuary. *United States National Marine Fisheries Service, Fisheries Bulletin* **80**, 827–40.
- Levings, S.C. & Garrity, S.D. 1983. Diel and tidal movement of two co-occurring neritid snails; differences in grazing patterns on a tropical rocky shore. *Journal of Experimental Marine Biology and Ecology* **67**, 261–78.
- Levinton, J.S. 1995. *Marine biology: function, biodiversity, ecology*. Oxford: Oxford University Press.
- Lewis, J.B. 1992. Recruitment, growth and mortality of a coral-inhabiting barnacle *Megabalanus stultus* (Darwin) upon the hydrocoral *Millepora complanata* Lamarck. *Journal of Experimental Marine Biology and Ecology* **162**, 51–64.
- Lewis, J.R. 1964. *The ecology of rocky shores*. London: The English Universities Press.
- Lewis, J.R. 1976. Long-term ecological surveillance: practical realities in the rocky littoral. *Oceanography and Marine Biology: an Annual Review* **14**, 371–90.
- Lively, C.M. 1986. Predator-induced shell dimorphism in the acorn barnacle *Chthamalus anisopoma*. *Evolution* **40**, 232–42.
- Lively, C.M. & Raimondi, P.T. 1987. Desiccation, predation, and mussel-barnacle interactions in the northern Gulf of California. *Oecologia (Berlin)* **74**, 304–9.
- Loosey, G.S., Balazs, G.H. & Privitera, L.A. 1994. Cleaning symbiosis between the wrasse, *Thalassoma duperry*, and the green turtle, *Chelonia mydas*. *Copeia* **1994**, No. 3, 684–90.
- Luckens, P.A. 1970a. Breeding, settlement and survival of barnacles at artificially modified shore levels at Leigh, New Zealand. *New Zealand Journal of Marine and Freshwater Research* **4**, 497–514.
- Luckens, P.A. 1970b. Predation and intertidal zonation at Asamushi. *Bulletin of the Marine Biological Station of Asamushi* **14**, 33–52.
- Luckens, P.A. 1975a. Predation and intertidal zonation of barnacles at Leigh, New Zealand. *New Zealand Journal of Marine and Freshwater Research* **9**, 355–78.
- Luckens, P.A. 1975b. Competition and intertidal zonation of barnacles at Leigh, New Zealand. *New Zealand Journal of Marine and Freshwater Research* **9**, 379–94.
- Luckens, P.A. 1976. Settlement and succession on rocky shores at Auckland, North Island, New Zealand. *New Zealand Oceanographic Institute Memoir* No. 70, 64 pp.
- Magre, E.J. 1974. *Ulva lactuca* L. negatively affects *Balanus balanoides* (L.) (Cirripedia Thoracica) in tidepools. *Crustaceana* **27**, 231–4.
- Malusa, J.R. 1985. Attack mode in a predatory gastropod: labial spine length and the method of prey capture in *Acanthina angelica* Oldroyd. *The Veliger* **28**, 1–5.
- Malusa, J.R. 1986. Life history and environment in two species of intertidal barnacles. *Biological Bulletin* **170**, 409–28.
- Marcus, E. 1961. Opisthobranch mollusks from California. *The Veliger* **3** (Suppl., Part 1), 1–85.
- Marsh, C.P. 1986. Impact of avian predators on high intertidal limpet populations. *Journal of Experimental Marine Biology and Ecology* **104**, 185–201.
- Mauzey, K.P. 1966. Feeding behaviour and reproductive cycles in *Pisaster ochraceus*. *Biological Bulletin* **131**, 127–44.
- Mauzey, K.P., Birkeland, C. & Dayton, P.K. 1968. Feeding behavior of asteroids and escape responses of their prey in the Puget Sound region. *Ecology* **49**, 603–19.
- McCook, L.J. & Chapman, A.R.O. 1997. Patterns and variations in natural succession following massive ice-scour of a rocky intertidal seashore. *Journal of Experimental Marine Biology and Ecology* **214**, 121–47.

- McDermott, J.J. 1960. The predation of oysters and barnacles by crabs of the family Xanthidae. *Proceedings of the Pennsylvania Academy of Science* **34**, 199–211.
- McDougall, K.D. 1943. Sessile marine invertebrates at Beaufort, N.C. *Ecological Monographs* **13**, 323–74.
- McKechnie, R.J. & Fenner, R.B. 1971. Food habits of white sturgeon, *Acipenser transmontanus*, in San Pablo and Suisun Bays, California. *California Fish and Game* **57**, 209–12.
- McQuaid, C.D. 1985. Differential effects of predation by the intertidal whelk *Nucella dubia* (Kr.) on *Littorina africana knysnaensis* (Phillipi) and the barnacle *Tetraclita serrata* Darwin. *Journal of Experimental Marine Biology and Ecology* **89**, 97–107.
- Meese, R.J. 1993. Effects of predation by birds on gooseneck barnacle *Pollicipes polymerus* Sowerby distribution and abundance. *Journal of Experimental Marine Biology and Ecology* **166**, 47–64.
- Menge, B.A. 1972a. Competition for food between two intertidal starfish species and its effect on body size and feeding. *Ecology* **53**, 635–44.
- Menge, B.A. 1972b. Foraging strategy of a starfish in relation to actual prey availability and environmental predictability. *Ecological Monographs* **42**, 25–50.
- Menge, B.A. 1976. Organization of the New England rocky intertidal community: role of predation, competition, and environmental heterogeneity. *Ecological Monographs* **46**, 355–93.
- Menge, B.A. 1978a. Predation intensity in a rocky intertidal community. Relation between predator foraging activity and environmental harshness. *Oecologia (Berlin)* **34**, 1–16.
- Menge, B.A. 1978b. Predation intensity in a rocky intertidal community. Effect of an algal canopy, wave action and desiccation on predator feeding rates. *Oecologia (Berlin)* **34**, 17–35.
- Menge, B.A. 1982a. Reply to a comment by Edwards, Conover, and Sutter. *Ecology* **63**, 1180–84.
- Menge, B.A. 1982b. Effects of feeding on the environment: Asteroidea. In *Echinoderm nutrition*, M.Jangoux & J.M.Lawrence (eds). Rotterdam: A.A.Balkema, 521–51.
- Menge, B.A. 1983. Components of predation intensity in the low zone of the New England rocky intertidal region. *Oecologia (Berlin)* **58**, 141–55.
- Menge, B.A. & Sutherland, J.P. 1976. Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. *The American Naturalist* **110**, 351–69.
- Menge, J.L. 1974. Prey selection and foraging period of the predaceous rocky intertidal snail, *Acanthina punctulata*. *Oecologia (Berlin)* **17**, 293–316.
- Menge, J.L. & Menge, B.A. 1974. Role of resource allocation, aggression and spatial heterogeneity in coexistence of two competing intertidal starfish. *Ecological Monographs* **44**, 189–209.
- Mercier, L. 1921. La larve de *Limnophora aestuum* Villen., Diptère marin. *Comptes Rendus de l'Académie des Sciences, Paris*, **173**, 1410–13.
- Miller, K.M. & Carefoot, T.H. 1989. The role of spatial and size refuges in the interaction between juvenile barnacles and grazing limpets. *Journal of Experimental Marine Biology and Ecology* **134**, 157–74.
- Miller, M.C. 1961. Distribution and food of the nudibranchiate Mollusca of the south of the Isle of Man. *Journal of Animal Ecology* **30**, 95–116.
- Moore, H.B. 1938. The biology of *Purpura lapillus*. Part III. Life history and relation to environmental factors. *Journal of the Marine Biological Association of the United Kingdom* **23**, 67–74.
- Morales, C. & Antezana, T. 1983. Diet selection of the Chilean stone crab *Homalaspis plana*. *Marine Biology* **77**, 79–83.
- Moran, M.J. 1985a. Effects of prey density, prey size and predator size on rates of feeding by an intertidal predatory gastropod *Morula marginalba* Blainville (Muricidae), on several species of prey. *Journal of Experimental Marine Biology and Ecology* **90**, 97–105.
- Moran, M.J. 1985b. Distribution and dispersion of the predatory intertidal gastropod *Morula marginalba*. *Marine Ecology Progress Series* **22**, 41–52.
- Moran, M.J. 1985c. The timing and significance of sheltering and foraging behaviour of the predatory intertidal gastropod *Morula marginalba* Blainville (Muricidae). *Journal of Experimental Marine Biology and Ecology* **93**, 103–14.
- Moran, M.J., Fairweather, P.G. & Underwood, A.J. 1984. Growth and mortality of the predatory intertidal whelk *Morula marginalba* Blainville (Muricidae): the effects of different species of prey. *Journal of Experimental Marine Biology and Ecology* **75**, 1–17.
- Moran, P.J. 1980. Natural physical disturbance and predation: their importance in structuring a marine sessile community. *Australian Journal of Ecology* **5**, 193–200.

- Moreno, C.A., Lunecke, K.M. & Lépez, M.I. 1986. The response of an intertidal *Concholepas concholepas* (Gastropoda) population to protection from man in southern Chile and the effects on benthic sessile assemblages. *Oikos* **46**, 359–64.
- Morgan, P.R. 1972. The influence of prey availability on the distribution and predatory behaviour of *Nucella lapillus* (L.). *Journal of Animal Ecology* **41**, 257–74.
- Murdoch, W.W. 1969. Switching in general predators: experiments on predator specificity and stability of prey populations. *Ecological Monographs* **39**, 335–54.
- Murdoch, W.W. 1971. The developmental response of predators to change in prey density. *Ecology* **52**, 132–7.
- Murdock, G.R. & Currey, J.D. 1978. Strength and design of shells of the two ecologically distinct barnacles, *Balanus balanus* and *Semibalanus (Balanus) balanoides* (Cirripedia). *Biological Bulletin* **155**, 169–92.
- Navarrete, S.A. 1996. Variable predation: effects of whelks on a mid-intertidal successional community. *Ecological Monographs* **66**, 301–21.
- Navarrete, S.A. & Castilla, J.C. 1988. Foraging activities of Chilean intertidal crabs *Acanthocyclus gayi* Milne-Edwards et Lucas and *A. hassleri* Rathbun. *Journal of Experimental Marine Biology and Ecology* **118**, 115–36.
- Navarrete, S.A. & Menge, B.A. 1996. Keystone predation and interaction strength: interactive effects of predators on their main prey. *Ecological Monographs* **66**, 409–29.
- Nelson, B.V. & Vance, R.R. 1979. Diel foraging patterns of the sea urchin *Centrostephanus coronatus* as a predator avoidance strategy. *Marine Biology* **51**, 251–8.
- Newman, W.A. 1960. On the paucity of intertidal barnacles in the tropical western Pacific. *The Veliger* **2**, 89–94.
- Newman, W.A. & Ross, A. 1976. Revision of the balanomorph barnacles; including a catalog of the species. *San Diego Society of Natural History* Memoir No. 9, 108 pp.
- Newman, W.A. & Ross, A. 1977. Superfamilies of the Balanomorphs (Cirripedia, Thoracica). *Crustaceana* **32**, 102 only.
- Newman, W.A. & Stanley, S.M. 1981. Competition wins out overall: reply to Paine. *Paleobiology* **7**, 561–9.
- Newman, W.A., Zullo, V.A. & Wainwright, S.A. 1967. A critique on recent concepts of growth in Balanomorphs (Cirripedia, Thoracica). *Crustaceana* **12**, 167–78.
- Nixon, M. & Macconnachie, E. 1988. Drilling by *Octopus vulgaris* (Mollusca: Cephalopoda) in the Mediterranean. *Journal of Zoology* **216**, 687–716.
- O'Brien, F.X. 1976. Some adaptations of the seastar, *Leptasterias littoralis* (Stimpson) to life in the intertidal zone. *Thalassia Jugoslavica* **12**, 237–43.
- Olla, B.L., Bejda, A.J. & Martin, A.D. 1974. Daily activity, movements, feeding, and seasonal occurrence in the tautog, *Tautoga onitis*. *United States Fish and Wildlife Service, Fishery Bulletin* **72**, 27–35.
- Olla, B.L., Bejda, A.J. & Martin, A.D. 1975. Activity, movements, and feeding behavior of the cunner, *Tautoglabrus adspersus*, and comparison of food habits with young tautog, *Tautoga onitis*, off Long Island, New York. *United States Fish and Wildlife Service, Fishery Bulletin* **73**, 895–900.
- Ortega, S. 1981. Environmental stress, competition and dominance of *Crassostrea virginica* near Beaufort, North Carolina, USA. *Marine Biology* **62**, 47–56.
- Ortega, S. 1987. Habitat segregation and temporal variation in some tropical intertidal populations. *Journal of Experimental Marine Biology and Ecology* **113**, 247–65.
- Otway, N.M. & Anderson, D.T. 1985. Variability of shell growth and morphology of the wall-plate junctions in the intertidal barnacle *Tesseropora rosea* (Cirripedia: Tetraclitidae). *Marine Biology* **85**, 171–83.
- Ozawa, S., Hagiwara, S. & Nicolaysen, K. 1977. Neural organization of shadow reflex in a giant barnacle, *Balanus nubilus*. *Journal of Neurophysiology* **40**, 982–95.
- Paine, R.T. 1962. Ecological diversification in sympatric gastropods of the genus *Busy con*. *Evolution* **16**, 515–23.
- Paine, R.T. 1963. Trophic relationships of 8 sympatric predatory gastropods. *Ecology* **44**, 63–73.
- Paine, R.T. 1966a. Food web complexity and species diversity. *The American Naturalist* **100**, 65–75.
- Paine, R.T. 1966b. Function of labial spines, composition of diet, and size of certain marine gastropods. *The Veliger* **9**, 17–24.

- Paine, R.T. 1971. A short-term experimental investigation of resource partitioning in a New Zealand rocky intertidal habitat. *Ecology* **52**, 1096–106.
- Paine, R.T. 1974. Intertidal community structure. Experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia (Berlin)* **15**, 93–120.
- Paine, R.T. 1980. Food webs: linkage, interaction strength, and community infrastructure. *Journal of Animal Ecology* **49**, 667–85.
- Paine, R.T. 1981. Barnacle ecology: is competition important? The forgotten roles of disturbance and predation. *Paleobiology* **7**, 553–60.
- Paine, R.T. & Palmer, A.R. 1978. *Sicyases sanguineus*: a unique trophic generalist from the Chilean intertidal zone. *Copeia* **1978**, 75–81.
- Palmer, A.R. 1982. Predation and parallel evolution: recurrent perietal plate reduction in balanomorph barnacles. *Paleobiology* **8**, 31–44.
- Palmer, A.R. 1983. Growth rate as a measure of food value in thaidid gastropods: assumptions and implications for prey morphology and distribution. *Journal of Experimental Marine Biology and Ecology* **73**, 95–124.
- Palmer, A.R. 1984. Prey selection by thaidid gastropods: some observational and experimental field tests of foraging models. *Oecologia (Berlin)* **62**, 162–72.
- Palmer, A.R. 1990. Predator size, prey size, and the scaling of vulnerability: hatchling gastropods vs. barnacles. *Ecology* **71**, 759–75.
- Palmer, A.R., Szymanska, J. & Thomas, L. 1982. Prolonged withdrawal: a possible predator evasion behavior in *Balanus glandula* (Crustacea: Cirripedia). *Marine Biology* **67**, 51–5.
- Paul, A.J., Feder, H.M. & Jewett, S.C. 1979. Food of the snow crab, *Chionoecetes bairdi* Rathbun, 1924, from Cook Inlet, Alaska (Decapoda, Majidae). *Crustaceana Supplement* **5**, 62–8.
- Pearse, A.S. & Wharton, G.W. 1938. The oyster “leech”, *Stylochus inimicus* Palombi, associated with oysters on the coasts of Florida. *Ecological Monographs* **8**, 605–55.
- Pentcheff, N.D. 1991. Resistance to crushing from wave-borne debris in the barnacle *Balanus glandula*. *Marine Biology* **110**, 399–408.
- Perkins, R.J. 1974. Energy flow through a marine intertidal association. *International Journal of Ecology and Environmental Science* **1**, 71–87.
- Perry, D.M. 1985. Function of the shell spine in the predaceous rocky intertidal snail *Acanthina spirala* (Prosobranchia: Muricea). *Marine Biology* **88**, 51–8.
- Perry, D.M. 1987. Optimal diet theory: behavior of a starved predatory snail. *Oecologia (Berlin)* **72**, 360–65.
- Peterson, C.H. 1979. The importance of predation and competition in organizing the intertidal epifaunal communities of Barnegat Inlet, New Jersey. *Oecologia (Berlin)* **39**, 1–24.
- Petraitis, P.S. 1983. Grazing patterns of the periwinkle and their effect on sessile intertidal organisms. *Ecology* **64**, 522–33.
- Petraitis, P.S. 1987. Factors organizing rocky intertidal communities of New England: herbivory and predation in sheltered bays. *Journal of Experimental Marine Biology and Ecology* **109**, 117–36.
- Phillips, B.F. 1969. The population ecology of the whelk *Dicathais aegrota* in Western Australia. *Australian Journal of Marine and Freshwater Research* **20**, 225–65.
- Phillips, B.F. & Campbell, N.A. 1974. Mortality and longevity of the whelk *Dicathais orbita* (Gmelin). *Australian Journal of Marine and Freshwater Research* **25**, 25–33.
- Porumb, I.I. 1961. Contribuții la cunoașterea biologiei guvizilor (*Gobius batrachocephalus*, *Gobius cephalarges* și *Gobius melanostomus*) din dreptul litoralului românesc al Mării Negre (Date preliminare). *Hidrobiologia* **3**, 271–82.
- Potts, G.W. 1970. The ecology of *Onchidoris fusca* (Nudibranchia). *Journal of the Marine Biological Association of the United Kingdom* **50**, 269–92.
- Povey, A. & Keough, M.J. 1991. Effects of trampling on plant and animal populations on rocky shores. *Oikos* **61**, 355–68.
- Pratt, D.M. 1974. Attraction to prey and stimulus to attack in the predatory gastropod *Urosalpinx cinerea*. *Marine Biology* **27**, 37–45.
- Purcell, J.E. 1977. The diet of large and small individuals of the sea anemone *Metridium senile*. *Bulletin of the Southern California Academy of Sciences* **76**, No. 3, 168–72.
- Qasim, S.Z. 1957a. The biology of *Blennius pholis* L. (Teleostei). *Proceedings of the Zoological Society of London* **128**, 161–208.

- Qasim, S.Z. 1957b. The biology of *Centronotus gunnellus* (L.) (Teleostei). *Journal of Animal Ecology* **26**, 389–401.
- Raimondi, P.T. 1988. Settlement cues and determination of the vertical limit of an intertidal barnacle. *Ecology* **69**, 400–407.
- Randall, R.M. & Randall, B.M. 1982. The hard-shelled diet of African black oystercatcher chicks at St. Croix Island, South Africa. *Ostrich* **53**, 157–63.
- Rangeley, R.W. & Thomas, M.L.H. 1987. Predatory behaviour of juvenile shore crab *Carcinus maenas* (L.). *Journal of Experimental Marine Biology and Ecology* **108**, 191–7.
- Rao, K.S. & Sundaram, K.S. 1972/74. Ecology of intertidal molluscs of the Gulf of Mannar and Palk Bay. *Proceedings of the Indian National Science Academy, Part B* **38**, 462–74.
- Reed, P.H. 1969. Culture methods and effects of temperature and salinity on survival and growth of Dungeness crab (*Cancer magister*) larvae in the laboratory. *Journal of the Fisheries Board of Canada* **26**, 389–97.
- Rittschof, D. & Gruber, G. 1988. Response to prey odors by oyster drills, *Urosalpinx cinerea cinerea*, *Urosalpinx cinerea follyensis* and *Eupleura caudata etterae*. *Marine Behaviour and Physiology* **13**, 185–99.
- Rittschof, D., Hooper, I.R., Branscomb, E.S. & Costlow, J.D. 1985. Inhibition of barnacle settlement and behavior by natural products from whip corals, *Leptogorgia virgulata* (Lamarck, 1815). *Journal of Chemical Ecology* **11**, 551–63.
- Rittschof, D., Shepherd, R. & Williams, L.G. 1984. Concentration and preliminary characterization of a chemical attractant of the oyster drill, *Urosalpinx cinerea*. *Journal of Chemical Ecology* **10**, 63–79.
- Rittschof, D., Williams, L.G., Brown, B. & Carriker, M.R. 1983. Chemical attraction of newly hatched oyster drills. *Biological Bulletin* **164**, 493–505.
- Ropes, J.W. 1968. The feeding habits of the green crab, *Carcinus maenas* (L.). *United States Fish and Wildlife Service, Fishery Bulletin* **67**, 183–203.
- Rosenthal, H. & Hempel, G. 1970. Experimental studies in feeding and food requirements of herring larvae (*Clupea harengus* L.). In *Marine food chains*, J.H. Steele (ed.). Edinburgh: Oliver & Boyd, 344–64.
- Runham, N.W. 1969. The use of the scanning electron microscope in the study of the gastropod radula: the radulae of *Agriolimax reticulatus* and *Nucella lapillus*. *Malacologia* **9**, 179–85.
- Russ, G.R. 1982. Overgrowth in a marine epifaunal community: competitive hierarchies and competitive networks. *Oecologia (Berlin)* **53**, 12–19.
- Schmidt, G.H. & Warner, G.F. 1984. Effects of caging on the development of a sessile epifaunal community. *Marine Ecology Progress Series* **15**, 251–64.
- Seapy, R.R. & Littler, M.M. 1982. Population and species diversity fluctuations in a rocky intertidal community relative to severe aerial exposure and sediment burial. *Marine Biology* **71**, 87–96.
- Sebens, K.P. 1985. Community ecology of vertical rock walls in the Gulf of Maine, USA: small-scale processes and alternative community states. In *Ecology of rocky coasts: essays presented to J.R. Lewis, D.Sc.*, P.G. Moore & R. Seed (eds). London: Hodder & Stoughton, 346–71.
- Sebens, K.P. & Lewis, J.R. 1985. Rare events and population structure of the barnacle *Semibalanus cariosus* (Pallas, 1788). *Journal of Experimental Marine Biology and Ecology* **87**, 55–65.
- Shanks, A.L. & Wright, W.G. 1986. Adding teeth to wave action: the destructive effects of wave-borne rocks on intertidal organisms. *Oecologia (Berlin)* **68**, 420–28.
- Shelford, V.E. 1930. Geographic extent and succession in Pacific North American intertidal (*Balanus*) communities. *Publications of the Puget Sound Biological Station, University of Washington* **7**, 217–23.
- Shumway, S.E. & Stickney, R.R. 1975. Notes on the biology and food habits of the cunner. *New York Fish and Game Journal* **22**, 71–9.
- Sih, A. 1987. Predators and prey lifestyles: an evolutionary and ecological overview. In *Predation: direct and indirect impacts on aquatic communities*, W.C. Kerfoot & A. Sih (eds). London, USA: University Press of New England, 203–24.
- Skerman, T.M. 1960. Note on *Stylochus zanzibaricus* Laidlaw (Turbellaria, Polycladida), a suspected predator of barnacles in the Port of Auckland, New Zealand. *New Zealand Journal of Science* **3**, 610–14.
- Sleder, J. 1981. *Acanthina punctulata* (Neogastropoda: Muricacea) its distribution, activity, diet, and predatory behavior. *The Veliger* **24**, 172–80.

- Sloan, N.A. 1980. Aspects of the feeding biology of asteroids. *Oceanography and Marine Biology: an Annual Review* **18**, 57–124.
- Sloan, N.A. & Robinson, S.M.C. 1983. Winter feeding by asteroids on a subtidal sandbed in British Columbia. *Ophelia* **22**, 125–41.
- Šoljan, T. 1932. *Blennius gallerita* L., poisson amphibien des zones supralittorale et littorale exposées de l'Adriatique. *Acta Adriatica* **1**, No. 2, 1–14.
- Sousa, W.P. 1979. Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. *Ecology* **60**, 1225–39.
- Southward, A.J. & Southward, E.C. 1978. Recolonization of rocky shores in Cornwall after use of toxic dispersant to clean up the Torrey Canyon spill. *Journal of the Fisheries Research Board of Canada* **35**, 682–706.
- Spight, T.M. 1973. Ontogeny, environment, and shape of a marine snail *Thais lamellosa* Gmelin. *Journal of Experimental Marine Biology and Ecology* **13**, 215–28.
- Spight, T.M. 1981. How three rocky shore snails coexist on a limited food resource. *Researches on Population Ecology (Kyoto)* **23**, 245–61.
- Spight, T.M. 1982. Population sizes of two marine snails with a changing food supply. *Journal of Experimental Marine Biology and Ecology* **57**, 195–217.
- Standing, J.D. 1976. Fouling community structure: effects of hydroid, *Obelia dichotoma*, on larval recruitment. In *Coelenterate ecology and behavior*, G.O.Mackie (ed.). New York: Plenum Press, 155–64.
- Standing, J.D., Hooper, I.R. & Costlow, J.D. 1984. Inhibition and induction of barnacle settlement by natural products present in octocorals. *Journal of Chemical Ecology* **10**, 823–34.
- Stanley, S.M. & Newman, W.A. 1980. Competitive exclusion in evolutionary time: the case of the acorn barnacles. *Paleobiology* **6**, 173–83.
- Stepien Jr, W.P. 1976. Feeding of laboratory-reared larvae of the sea bream *Arcosargus rhomboidalis* (Sparidae). *Marine Biology* **38**, 1–16.
- Stickle, W.B. 1973. The reproductive physiology of the intertidal prosobranch *Thais lamellosa* (Gmelin). I. Seasonal changes in the rate of oxygen consumption and body component indexes. *Biological Bulletin* **144**, 511–24.
- Stimson, J. 1970. Territorial behavior of the owl limpet *Lottia gigantea*. *Ecology* **51**, 113–18.
- Stubbings, H.G. 1975. *Balanus balanoides*. *Liverpool Marine Biology Committee Memoirs on Typical British Marine Plants and Animals* No. 37, 175 pp.
- Sutherland, J.P. & Ortego, S. 1986. Competition conditional on recruitment and temporary escape from predators on a tropical rocky shore. *Journal of Experimental Marine Biology and Ecology* **95**, 155–66.
- Swennen, C. 1961. Data on distribution, reproduction and ecology of the nudibranchiate molluscs occurring in the Netherlands. *Netherlands Journal of Sea Research* **1**, 191–240.
- Taylor, J.D. 1976. Habitats, abundance and diets of muricacean gastropods at Aldabra Atoll. *Zoological Journal of the Linnean Society* **59**, 155–93.
- Taylor, J.D. 1983. The food of coral-reef *Drupa* (Gastropoda). *Zoological Journal of the Linnean Society* **78**, 299–316.
- Thompson, M.-F., Nagabhushanam, R., Sarojini, P. & Fingerman, M. (eds) 1994. *Recent developments in biofouling control*. New Delhi: Oxford and IBH Publishing.
- Thompson, T.E. 1964. Grazing and life cycles of British nudibranchs. In *British Ecological Society Symposium No. 4: Grazing in terrestrial and marine environments*, D.J.Crisp (ed.). Oxford: Blackwell, 275–97.
- Thompson, T.E. 1976. *Biology of opisthobranch molluscs, Vol. I*, Ray Society Series No. 151. London: The Ray Society.
- Thompson, T.E. & Brown, G.H. 1984. *Biology of opisthobranch molluscs, Vol. II*, Ray Society Series No. 156. London: The Ray Society.
- Todd, C.D. 1979. The population ecology of *Onchidoris bilamellata* (L.) (Gastropoda: Nudibranchia). *Journal of Experimental Marine Biology and Ecology* **41**, 213–55.
- Todd, C.D. 1981. The ecology of nudibranch molluscs. *Oceanography and Marine Biology: an Annual Review* **19**, 141–234.
- Todd, C.D. & Doyle, R.W. 1981. Reproductive strategies of marine benthic invertebrates: a settlement-timing hypothesis. *Marine Ecology Progress Series* **4**, 75–83.
- Underwood, A.J. 1979. The ecology of intertidal gastropods. *Advances in Marine Biology* **16**, 111–210.

- Underwood, A.J. 1985. Physical factors and biological interactions: the necessity and nature of ecological experiments. In *The ecology of rocky coasts: essays presented to J.R.Lewis, D.Sc.*, P.G. Moore & R.Seed (eds). London: Hodder & Stoughton, 372–90.
- Underwood, A.J., Denley, E.J. & Moran, M.J. 1983. Experimental analyses of the structure and dynamics of mid-shore rocky intertidal communities in New South Wales. *Oecologia (Berlin)* **56**, 202–19.
- Underwood, A.J. & Fairweather, P.G. 1985. Intertidal communities: do they have different ecologies or different ecologists? *Proceedings of the Ecological Society of Australia* **14**, 7–16.
- Vance, R.R. 1978. A mutualistic interaction between a sessile marine clam and its epibionts. *Ecology* **59**, 679–85.
- Vance, R.R. 1979. Effects of grazing by the sea urchin, *Centrostephanus coronatus*, on prey community composition. *Ecology* **60**, 537–46.
- Varas, E. & Ojeda, F.P. 1990. Intertidal fish assemblages of the central Chilean coast: diversity, abundance and trophic patterns. *Revista de Biología Marina* **25**(2), 59–70.
- Vasserot, J. 1983. Un crabe prédateur de Balanes: le 'Tourteau' *Cancer pagurus*. *Journal de Recherche Oceanographique* **8**, 51–3.
- Vevers, H.G. 1949. The biology of *Asterias rubens* L.: growth and reproduction. *Journal of the Marine Biological Association of the United Kingdom* **28**, 165–87.
- Villalobos, C.R. 1979a. Variations in population structure in the genus *Tetraclita* (Crustacea: Cirripedia) between temperate and tropical populations. I. Fecundity, recruitment, mortality and growth in *T. rubescens*. *Revista de Biología Tropical* **27**, 279–91.
- Villalobos, C.R. 1979b. Variations in population structure in the genus *Tetraclita* (Crustacea: Cirripedia) between temperate and tropical populations. II. The age structure of *T. rubescens*. *Revista de Biología Tropical* **27**, 293–300.
- Villalobos, C.R. 1980. Variations in population structure in the genus *Tetraclita* (Crustacea: Cirripedia) between temperate and tropical populations. III. *T. stalactifera* in Costa Rica. *Revista de Biología Tropical* **28**, 193–201.
- Vitalina, Sr M., Avelin, Sr M., Rittschof, D., Sarojini, R. & Nagabhushanam, R. 1991. Compounds from octocorals that inhibit barnacle settlement: isolation and biological potency. In *Bioactive compounds from marine organisms, with emphasis on the Indian Ocean*, M.-F.Thompson et al. (eds). New Delhi: Oxford and IBH Publishing, 331–9.
- Viviani, C.A. 1978. *Interspecific predation, cannibalism and autotomy as an escape method among asteroid species (Echinodermata) in the intertidal zone of northern Chile*. Iquique, Chile: (published by the author, in Spanish, English abstract).
- Wagh, A.B. & Bal, D.V. 1970a. Various associates of sessile barnacles in Bombay waters. *Journal, Bombay Natural History Society* **67**, 351–4.
- Wagh, A.B. & Bal, D.V. 1970b. Diametrically opposite result of human activity on barnacle populations. *Journal, Bombay Natural History Society* **67**, 589–92.
- Wailes, G.H. 1936. Food of *Clupea pallasii* in Southern British Columbia waters. *Journal of the Biological Board of Canada* **1**, 477–86.
- Ward, S. & Quinn, G.P. 1988. Preliminary investigations of the ecology of the intertidal predatory gastropod *Lepsiella vinosa* (Lamarck) (Gastropoda, Muricidae). *Journal of Molluscan Studies* **54**, 109–17.
- West, L. 1986. Interindividual variation in prey selection by the snail *Nucella (=Thais) emarginata*. *Ecology* **67**, 798–809.
- Wieters, E.A. & Navarrete, S.A. 1998. Spatial variability in prey preferences of intertidal whelks *Nucella canaliculata* and *Nucella emarginata*. *Journal of Experimental Marine Biology and Ecology* **222**, 133–48.
- Wiley, A. 1910. Association of barnacles with snakes and worms. *Spolia Zeylanica* **6**, 180–81.
- Williams, L.G., Rittschof, D., Brown, B. & Carriker, M.R. 1983. Chemotaxis of oyster drill *Urosalpinx cinerea* to competing prey odors. *Biological Bulletin* **164**, 536–48.
- Wood, L. 1968. Physiological and ecological aspects of prey selection by the marine gastropod *Urosalpinx cinerea* (Prosobranchia: Muricidae). *Malacologia* **6**, 267–320.
- Wootton, J.T. 1992. Indirect effects, prey susceptibility, and habitat selection: impacts of birds on limpets and larvae. *Ecology* **73**, 981–91.
- Wootton, J.T. 1993. Size-dependent competition: effects on the dynamics vs. the end point of mussel bed succession. *Ecology* **74**, 195–206.

- Wootton, J.T. 1994. Predicting direct and indirect effects: an intertidal approach using experiments and path analysis. *Ecology* **75**, 151–65.
- Yoshiyama, R.M. 1980. Food habits of three species of rocky intertidal sculpins (Cottidae) in Central California. *Copeia* **1980**, 515–25.
- Yule, A.B. & Crisp, D.J. 1983. Adhesion of cyprid larvae of the barnacle, *Balanus balanoides*, to clean and arthropod treated surfaces. *Journal of the Marine Biological Association of the United Kingdom* **63**, 261–71.
- Yule, A.B. & Walker, G. 1984a. The adhesion of the barnacle, *Balanus balanoides*, to slate surfaces. *Journal of the Marine Biological Association of the United Kingdom* **64**, 147–56.
- Yule, A.B. & Walker, G. 1984b. The temporary adhesion of barnacle cyprids: effects of some differing surface characteristics. *Journal of the Marine Biological Association of the United Kingdom* **64**, 429–39.
- Yule, A.B. & Walker, G. 1987. Adhesion in barnacles. In *Crustacean issues. 5. Barnacle biology*, A.J.Southward (ed.), Rotterdam: A.A.Balkema, 389–402.
- Zander, C.D. 1979. On the biology and food of small-sized fish from the North and Baltic Sea areas. II. Investigation of a shallow stony ground off Møn, Denmark. *Ophelia* **18**, 179–90.
- Zander, C.D. & Heymer, A. 1977. Analysis of ecological equivalents among littoral fish. In *Biology of benthic organisms*, B.F.Keegan et al. (eds). Oxford: Pergamon Press, 621–30.

THE BIOLOGY OF SIPHONARIID LIMPETS (GASTROPODA: PULMONATA)

ALAN N. HODGSON

*Department of Zoology and Entomology, Rhodes University, Grahamstown, 6140
South Africa*

Abstract The Siphonariidae are regarded as a primitive family of basommatophoran pulmonate limpets which probably have a marine ancestry. They have a broad global distribution but are most abundant on rocky shores in lower latitudes of the Indo-Pacific, especially within the southern hemisphere. This review examines a number of aspects of the physiology, behaviour, ecology and reproduction of these pulmonates in relation to their intertidal existence.

Despite limpets being poorly designed to minimize heat stress and desiccation, siphonariids are particularly abundant in warmer climates, unlike many prosobranch limpet taxa which decline towards the tropics. The success of siphonariids in lower latitudes, when compared with patellogastropods, does not appear to be due to greater temperature or desiccation tolerances, although important data from subtropical and tropical species are lacking. However, a number of physiological adaptations that may contribute to their successful occupation of lower latitudes are discussed including: a) efficient respiration in air and water; b) facultative metabolic rate depression; c) anaerobiosis; d) rapid re-hydration after water loss. Siphonariids are osmoconformers, but have a wide tolerance to hypo- and hyper-osmotic conditions. Such tolerance has enabled these limpets to exploit habitats (e.g. rock pools and estuaries) generally not utilized by patellogastropods.

The behavioural adaptations of siphonariids also help them reduce the physical and biological stresses of the intertidal zone. These adaptations (with few exceptions) include rigid homing to a scar or crevice, and confining foraging activity to moist or humid conditions often when wave activity is minimal. High shore species tend to be active when exposed at night, whereas lower shore species are more active when awash. Foraging is adjusted both in duration and distance in relation to day/night and spring/neap cycles. Although the timing of foraging may also serve to minimize predation, nearly all siphonariids are unpalatable to predators, possessing multicellular epidermal glands that produce polypropionate chemicals. This ability to avoid the many predators of lower latitudes may be a major factor in explaining the success of siphonariids in these habitats.

Siphonariids primarily feed on foliose macroalgae, cropping the algae but never removing them completely. On the whole they do not influence algal community structure in the same way as patellogastropods. Even though siphonariids and patellogastropods generally do not compete for the same food resource, on many temperate shores direct and indirect interactions between the two limpet taxa occurs. Because of their weaker radula, siphonariids are often out-competed, but never completely eliminated, by the patellogastropod fauna. There are, however, examples of siphonariids outcompeting the patellogastropod fauna. *Siphonaria* spp. can also interact with fissurellid gastropods, the outcomes of these interactions being variable. The grazing activities of *Siphonaria* may be crucial to the survival of other limpets as well as other intertidal invertebrates (e.g. barnacles). These are discussed.

Like all pulmonates the Siphonariidae are hermaphrodites which have internal fertilization. Eggs are laid in egg capsules which are embedded in a protective gelatinous matrix. Ribbons of eggs are usually cemented to rocks within the intertidal, although in two species, pelagic egg ribbons are produced. Two reproductive strategies have evolved; most species produce numerous small eggs which hatch into planktotrophic larvae within seven days of being laid; several species deposit fewer, larger eggs which undergo direct development, crawling larvae emerging from the egg ribbons within 35 days. Both adaptive and phylogenetic hypotheses have been proposed to explain these two life history strategies and these are discussed. Whatever the reproductive strategy, most species studied have a seasonal pattern of reproduction with individuals laying more than one ribbon per season. Copulation and spawning are often linked to tidal and/or lunar cycles which are not only thought to provide the maximum time for egg laying, but may also improve the chances of survival of the eggs and the larvae.

Introduction

The influence of limpets as grazers, and their interactions with other organisms in shallow-water intertidal marine ecosystems, has resulted in these gastropods being the subjects of extensive investigations. A further stimulating factor for research is the ability of limpets to exist in an environment (i.e. the intertidal zone) that is both physically and biologically challenging. Aspects of the ecology, behaviour, physiology and evolution of limpets in general have been reviewed by Branch (1981, 1985, 1986), Hawkins & Hartnoll (1983) and Little (1989). Although these reviews included information on both prosobranch and pulmonate limpets, their focus was primarily on the prosobranch patellogastropods, of which there was a more extensive literature. As well as being excellent summaries of limpet biology, the reviews highlighted many important gaps in our knowledge, not only of limpets but also of marine intertidal ecology. Research involving limpets has not abated, and in addition to the continued studies on patellogastropods, more researchers have studied the Siphonariidae (a family of intertidal pulmonate limpets) and the habitats in which they are found.

Siphonariid limpets are particularly successful on warm temperate to tropical rocky shores, where they can reach densities of 3000–6000 m⁻² (e.g. Menge 1973). They have featured in many ecological studies that have examined grazer-algal interactions, as well as intra- and interspecific competition. In addition, numerous authors have used siphonariids to further our knowledge of gastropod physiology, morphology, behaviour and life history strategies. Phylogenetically the Siphonariidae are of interest as many invertebrate biologists regard them as a primitive family of pulmonates (Hyman 1967, Purchon 1979), and whereas some authors have suggested that siphonariids were derived from terrestrial ancestors which invaded the intertidal (e.g. Borland 1950, Yonge 1952), others claim that they have a marine ancestry (Purchon 1979). The aim of this review is to draw together information on the ecology, behaviour, physiology and life histories of the Siphonariidae. I have avoided a detailed review of the taxonomy and morphology of these gastropods although of necessity have included some information on these subjects. Details on these topics can be found in papers by Köhler (1893), Cottrell (1910, 1914), Hubendick (1946, 1947, 1978), Yonge (1952), Allanson (1959, 1963), Marcus & Marcus (1960), Morrison (1963), Christiaens (1973, 1980), Jenkins (1981, 1983, 1984), Marshall (1981), de Villiers et al. (1985),

Hodgson et al. (1990), Frescura (1991), Frescura & Hodgson (1992), Chambers & McQuaid (1994a), McLean (1998), and the general texts of Hyman (1967) and Purchon (1979).

This introduction is followed by a brief overview of some of the recent debate on the higher classification and phylogeny of the Siphonariidae, which is far from settled. The biogeographic distribution of the siphonariid genera is then outlined in the next section. The third section examines the physiological and behavioural adaptations of these limpets to intertidal habitats and in particular explores possible reasons why these gastropods are more successful in lower latitudes than most prosobranch limpets. Immediately following, is a look at the behavioural biology, particularly activity rhythms and homing. Interactions between intertidal organisms and the way in which such interactions may shape intertidal communities has been a major field of study by many marine ecologists. The fifth component of the review, therefore, looks at the interactions between siphonarian limpets, algae and other intertidal organisms. The final section of the review concentrates on aspects of their life history.

Systematic and evolutionary relationships of the Siphonariidae

While a detailed examination of the systematics of the Siphonariidae is beyond the scope of this review, some background information on the higher taxonomy and their relationships to other pulmonate taxa would seem appropriate. Hyman (1967) suggested that the Siphonariidae are the most primitive of pulmonates. In recent years the phylogeny and classification of pulmonates have been re-examined extensively (for reviews see Salvini-Plawen 1990, Bieler 1992, Nordsieck 1992, Tillier & Ponder 1992, Salvini-Plawen & Steiner 1996, Tillier et al. 1996). The stimulation for these investigations has been new sources of information in the form of ultrastructural and molecular data. Traditionally the Pulmonata have been divided into two principal orders, the Basommatophora and Stylommatophora, although several authors have suggested that the Basommatophora might not be a monophyletic group (Morton 1955, Hubendick 1978, Healy 1983). Within the Basommatophora *sensu lato*, a number of taxa have patelliform shells including the marine Siphonariidae and Trimusculidae as well as a number of fresh water families (Hubendick 1947, 1978, Boss 1982). The Siphonariidae and Trimusculidae were placed within the Siphonarioidea (Hubendick 1978, Boss 1982, also Patelliformia of Thiele 1931). Tillier (1984) proposed removing both the Siphonariidae and Trimusculidae from the Basommatophora and including them with the Amphibolidae in a redefined and expanded Amphiboloidea, reserving the Basommatophora for the limnic groups only. Haszprunar & Huber (1990) removed the Trimusculidae from the Basommatophora *sensu lato*, and placed them together with the Ellobiidae and Stylommatophora in a higher rank taxon, the Eupulmonata. Nordsieck (1992) proposed a classification of the Pulmonata in which the Siphonariidae and Amphibolidae were included in the higher taxon Thalassophila of the Basommatophora (Fig. 1). Nordsieck also removed the Trimusculiformes from the Basommatophora and placed them in the Superorder Eupulmonata (Fig. 1). Hodgson & Healy (1998) suggested that the differences in the sperm morphology between *Siphonaria*, *Trimusculus* and the amphibolid *Salinator* supported the distant relationship of siphonariid and trimusculid limpets. Their results, however, also cast considerable doubt over the validity of the higher taxon Thalassophila, lending support to the results of rRNA sequence studies by Tillier et al. (1996) who concluded that the Thalassophila were at best a paraphyletic and not a monophyletic grouping. Tillier et al. (1996) further suggested that the Amphibolidae may even belong outside the Pulmonata. Current consensus is that the Siphonariidae is the

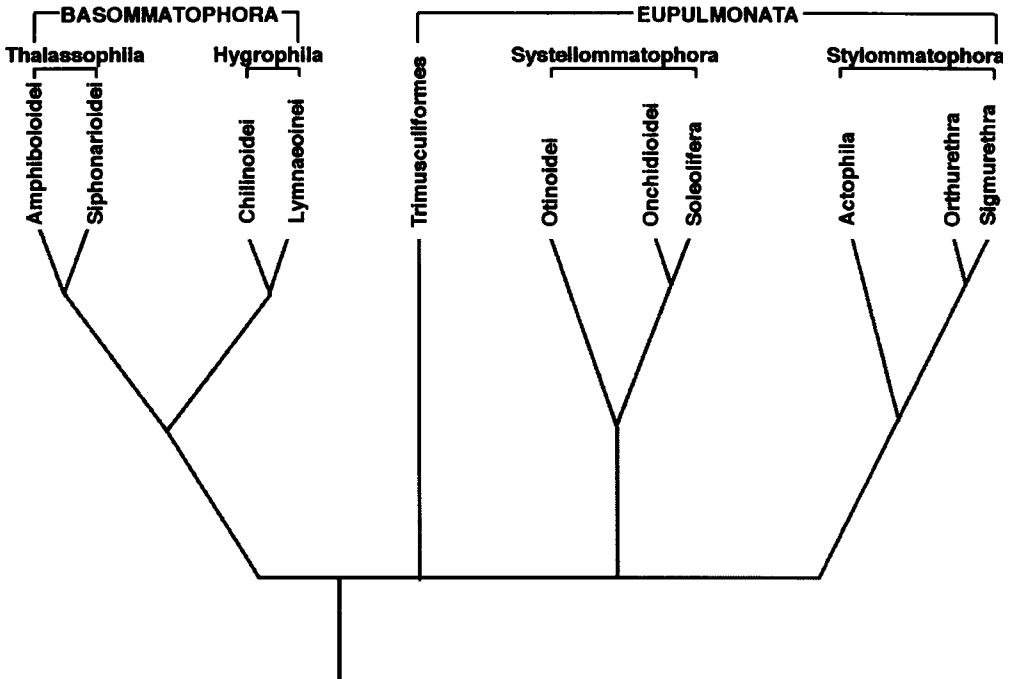


Figure 1 Phylogeny of the higher taxa within the Pulmonata as proposed by Nordsieck (1992). Diagram has been redrawn and simplified for clarity from Nordsieck (1992).

most primitive family (primitive features include: monaully, lack of tentacles, planktonic veliger larva, chromosome number $n=16$) of Basommatophora (Salvini-Plawen 1990, Nordsieck 1992). As most authors at present agree that the Siphonariidae are not closely related to the Trimusculiidae and Amphibolidae, this review has been restricted to the siphonariid limpets only. I have, however, not hesitated to introduce a small amount of information on trimusculids where aspects of their biology and adaptations to a marine lifestyle overlap with those of the siphonariid limpets.

The Siphonariidae is a diverse family, with over 60 species being recorded by Hubendick (1946). Aspects of the taxonomy of this family are still unresolved and even the number of genera is contentious. Hubendick (1946) recognized two genera only (*Siphonaria* and *Williamia*), with two subgenera (*Liriola* and *Siphonaria*) each containing five "sectia". Other authors have recognized four genera, *Siphonaria*, *Williamia*, *Kerguelenella* and *Benhamina*. As these generic names have been used in much of the literature, this system has been adopted to avoid potential confusion.

Geographic distribution

As the zoogeography of the Siphonariidae was reviewed by Hubendick (1947), a brief overview of some aspects only is presented. Hubendick suggested that the present day distribution of the family reflects an origin in the Tethys Sea of the Miocene period. This view was supported by Marcus & Marcus (1960). The majority of species are found in the

Indo-Pacific region (especially of the southern hemisphere), nine species (seven species of *Siphonaria* and two species of *Williamia*) only having been recorded from the Atlantic, Caribbean, and Mediterranean combined (Hubendick 1946). Of the seven species of *Siphonaria*, three, *S. compressa*, *S. capensis* and *S. serrata*, have an Atlantic distribution restricted to the west coast of southern Africa, the latter two species being also found along the Indian Ocean coastline of South Africa. This suggests that these species were part of an Indo-Pacific radiation, with some taxa migrating around the southern Cape to the southeast Atlantic. A similar migratory route has been suggested for some species of patellid limpet (Ridgway et al. 1998). *S. compressa* is only found as a single west coast population in Langebaan lagoon, being the only siphonariid to live on eelgrass blades (Kilburn & Rippey 1982). This is probably a relict population, and the species is thought to be in serious danger of extinction. *S. lessoni*, which is found in the west Atlantic from Uruguay southwards, has a more extensive distribution on the Pacific coast of the Americas from the Strait of Magellan northwards to 12°S (Hubendick 1946). This distribution pattern indicates that this species also had Pacific origins, migrating into the southwest Atlantic after the formation of the Panamanian land bridge. *S. pectinata* is unusual among the Atlantic-Mediterranean species in that it is found on both sides of the Atlantic (Voss 1959, Allanson 1963). Morrison (1963) proposed that this limpet was introduced by humans from West Africa to the western Atlantic, citing its patchy distribution in the Caribbean as evidence. Although Vermeij & Rosenberg (1993) agreed that *S. pectinata* had a westward dispersal, they challenged the view that it was by human introduction. They have proposed that under favourable conditions the planktotrophic larvae could have been transported in oceanic currents to the Americas in relatively recent times. This view is supported by the analysis of Scheltema (1995) who concluded that the major ocean currents in the tropical Atlantic Ocean have, and continue to play, an important role in the passive dispersal of molluscan larvae. Until evidence is presented that larvae of some species of *Siphonaria* are teleplanic, such dispersal will remain speculative for this genus.

Although some species of *Siphonaria* are found in cool temperate waters (e.g. New Zealand, South African west coast, North American west coast, South American south coasts) species diversity is greatest in warm temperate to subtropical regions (Vermeij 1973). This trend of increasing species diversity in warmer waters is admirably demonstrated along the coastline of southern Africa. In the cool temperate waters of the west coast of South Africa, three species only are found, the warm temperate south coast has four species, whereas the subtropical east coast has seven species. In the more tropical waters of the northeast coast, the number of species declines to five.

The genus *Kerguelenella* has a circum-Antarctic distribution and is common to many cool temperate and sub-Antarctic shores, including sub-Antarctic islands. *Benhamina* is more restricted, being found around the South Island and part of the North Island of New Zealand (Hubendick 1946). The few species of *Williamia* are largely Pacific in their distribution, although one or two species have been recorded from the Mediterranean and adjoining part of the eastern Atlantic (Hubendick 1946, McLean 1998).

Physiological and morphological adaptations to intertidal habitats

When compared with gastropods with coiled shells, limpets are poorly adapted for minimizing desiccation and heat stress (Vermeij 1973, Branch 1981). Limpets have a shell

with a large surface area for heat absorption relative to that for heat emission, a large flat foot that cannot be withdrawn from the substratum thus increasing heat uptake by conduction, and finally a shell shape that allows relatively little storage of water (compared with some other gastropods). Limpets are, therefore, not particularly well designed for living on rocky shores of warmer latitudes and it has been suggested that this is why there is a decrease in diversity and abundance of some limpet taxa (e.g. patellids and acmaeids) towards the tropics (see Branch 1981, 1985). Despite the poor thermal design of limpets, there are a number of taxa which are successful inhabitants of warmer latitudes and, unlike the patellids, siphonariid limpets increase in diversity towards the tropics (Vermeij 1973). Furthermore, in lower latitudes, siphonariids are not restricted to lower regions of intertidal ecosystems where the risk of desiccation would be reduced. There are a number of possible physiological, behavioural or ecological reasons that could explain the success of siphonariids in lower latitudes. The larvae, juveniles or adults of siphonariids could have higher physiological tolerances to elevated temperatures and desiccation than most prosobranch limpets. Alternatively, siphonariids may have morphological and/or behavioural mechanisms for reducing heat uptake and water loss. Branch (1981) has also suggested that competition for food with herbivorous fishes could explain the absence of patellids from subtropical and tropical shores. Finally, predation may explain the absence of some limpet taxa from lower latitudes, Palmer (1979) noting that in the tropics there are a greater number of fishes which are specialized for feeding on shelled molluscs. Data currently available do not allow all of these hypotheses to be explored adequately. Nevertheless, there are some studies on the physiology and morphology of adult siphonariid limpets which allow some comment to be made.

Respiration

As pulmonates, siphonariids have a lung cavity that opens to the outside on the right side of the body via a pneumostome. In addition, the dorsal mantle of the pulmonary cavity is elaborated into a series of folds that form a secondary gill (Köhler 1893, Cottrell 1910, Hubendick 1947, 1978, Yonge 1952, Marcus & Marcus 1960). The gill (Fig. 2) has a series of triangular leaflets (up to 30 in some species, Allanson 1958, Hyman 1967), the wall of which consists of a single layer of small cuboidal epithelial cells (about 4 μm in size) that surround a central haemocoelic space (De Villiers & Hodgson 1987). Each gill lamella bears ciliary tufts which have a density of about 400 mm^{-2} (De Villiers & Hodgson 1987). The cilia of the tufts, along with those of the dorsal and ventral ridges (Yonge 1952), draw water through the inhalant opening of a short siphon, across the gills, expelling the water through the exhalant opening of the same siphon. A number of authors have suggested that the possession of both a pulmonary cavity and gill would allow siphonariids to respire aerobically both in air and water. The thin epithelium of the gill, and a counter-current system (Yonge 1952), must allow efficient and rapid diffusion of gases into, or out of, the haemolymph which contains haemocyanin (Wells & Wong 1978). In addition, like many gastropods, siphonariids also have myoglobin but this is restricted to the radular muscle (Read 1968, Wells & Wong 1978). The relative importance of the gill as a respiratory surface, when compared with other epithelial surfaces, is unknown, although Innes et al. (1984) calculated that 25% of gaseous exchange in *Siphonaria zelandica* occurs across the side of the foot.

Whereas there have been a considerable number of studies on respiration in prosobranch limpets (see Branch 1981 for review), such investigations on siphonariids are limited. Initial studies were short-term experiments, comparing oxygen consumption at the same or different

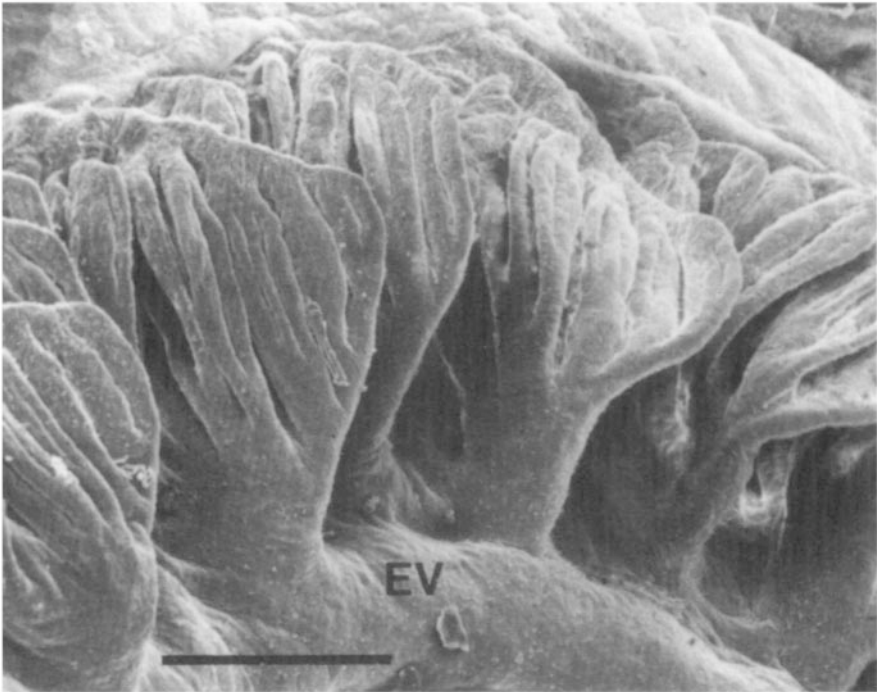


Figure 2 Scanning electron micrograph of the secondary gill lamellae of *Siphonaria capensis*. EV, position of efferent branchial blood vessel. Scale bar=0.5 μ m. (From de Villiers & Hodgson 1987).

temperatures in air and water (Innes et al. 1984, Dye 1987). Results from *S. zelandica* (at 10°C), *S. concinna* and *S. capensis* (both at 12°C), showed that oxygen consumption was significantly higher (1.5–1.6 times) in air than in water, and in *Benhamina obliquata* there was no difference in aerial and aquatic respiratory rates (Innes et al. 1984, Dye 1987). This latter result may have been due to the experimental conditions, as the difference between aerial and aquatic respiration can be temperature dependent (Fig. 3) (Dye 1987). A comparison of the ratios of aquatic to aerial respiration in species of aquatic pulmonates possessing and lacking a secondary gill (Table 1) reveals that although aquatic respiration may be significantly lower in water than in air in pulmonates with a gill, the depression in the rate of oxygen consumption when submerged in species with a gill is far greater (Table 1). These findings support the idea that the gill bearing pulmonates such as siphonariids respire efficiently in both air and water. Further evidence has been provided more recently by Marshall & McQuaid (1994) who recorded *in situ* heart rates of *Siphonaria oculus*. Heart rate and metabolic rate are closely correlated in this species (Marshall & McQuaid 1992a). The heart rates of limpets in air were not significantly different from those of submerged limpets in summer, and in winter were only different at a low level of significance.

One of the problems of aerial respiration for siphonariids is a lung cavity that can only be ventilated through a small pneumostome. This probably causes an elevation in pulmonary pCO₂ levels, which may be further increased by the activity of these animals at low tide (Wells & Wong 1978). Wells & Wong (1978) found that the oxygen combining properties of the haemocyanin of *S. zelandica* were similar to that reported for terrestrial pulmonates,

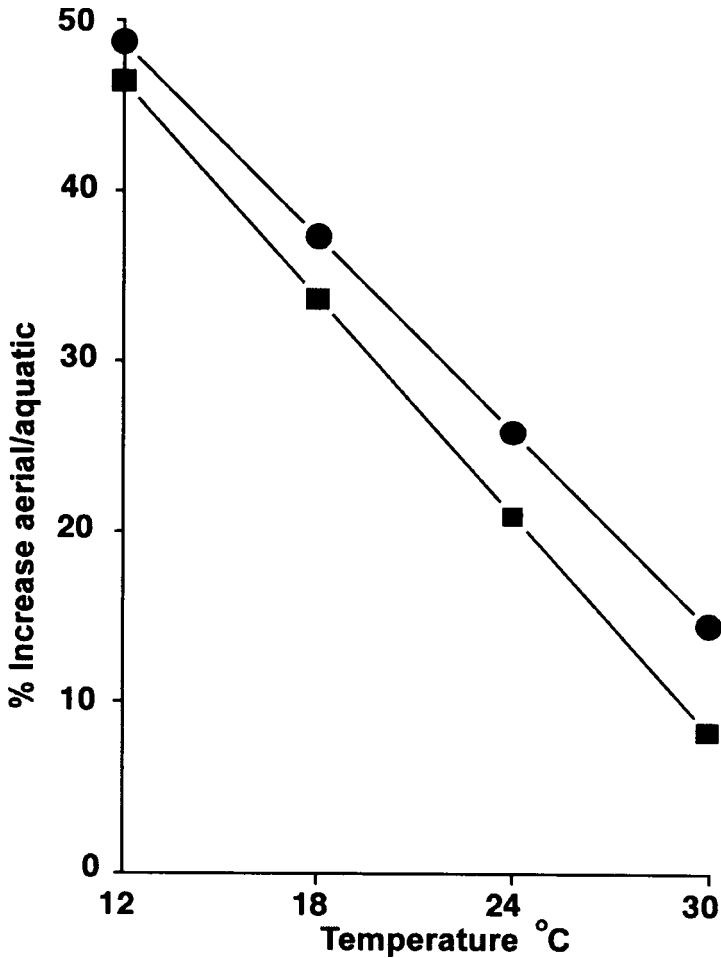


Figure 3 Percentage increase in aerial over aquatic respiration in *Siphonaria capensis* (●) and *S. concinna* (■) as a function of temperature. (Redrawn from Dye 1987).

Table 1 Comparison of ratios of aquatic to aerial oxygen consumption for a number of pulmonates with and without a secondary gill. Table modified and expanded from Innes et al. 1984. * Indicates no significant difference between aquatic and aerial respiration.

Species	Habitat	Temperature (°C)	Aquatic to aerial ratio	Reference
NO GILL				
<i>Melampus bidentatus</i>	High tidal salt marsh	10–20	1:3.0–5.0	McMahon & Russell-Hunter 1981
<i>Cassidula aurisfelis</i>	High tidal mangroves	28	1:6.01	Houlihan 1979
GILL PRESENT				
<i>Amphibola crenata</i>	High tidal mud flats	15	1:0.94*	Shumway 1981
<i>Benhamina obliquata</i>	Mid-upper intertidal	10	1:1.16*	Innes et al. 1984
<i>Siphonaria zelandica</i>	Mid-upper intertidal	10	1:1.6	Innes et al. 1984
<i>Siphonaria capensis</i>	Mid-upper intertidal	12–30	1:1.13–1.49*	Dye 1987
<i>Siphonaria concinna</i>	Mid-upper intertidal	12–30	1:1.07–1.45*	Dye 1987

having a sigmoidal equilibrium curve that would enable the circulating blood to deliver most of the combined oxygen for a relatively small decrease in pO_2 . Furthermore, at pH 7.2 (25°C), the haemocyanin had a half-saturation value of 12.7 mm Hg. At pH 7.6, the oxygen affinity decreased to 17.3 mm Hg. Wells & Wong proposed that this reverse (positive) Bohr effect would facilitate oxygen uptake in the lung while the limpet was active during low tide.

While siphonariids are undoubtedly able to respire aerobically in air, and have blood pigments that are similar to those of terrestrial pulmonates (Wells & Wong 1978), some species of *Siphonaria* can reduce their metabolic rate when exposed to air for long periods (Marshall & McQuaid 1991, 1992a). The decrease in metabolic rate is reflected both in the level of oxygen consumption and heart rate (Fig. 4), which are closely correlated in these limpets (Marshall & McQuaid 1992a). After 4–8 h of exposure to air with a relative humidity of 80% (constant subdued illumination; 25 °C), the heart rate of *S. oculus* decreases from about 50 to <20 beats per minute (Fig. 4), remaining at this low level until animals are re-immersed 72 h later. The depression of aerobic metabolism, which is accompanied by withdrawal of the mantle skirt and closure of the pneumostome, can be as low as 18% of the normal rate (Marshall & McQuaid 1991). Both heart rate and oxygen consumption returned to normal on re-immersion in water. Metabolic rate depression is probably stimulated by desiccation rather than exposure to air *per se*, as when the same species is kept in air with a 100% relative humidity (constant subdued illumination; 20°C) there is no significant decline in metabolic rate (Marshall & McQuaid 1992a). Temperature independent metabolic rate depression has also been observed in animals in the field, Marshall & McQuaid (1994) recording bradycardia (=reduction in heart rate) during daytime emersion.

Marshall & McQuaid (1991) point out that the level of metabolic rate depression of *S. oculus* can be similar to that of aestivating land and fresh water pulmonates, a physiological strategy that allows these gastropods to survive adverse environmental conditions. Depression of metabolic rate during daytime low tides could be a particular advantageous strategy for saving energy. Winter and summer measurements of the heart rates of animals *in situ* by Marshall & McQuaid (1994) have shown that unlike many intertidal limpet species, *S. oculus* does not exhibit any seasonal metabolic acclimation to declining temperatures. They therefore proposed this observed non-acclimation would further reduce energy expenditure.

Metabolic rate depression, along with non-acclimation to temperature, is seen as an energy conservation strategy that allows *S. oculus* to inhabit the upper regions of the intertidal zone where food availability is low. The suggestion that some siphonariids are able to conserve energy is supported by studies on the effect of temperature on oxygen consumption and heart rate, and of body size on metabolic rate.

Dye (1987) has found that the Q_{10} of the mid- to upper-shore species *S. capensis* and *S. concinna* is low, ranging from 0.4 to 1.6 (depending on temperature range tested and whether animals were in air or water) (Fig. 5). Low Q_{10} values are also a feature of upper intertidal prosobranch limpets, and are regarded as a physiological adaptation to minimize metabolic expenditure (Branch 1981). These results are reinforced by the work of Marshall & McQuaid (1991, 1992b, 1994) who demonstrated that metabolic rate depression during emersion was temperature independent in *S. oculus*. This, they argued, would allow enhanced conservation of energy resources.

For ectotherms, a value of 0.75 has been suggested for the slope (b) of the logarithmic relationship between mass and oxygen consumption (see Branch 1981 for more complete explanation). Most limpets, and the marine pulmonate *Amphibola crenata*, have a value for

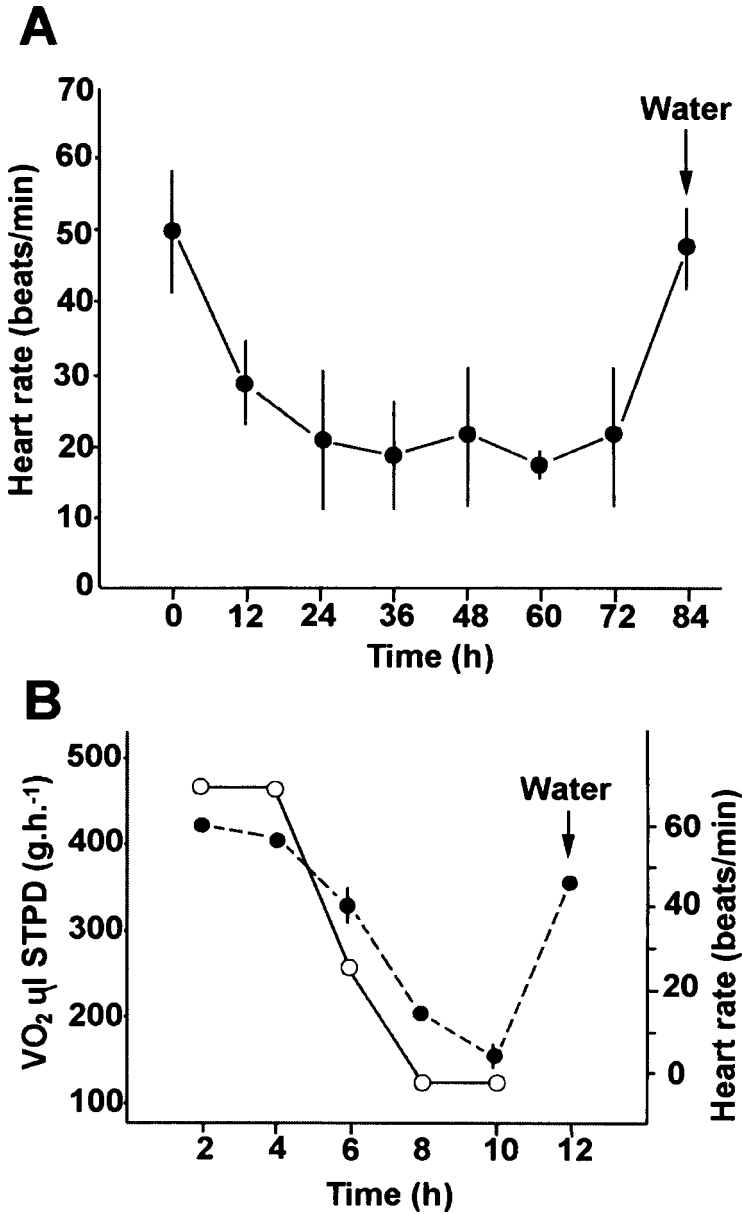


Figure 4 A, heart rate ($\bar{x}\pm$ SD) of *Siphonaria oculus* ($n=12$) during continuous exposure in air ($25\pm 0.5^{\circ}\text{C}$, $80\pm 5\%$ R.H.), and following 12 h re-immersion in water. B, simultaneous measurements of heart rate (\bullet) and oxygen consumption (VO_2 at 25°C ; \circ) for an individual *Siphonaria oculus*, measured after intervals of exposure to a dry airstream (25°C), and following 2 h re-immersion in water. Heart rate is given as $\bar{x}\pm$ SD. (Redrawn from Marshall & McQuaid 1991).

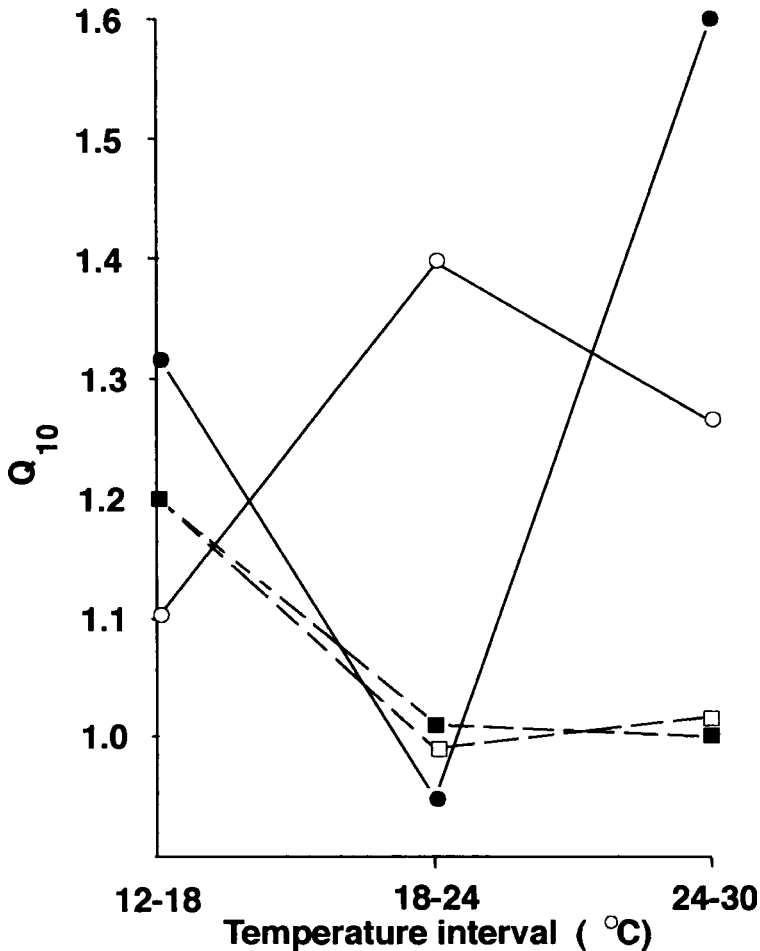


Figure 5 Relationship between temperature and Q_{10} for a 100 mg animal. Aerial ———; aquatic———; *Siphonaria capensis*, ● ■; *S. concinna*, ○ □. (Redrawn from Dye 1987).

b lower than this, which indicates that metabolic rate is less responsive to temperature in larger animals (Branch 1981, Dye 1987). Mid- to upper-shore siphonariids are no exception, Dye (1987) calculating b values of 0.1 to 0.67 for *Siphonaria capensis* and *S. concinna*. Like many other high shore limpets, respiration is less size dependent in *Siphonaria*.

The respiratory studies carried out to date raise the intriguing question as to whether all siphonariids exhibit metabolic rate depression and seasonal non-acclimation of metabolic rate, i.e. are the metabolic responses adaptive, and linked to position on the shore (as in patellid limpets), or are they phylogenetic, and a feature of all species of *Siphonaria*? To help answer this, work on low shore species is required. Because facultative aerobic depression and seasonal non-acclimation are features of some fresh water and terrestrial pulmonates, Marshall & McQuaid (1991) have suggested that it is a phylogenetic character. Metabolic rate depression thus pre-adapted primitive marine pulmonates for a more terrestrial existence, which would imply that all siphonariids will have such physiological

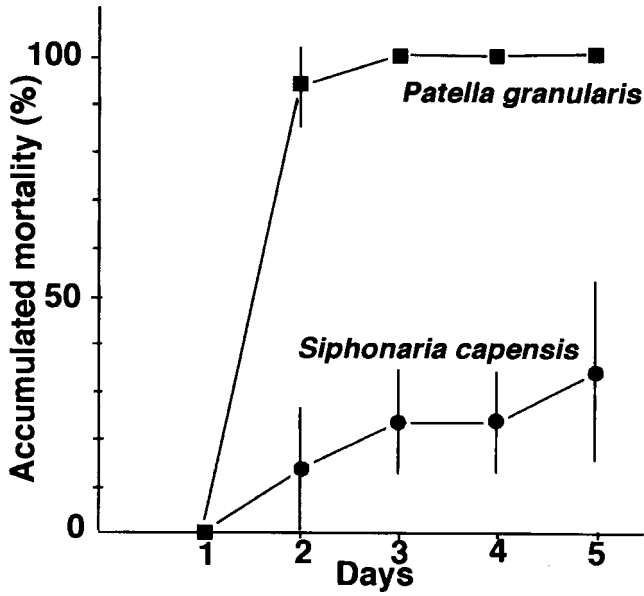


Figure 6 Mean cumulative percentage mortality (\pm SD) of *Siphonaria capensis* and *Patella granularis* at a water oxygen tension of $<0.8\text{ ml l}^{-1}\text{ O}_2$. (Redrawn from Marshall & McQuaid 1989).

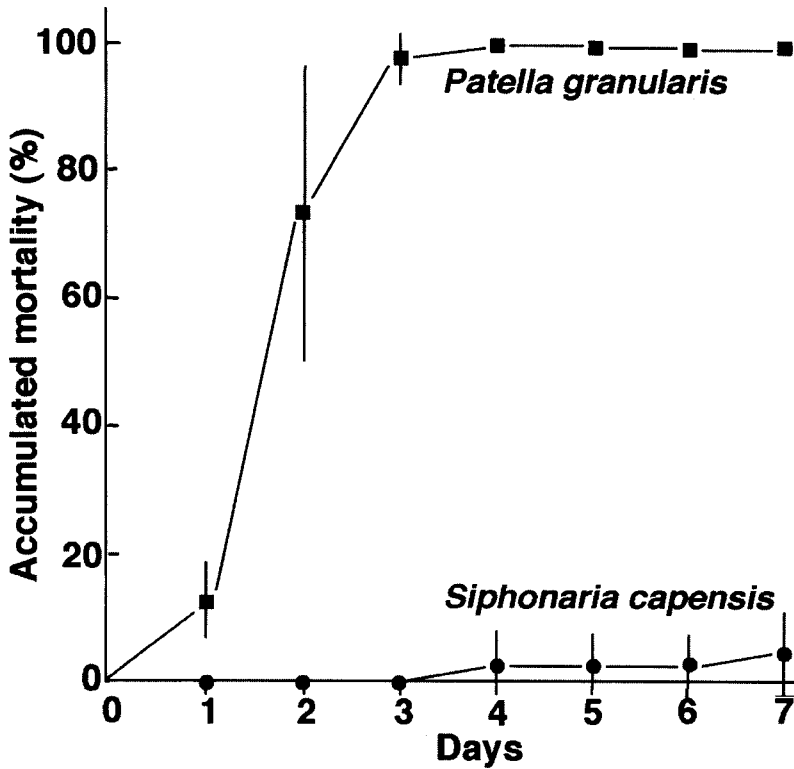


Figure 7 Mean cumulative percentage mortality (\pm SD) of *Siphonaria capensis* and *Patella granularis* when inundated by sand. Controls suffered no mortality. (Redrawn from Marshall & McQuaid 1989).

abilities. Conservation of energy would be a valuable adaptation in physiological stressful environments such as those encountered in lower latitudes.

Many bivalve molluscs are able to survive unfavourable conditions by using anaerobic metabolism (de Zwaan 1977). Marshall & McQuaid (1989, 1993) believe that one species of *Siphonaria* at least (*S. capensis*), can respire anaerobically. When compared with the prosobranch limpet *Patella granularis* (which lives at a similar height on South African shores as *Siphonaria capensis*), the survival rate of *S. capensis* in hypoxic conditions is significantly greater (Fig. 6). *S. capensis* is also able to live for 24 h in an anoxic environment, whereas *Patella granularis* survives for less than 11 h. The survival of *Siphonaria capensis* under anoxic conditions, together with the accumulation of succinate (an end product of anaerobiosis) in its tissues, provides some evidence that this limpet is able to respire anaerobically. Whether other siphonariids possess this ability is not known. Marshall & McQuaid (1989) concluded that in *S. capensis* at least, anaerobiosis enables adults to survive on shores that are subjected to frequent sand inundation. Even after 7 days under sand there are very few mortalities in this limpet whereas *Patella granularis* suffers 100% mortality in less than half this time (Fig. 7).

Temperature and desiccation tolerances

Tolerance to high and low temperatures can be correlated to the environmental conditions experienced by organisms. Thus tolerances can be related to intertidal zonation and geographical position. Branch (1981) concluded that in patellogastropods, upper lethal temperatures did not vary much between species that inhabit very different latitudes. A better correlation was apparent if sublethal effects (e.g. detachment or loss of movement) were considered. Unfortunately, there are very few data on either lethal tolerances to, or sublethal effects of, temperature to make such comparisons within the Siphonariidae. Information on upper thermal tolerances is restricted to three species from the Cape Peninsula of South Africa (Allanson 1958) and one species from sub-Antarctic islands (Simpson 1976, Davenport & McAlister 1996). The South African species have a thermal tolerance of 40–46°C (Table 2), which is similar to patellogastropods (see Table IV in Branch 1981), but greater than *Kerguelenella lateralis*. Whether subtropical and tropical species of *Siphonaria* can tolerate even higher temperatures remains to be determined. There is some evidence that high shore species of *Siphonaria* are more tolerant of higher temperatures than species inhabiting the lower regions of the intertidal zone. Allanson (1958) found that the upper lethal temperature of *S. capensis* (which has its greatest density 2.1 m above mean sea level) is 42.5–46.5°C, whereas for *S. serrata* (greatest density 1 m above mean sea level) it is 40°C (Table 2).

Siphonariid limpets which inhabit sub-Antarctic environments face the problem of potentially lethal subzero temperatures. *Kerguelenella lateralis* lives in mid shore pools at a number of sub-Antarctic sites and on South Georgia it can experience temperatures ranging from -2.43°C to 19.18°C (Davenport & MacAlister 1996, Davenport 1997). The thermal niche of this limpet is quite remarkable, ranging from -17.8°C to +31.8°C (= thermal niche width of 49.6°C). This niche width is nearly twice that of the prosobranch limpet *Nacella concinna* which is found lower on the shore (Davenport 1997). Below -2°C the tissues of *Kerguelenella lateralis* freeze, but how they tolerate this condition is unknown. Mucous secretion, which lowers the intercellular space fluid volume, may play a role as demonstrated in some prosobranch limpets (Branch 1981, 1985).

Table 2 Temperature and desiccation tolerances of some siphonariid limpets, nd, indicates no data.

Species	Upper lethal temperature °C	Lower lethal temperatures °C	Tolerance of % water loss	Rate of water loss (%/h)	References
<i>Siphonaria capensis</i>	In saturated air and submerged, 42.5–46.5	nd	11–20 at 0% R.H., room temp., and at 30°C	2.1 <i>in situ</i> = 35–77% R.H., 20–29°C	Allanson 1958
<i>S. serrata</i>	In saturated air and submerged, 40	nd	14–27 at 0% R.H. and room temp. 35 at 30°C	2.8 <i>in situ</i> = 35–77% R.H., 20–29°C	Allanson 1958
<i>S. concinna</i>	In saturated air and submerged, 43–44.5	nd	11–20 at 0% R.H., room temp., and 30°C		Allanson 1958
<i>Kerguelenella lateralis</i>	In water, 31.8	In water, –17.8	At least 13.5%	2.25 at 10°C; 75% R.H. in moving air	Davenport & MacAlister 1996 Simpson 1976
<i>S. oculata</i>	nd	In air, –7.8	48–55 at 0%? R.H., 17–19°C 52–59 at 0%? R.H., 5–7°C 59 at 20°C; 80% R.H.	nd 0.5–1.1	Marshall & McQuaid 1992a
<i>S. siphonaria</i>	nd	nd	Adult 33–40 at 23°C, R.H. not given Juvenile 51 at 23°C, R.H. not given	1.6–2 8.4	Malli et al. 1982
<i>S. pectinata</i>	nd	nd	~13% at 24°C, R.H. not given	0.24	McAlister & Fisher 1968
<i>S. thersites</i>	nd	nd	70–75 at 29°C; 50% R.H. and air speed 2.5 m.s ⁻¹	About 60	Branch 1988

Whereas some species of *Siphonaria* have been found to have a limited ability to control their body temperature, others have no thermoregulatory capabilities. Thus, the tropical limpets *S. normalis*, *S. gigas* and *S. maura* can have body temperatures slightly lower than the substratum (Vermeij 1971a, Garrity 1984), whereas in *S. guamensis*, *S. javanica*, *S. laciniosa* and *Kerguelenella lateralis* the body temperatures are higher than rock temperatures (Vermeij 1971a, Simpson 1976). Garrity (1984) suggested that *Siphonaria gigas* and *S. maura* lower their body temperatures by the use of evaporative cooling, as limpets were observed to elevate their shells and trickle water out of the pallial cavity through the pneumostome. Evaporative cooling, however, carries the cost of increased desiccation and is probably of limited value. Shell colour and elaborations may help some species thermoregulate to a limited degree. Vermeij (1971a) found that *S. normalis* that had light coloured shells were better at regulating temperatures, presumably because of increased reflection. Vermeij (1973) also noted that tropical limpets which lived in places that are exposed to direct sunlight have more sculptured shells and Black (1979) found that the shells of high shore *S. kurracheensis* are more ribbed (although the ribs are less prominent). Shell ornamentation may play a role in maximizing convection and increasing the area of heat loss (for re-radiation) from the shell surface (see also Branch 1981, 1986), although this hypothesis remains to be tested by rigorous experimentation. Rock type and orientation of the rock habitat is also important. Some species of tropical limpet are restricted to a narrow range of rock types, which Vermeij (1971b) believes is related to the overall adaptive strategies. Heat uptake is greatest on horizontal surfaces and least on vertical surfaces (Garrity 1984). On Panamanian rocky shores, 50% of *S. gigas* were found on vertical surfaces and only 10% on horizontal surfaces. *S. gigas* also avoids grazing on large expanses of flat rock (Levings & Garrity 1984). *S. maura* avoids horizontal rock completely and if transferred to such a habitat has a 94% mortality (Garrity 1984). The same two species on Costa Rican shores, however, can be found on horizontal substrata (Ortega 1987b). One possible reason for this is the greater abundance of algae which may offer more protective cover to the limpets.

Temperature and desiccation stress are closely linked and often exacerbate each other. Although it is often impossible to separate their effects in the field, desiccation is considered to be the more important in influencing the distribution of intertidal organisms (Branch 1981). Results of desiccation tolerances of siphonariids are very variable. This observed variability is in part a result of using different experimental protocols (e.g. temperatures and humidities), sizes of animal (rate of water loss varies considerably with body size of limpets, Branch 1975) and the adaptations of species to a particular zone on the shore (Allanson 1958). Tolerances of water loss in South African species of *Siphonaria* range from 11–59% (Allanson 1958, Marshall & McQuaid 1992a) (Table 2). The tolerance to water loss of *S. siphonaria* from Indian shores lies between these values at 33–40% (Malli et al. 1982) with juveniles being more susceptible to desiccation than adults. The northern hemisphere species *S. thersites* has an even greater tolerance, surviving 70–75% water loss (Branch 1988). As a group, siphonariids do not have a greater tolerance of desiccation than patellogastropods (=13–70% in small limpets and 30–70% in adults, Branch 1975, 1981).

Controlling the rate of water loss may be more important to survival than total loss of water. Both size and shell shape of limpets influence the rate by which they lose water. Branch (1981, 1985, 1986) has discussed the reasons for this in detail. In short, larger limpets and those with a high-domed shell, have a physiological advantage (both in terms of temperature regulation and desiccation) with a smaller surface area to volume ratio. Limpets with domed shells also have a smaller aperture (and therefore smaller foot area) relative to their volume than limpets with less domed shells. Limpets with less domed shells

would not only lose water more rapidly, but also gain heat more rapidly via conduction through the foot. Limpets with flatter shells also retain less extravisceral water (Marshall & McQuaid 1992a). Very few studies have attempted to determine whether there is a relationship between shell shape and intertidal zonation in siphonariids. Nevertheless, the shells of high-shore siphonariids can be relatively high-domed, some species (e.g. *S. gigas*, *S. lessoni*, *S. hispida*, *S. kurracheensis*) do increase in size upshore (Borland 1950, Marcus & Marcus 1960, Olivier & Penchaszadeh 1968, Vermeij 1971a, 1973, Black 1979, Branch 1981) and *S. alternata*, which inhabits exposed ledges, are taller than those from pools (Cook 1979). High shore species, however, are not necessarily better at controlling water loss than those living lower down. Most siphonariids have been found to lose water at about 2–3% h⁻¹ (Table 2), which is very similar to the rate of water loss for several adult patellogastropods (Branch 1975, 1981, 1985). The high shore limpet *S. thersites*, however, has a rate of water loss which is 10 to 40 times faster than that of any other limpet (Table 2) (Branch 1988). Although this species has a high tolerance to desiccation, its microhabitat and behaviour is crucial for its survival (see below).

Branch (1981) has suggested that “the balance between rates of water loss and rates of recovery are more likely to determine zonation patterns than either factor alone”. While siphonariids are no more tolerant to desiccation, and lose water at a similar rate to that of patellogastropods, they have an ability to regain lost fluid rapidly when re-immersed. *S. pectinata* at 24°C survives emersion for about 54 h during which time it loses about 15% of its body weight. Upon re-submergence the lost water is regained after only 1 h (McAlister & Fisher 1968). Similarly, Davenport & MacAlister (1996) found that at 10°C, *Kerguelenella lateralis* lost 13.5% of its body weight in 6 h, but regained the weight within 90 min. By contrast, when *Patella vulgata* loses a similar amount of water (13.9% to 17.2%), the time taken to recover it is double that (2.9h to 3.1 h) of the siphonariids (Davies 1969). This ability of the pulmonate limpets to re-hydrate more rapidly may be one of the keys to the success of these limpets in certain habitats.

The timing of foraging activity also plays a crucial role in reducing heat stress and water loss. It is well established that active gastropods lose water more rapidly than inactive ones. Most siphonariids are inactive, therefore, during daytime low tides and active during moist or wet conditions only, e.g. early morning, at night, or when splashed by the ebbing and flooding tides (hereafter referred to as awash) (Table 3). Those that are active during daytime cease all movement when the substratum dries out (Bertness et al. 1981, Garrity 1984). While this behaviour will reduce water loss, inactive limpets will still lose water during the daytime low tides. After foraging, most species return to a refuge site. Both *Siphonaria japonica* and *S. thersites* often retreat beneath algae during low tide (Abe 1940, Branch 1988). Algae provides these limpets with a humid micro-environment and shields them from the direct effects of the sun. The importance of algal beds to the survival of *S. thersites* was demonstrated by Branch (1988) who removed limpets from the algae and placed them on bare rock at low tide. In just over 2 h, 100% mortality was recorded in the exposed animals, whereas those limpets left in the algae, where the relative humidity was 98%, all survived (Fig. 8). An alternative humid environment to retreat to during low tide is a crevice, and several species exhibit such behaviour. On the tropical shores of Panama, 20% of *S. gigas* and 67% of *S. maura* are found in crevices (Garrity 1984). The use of crevices is not restricted to tropical limpets, as *Kerguelenella lateralis* in the sub-Antarctic and *Siphonaria thersites* in the northwest Pacific both retreat to crevices in dry conditions (Simpson 1976, 1977, Branch 1988). Some species, e.g. *S. maura*, *S. capensis* and *Kerguelenella lateralis* avoid desiccation by inhabiting rock pools (Garrity 1984, Branch & Cherry 1985, Davenport

Table 3 Timing of foraging activity in some siphonariids. Homing, yes indicates homing to a scar unless noted otherwise. E, ebbing tide; R, rising tide; nd, no data.

Species	Observation site	Intertidal distribution	Day/Night	Activity	Homing	References
A. ACTIVE DURING ALL PHASES OF THE TIDE						
<i>Kerguelenella lateralis</i>	South Georgia (54°S) Macquarie island (54°38'S)	Mid-tide pools and mid-upper littoral	nd		No	Simpson 1976, 1977, Davenport 1997
<i>Siphonaria hispida</i>	Ubatuba, Brazil (23°27'S)	Mid-littoral	D and N?		Yes	Marcus & Marcus 1960
B. ACTIVE WHILE SUBMERGED ONLY						
<i>Siphonaria kurracheensis</i>	Rottnest island, W. Australia (37°S)	Lower and upper littoral	nd		Yes	Black 1979
<i>Siphonaria laciniosa</i>	Gulf of Aqaba, Jordan (29°N)	Mid-littoral	Night; E and R		Yes	Hulings 1985
C. ACTIVE WHILE AWASH & EMERSED						
<i>Siphonaria atra</i>	Palau (7°20'N)	Mid-littoral	Day < night; E		Yes	Abe 1935, 1940, 1941
<i>Siphonaria sipho</i>	Palau (7°20'N)	Mid-upper littoral	Day and night		?	Abe 1940, Hirano & Inaba 1980
<i>Siphonaria gigas</i>	Panama, Pacific coast (8°N)	Mid-littoral	Day < night; E > R		Yes	Bertness et al. 1981, Garrity 1984, Levings & Garrity 1984
<i>Siphonaria maura</i>	Panama, Pacific coast (8°N)	Mid-littoral	Day < night; E > R		Yes	Bertness et al. 1981, Garrity 1984
<i>Siphonaria palmata</i>	Panama, Pacific coast (8°N)	Mid-littoral	Day < night; E > R		Yes	Bertness et al. 1981
<i>Siphonaria alternata</i>	Florida & Bermuda (11°N)	Mid-littoral	Day and night; E v. R, site specific		Yes	Cook 1971, 1976; Verderber et al. 1983
<i>Siphonaria japonica</i>	Japan (40°55'N)	Mid-littoral	Day < night; E and R		Yes	Abe 1940, Ohgushi 1954, 1955, Hirano & Inaba 1980, Hirano 1981, Iwasaki 1994
<i>Siphonaria normalis</i>	Hawaii, Marshall islands (20°S)	Mid-upper littoral	Day/night; E v. R, site specific		Yes	Cook 1969, 1976, Cook & Cook 1978
<i>Siphonaria lessoni</i>	Mar del Plata, Argentina & Quequén, Argentina (38°S)	Mid-upper littoral	Day < night; E > R		No	Olivier & Penchaszadeh 1968; López Gappa et al. 1996

Table 3 continued

Species	Observation site	Intertidal distribution	Day/Night Activity	Homing	References
D. ACTIVE WHILE AWASH & IMMERSED					
<i>Siphonaria sirius</i>	Japan (33°N)	Lower littoral	Day	Yes	Ohgushi et al. 1953, Iwasaki 1993a
E. ACTIVE WHILE AWASH/SPLASHED ONLY					
<i>S. pectinata</i>	Florida (26°N)	Low – high littoral	Day and night? E > R	Yes	Thomas 1973
F. ACTIVE AT LOW TIDE ONLY					
<i>Siphonaria thersites</i>	NW USA (48°30'S)	High-upper littoral	Night, summer Morning, winter	Yes*	Branch 1988
<i>Siphonaria capensis</i>	South Africa (33°–34°S)	Mid-upper littoral	Night > early morning, day and night in pools	Yes	Branch & Cherry 1985, A. N. Hodgson unpubl.
<i>Siphonaria concinna</i>	South Africa (33°44'S)	Mid-upper littoral	Night > early morning in shade	Yes	Gray & Hodgson 1997
<i>Siphonaria serrata</i>	South Africa (33°44'S)	Mid-upper littoral	Night	Yes	Branch 1981
<i>Benhamina obliquata</i>	New Zealand (45°30'S)	Mid-upper littoral	Mainly night	Yes**	Borland 1950
E. PERIOD OF ACTIVITY NOT GIVEN					
<i>Siphonaria denticulata</i>	NSW, Australia (34°S)	Mid-littoral	?	Yes	Creese & Underwood 1982
<i>Siphonaria virgulata</i>	NSW, Australia (34°S)	Mid-littoral		No	Creese & Underwood 1982

* Home to a crevice;

** Mid-shore animals home to a scar, high shore to a crevice.

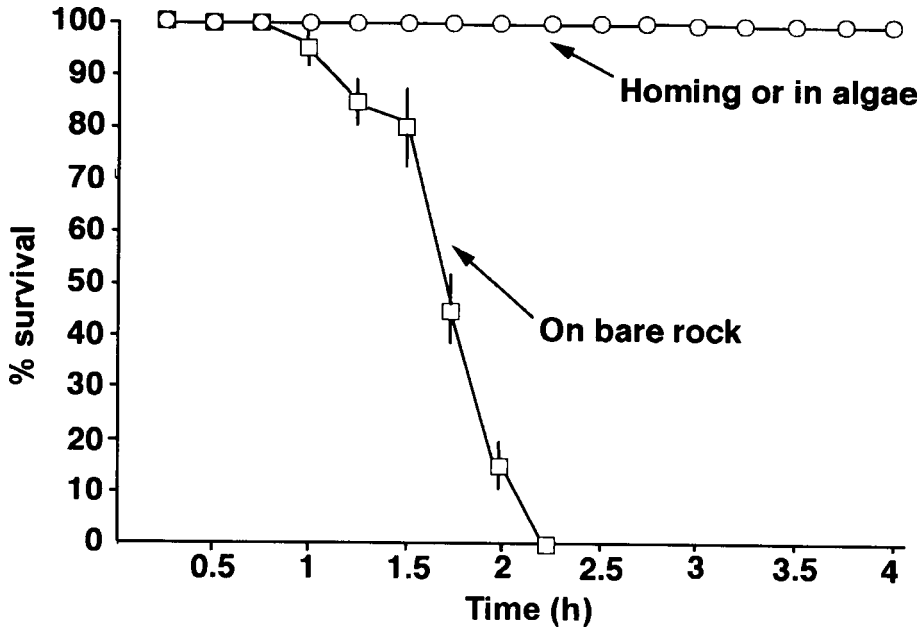


Figure 8 Survival of *Siphonaria thersites* during low tide when left exposed on bare rock, allowed to home to crevices, or left in beds of *Iridaea cornucopiae*. Error bars show standard deviations. (Redrawn from Branch 1988).

1997). Evidence that a crevice or pool is vital for preventing desiccation in *K. lateralis* is twofold. First, mortalities of animals exposed on rocks on calm sunny days have been noted, and secondly, the tissues of dead limpets appeared dehydrated (Simpson 1976).

After activity, the majority of siphonariid limpets retreat to a home scar on the rock (Table 3). At the scar, which is formed by mucoïd secretions (Branch 1981, Lindberg & Dwyer 1983), the margin of the shell matches the contours of the rock precisely. Several studies have now shown that occupation of a home scar reduces desiccation (Cook 1976, Verderber et al. 1983, Garrity 1984, Branch & Cherry 1985); but it should be noted that this is not the only function of the home scar and other functions are discussed elsewhere in the review. Cook (1976) found that transplanting *Siphonaria alternata* from their scars to the adjacent rock resulted in a 36% mortality within three days. The most likely cause of mortality was desiccation. Further work on this species showed that occupying a scar reduced water loss by up to 55% (Verderber et al. 1983). A further behaviour pattern observed in some species (e.g. *S. denticulata*, Creese 1980b; *S. concinna* and *S. serrata*, A.N.Hodgson, pers. obs.) is clustering, which may reduce desiccation (Branch 1981). The evidence for this is, however, circumstantial and needs to be investigated fully.

Despite physiological and behavioural adaptations to minimize both heat stress and desiccation, some species may still suffer mortality. It has been suggested that high temperatures in the summers of 1988–90 caused mortalities of *Siphonaria* on shores of Hong Kong (Liu 1994). However, it is possible that mortality was not due to the direct effects of heat and desiccation, but that the limpets starved to death. Quinn (1988a) showed that the increased mortality of high shore *S. diemenensis* in summer on Australian shores was a result of starvation (algae dying back during the summer months) not physiological stress. Summer algal die back also occurs on the shores of Hong Kong (Williams 1993).

Salinity tolerances and osmoregulation

Many intertidal organisms, including siphonariids, experience episodic fluctuations in environmental salinity, either owing to rainfall or evaporation during low tide. Such fluctuations can be particularly severe in shallow rock pools, a habitat favoured by a number of siphonarian species (Allanson 1958, Bedford 1969, Garrity 1984, Branch & Cherry 1985, Davenport & MacAlister 1996). In addition, desiccation can cause internal osmolarities to increase by the loss of water and resultant concentration of tissue ions. It is likely that all species of *Siphonaria* are either strict osmoconformers, as shown for *S. pectinata* (McAlister & Fisher 1968), or have limited capabilities of osmoregulation at low salinities only (Williams 1964, Bedford 1969). Both *S. serrata* (studied as *S. aspera*) and *S. zelandica* are able to maintain hyperosmotic haemolymph in reduced salinities (Fig. 9) (Williams 1964, Bedford 1969). Siphonariids, along with other marine gastropods can have high concentrations of non-essential amino acids (Simpson et al. 1959). *S. zelandica* regulates levels of the intracellular free amino acids alanine, glutamine and taurine, which decrease in concentration with decreasing salinities. Reduction of these non-essential amino acids presumably reduces the colloidal osmotic pressure as has been shown in many osmoconformers (Rankin & Davenport 1981).

Like their prosobranch relatives, *Siphonaria* spp. can buffer the immediate effects of salinity change by clamping their shell firmly against the substratum. In many species this is facilitated by the margin of the shell fitting the rock contours precisely. The effectiveness of clamping in reducing mortality in *Siphonaria* was first demonstrated by McAlister & Fisher (1968). Limpet survival at low (<20ppt) and high (>45 ppt) salinities was better when animals were undisturbed and left attached to rock. More recent experiments by Branch &

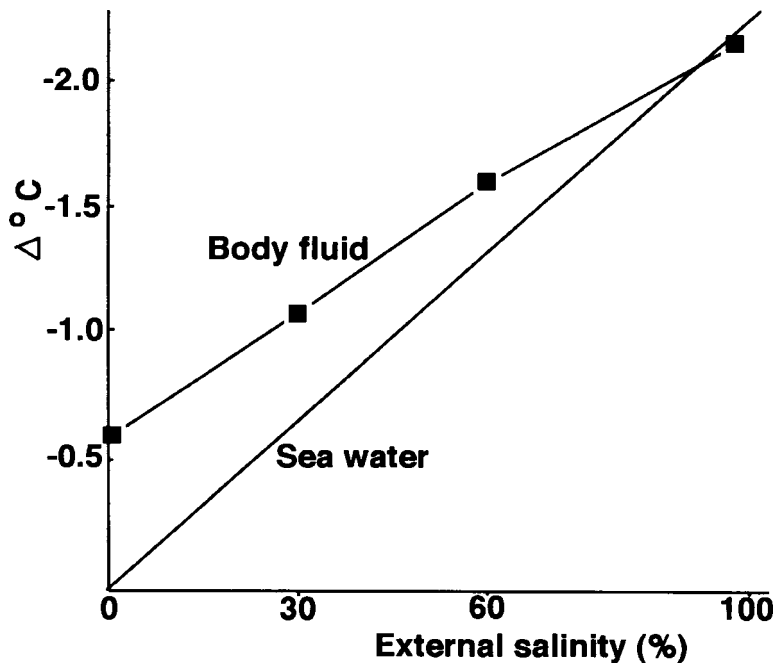


Figure 9 Depression of freezing points of the body fluid of *Siphonaria zelandica* in different salinities. (Redrawn from Bedford 1969).

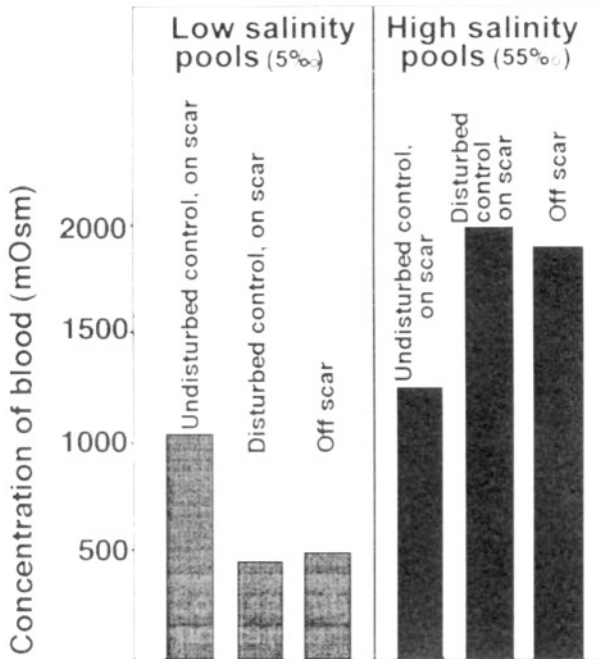


Figure 10 The osmotic concentration (mOsm) of pool-dwelling *Siphonaria capensis* subjected to hypo- and hypersaline water and left undisturbed on their scars, lifted and replaced on scars (disturbed) or denied access to a scar. Standard deviations left to right are (\pm) 36, 150, 121, 76, 142 and 96 mOsm. (Redrawn from Branch & Cherry 1985).

Cherry (1985) on pool dwelling *S. capensis* confirmed these findings. Those animals left on their home scar resisted changes to the osmotic concentration of their blood, compared with experimental animals that were deprived of their scars (Fig. 10). During clamping *Siphonaria* reduces its metabolic rate, Marshall & McQuaid (1993) showing that within 3 h exposure to low salinities (20 ppt) *S. capensis* undergoes bradycardia. Presumably such metabolic rate depression is accompanied by reduction in the flow of water through the mantle cavity, which would further reduce the impact of salinity change. McAlister & Fisher (1968) noted that during clamping in *S. pectinata* there was a reduction in pallial and mantle currents.

Although limited in their osmoregulatory capabilities, siphonariids on the whole have a greater tolerance to hyper- or hypo-osmotic conditions (Allanson 1958, 1959, McAlister & Fisher 1968, Simpson 1976, Prasad et al. 1988, Branch et al. 1990, Davenport 1997) than patellogastropods (see Branch 1981). Whereas *S. pectinata* tolerates salinities between 20 ppt and 40 ppt (McAlister & Fisher 1968), a tolerance range similar to that of some patellogastropods (Branch 1981), some South African species survive salinities of 16–79 ppt (Allanson 1958). *Kerguelenella lateralis*, which is common to mid shore pools on sub-Antarctic islands, has an equally wide salinity tolerance of 6 ppt and 68 ppt (Davenport 1997; see also results of Simpson 1976). As osmoconformers, siphonariids are therefore tolerant to high internal osmolarities which are not only caused by changes in the external environment but also by evaporative water loss. Wolcott (1973) suggested that it is the resulting internal osmotic stress which causes the death of prosobranch limpets. Marshall

& McQuaid (1992a), however, urge caution in attributing death after evaporative water loss to any one physiological cause. Nevertheless, tolerance to internal osmotic stress may be an important adaptation which enables siphonariids to inhabit warmer environments than those favoured by patellogastropods.

Tolerance to hypo-osmotic conditions enabled *Siphonaria capensis* and *S. serrata* to survive the extreme flooding of the Orange River on the west coast of South Africa in 1988 an event which killed most of the other rocky shore inhabitants. This flooding event reduced the salinities to 18 ppt at a distance of 4–8 n.mi. offshore of the mouth of the estuary (Branch et al. 1990). The greater salinity tolerances of siphonariids (when compared with patellogastropods) have not only enabled siphonariids to inhabit rock pools but also estuaries, habitats that are generally not favoured by patellogastropods. For example, four South African species (*S. capensis*, *S. serrata*, *S. oculus*, *S. concinna*), are commonly found on hard substrata well within many estuaries that are subjected to episodic floods of fresh water (Allanson 1959, A.N.Hodgson pers. obs.).

Thus salinity tolerances, coupled to the behavioural (shell clamping) and metabolic responses (metabolic rate depression) enable siphonariids to survive not only short-term exposures to adverse external salinities, but also changes in internal osmolarities.

Wave action, tenacity and pedal mucus

Shell shape and texture (which influence drag), as well as tenacity, are factors that are important in withstanding wave activity. As tall shells exert more frontal drag (Branch & Marsh 1978) it would be expected that low shore limpets (which experience the greatest wave activity) would have flatter, more streamlined, shells. Although this is true for some species, overall there is not a strong correlation between limpet shell height and exposure to wave action (Branch 1985, 1986). The possible relationship between shell shape, texture and degree of wave exposure has not been investigated in siphonariids. Bastida et al. (1971), however, have found that populations of *S. lessoni* from shores with less turbulent water have higher shells than those limpets from more wave beaten habitats.

Branch & Marsh (1978), working on patellogastropods, found that tenacity was inversely related to (a) the flexibility of the foot, (b) the speed of locomotion (high tenacity and high mobility are incompatible) and (c) the amount of mucus secreted by the foot. In addition, Frescura (1991) has suggested that the size of the columella (shell) muscle must be important for tenacity, as it is these muscles that clamp the shell firmly against the substratum and resist the lift caused by wave activity. When compared with prosobranch limpets, siphonariids have a tenacity that is 1.8 to 6.9 times lower (Branch & Cherry 1985, Branch 1988, Davenport 1997) (Table 4). This lower tenacity is in part a result of having a more flexible foot (Branch 1988) and a relatively smaller columellar muscle when compared with patellogastropods (A.N.Hodgson, unpubl. obs.). In addition, most siphonariids are highly mobile grazers and in some species tenacity is particularly poor when they are active (Table 4). *S. thersites*, for example, is a highly mobile limpet with a very low tenacity (Branch 1988). Siphonariids move using monotaxic retrograde waves (Abe 1935, 1941), and during locomotion limpets only have about 50% of their foot in contact with the substratum (Jones & Trueman 1970). In a comparison of six species of *Patella*, Branch & Marsh (1978) found an inverse relationship between speed of movement and limpet tenacity, i.e. species that moved slowly had a greater tenacity. This relationship, however, may not exist within a species; Davenport (1997) found no significant difference in the tenacity of highly mobile and sluggish individuals of *Kerguelenella lateralis*.

Table 4 Tenacity of some siphonariid and patellid limpets with a foot area of 30 mm². Data from Branch 1988 and Davenport 1997.

Species	Tenacity	Habitat
<i>Siphonaria capensis</i>	4.02N	On scars
	1.62N	Foraging
<i>Siphonaria thersites</i>	0.60N	On rock
	0.02N	On algae
<i>Kerguelenella lateralis</i>	0.60N	On rock
<i>Patella cochlear</i>	22.5N	On rock
<i>Patella granularis</i>	14.5N	On rock
<i>Patella longicosta</i>	13.8N	On rock
<i>Patella granatina</i>	7.60N	On rock

Limpets are largely able to attach to rocks because of a thin layer of pedal mucus which is tacky and visco-elastic (Branch 1981, 1985, 1986, Davies & Hawkins 1998 for literature on this subject). Mucus production by patellogastropods has been shown to be energetically expensive (Davies & Hawkins 1998 for review) and siphonariids are no exception. In a study on three species of *Siphonaria* from the shores of Hong Kong, Davies & Williams (1997) found that *S. japonica* (0.1 g whole DW) produced 2.7 µg dry mucus mm⁻¹ moved. This was about three times the amount (0.97 µg dry mucus mm⁻¹ moved) produced by active *S. atra* of the same size. However, the mucus of *S. japonica* had a lower calorific content (5.6 kJg⁻¹) than the pooled mucus of *S. sirius* and *S. atra* (9.1 kJg⁻¹). Davies & Hawkins (1998) suggest that these differences might reflect a trade off between quantity of mucus produced and energetic content. From their data, Davies & Williams (1997) calculated that depending on the size of the animal, estimates of energy export as locomotory mucus range from 0.55–128 J. day⁻¹ for *S. atra*, and 0.59–169 J. day⁻¹ for *S. japonica*. These values are similar to those obtained from earlier work on patellogastropods (e.g. *Cellana grata*= 23–164 J day⁻¹, Davies & Williams 1995). Using maximum population densities, Davies & Williams (1997) calculated that for Hong Kong siphonariid species, energy loss as mucus would range from 6.6 kJ m⁻² yr⁻¹ to 8026 kJ m⁻² yr⁻¹, estimates which are comparable with other studies on temperate and tropical molluscs (e.g. *C. grata*=892–6000 kJ m⁻² yr⁻¹; *Patella vulgata*=720–1624 kJ m⁻² yr⁻¹, Davies & Williams 1995). Branch & Marsh (1978) in their work on South African patellids found that high shore patellids had a thicker layer of pedal mucus than lower-shore species. Davies & Williams (1997) also found that *Siphonaria japonica*, which is found higher in the intertidal than *S. atra*, secretes significantly more mucus during locomotion (Fig. 11). Although it has not been measured it can be predicted that *S. japonica* will have a lower tenacity.

Because of their relatively low tenacity, many siphonariids maintain their positions by avoiding heavy wave activity. *Kerguelenella lateralis*, for example, probably gains some protection from the direct action of the waves by inhabiting rock pools (Davenport 1997). Other species are active during low tide only (Branch & Cherry 1985, Branch 1988, Davenport 1997, Gray & Hodgson 1997), retreating to crevices or home scars before they are subjected to the physical stresses of the waves. A crevice is essential for the survival of *Siphonaria thersites* which, along with *Kerguelenella lateralis*, has the lowest tenacity of all limpets (Table 4). If prevented from gaining this refuge *Siphonaria thersites* is rapidly

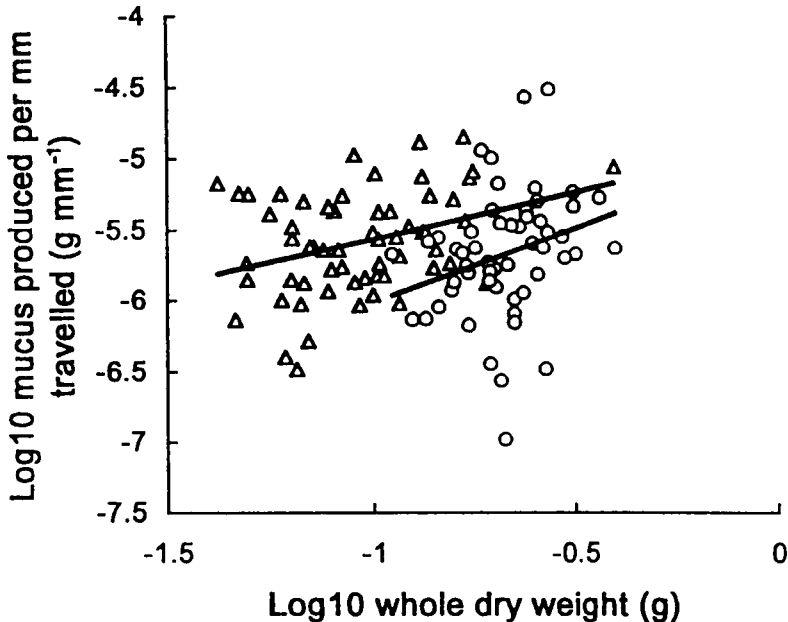


Figure 11 Pedal mucous production per unit distance travelled by *Siphonaria atra* (open circles) and *S. japonica* (open triangles) as a function of whole animal DW. (From Davies & Williams 1997, by kind permission of Hong Kong University Press).

washed off the rocks, a force of $<0.02\text{N}$ being sufficient to dislodge this limpet (Branch 1988). Homing to a scar helps the majority of siphonariids maintain their position on the shore as tenacity is about six times greater in limpets which are on a scar compared with those which are not (Branch & Cherry 1985). When *S. capensis* were removed from their scars, 40% of the limpets were lost to wave activity in 4 h (Branch & Cherry 1985).

Predation and predator avoidance

Whereas prosobranch limpets are commonly found in the diets of many predators (Branch 1985), siphonariids are consumed to a much lesser extent. The role of a home scar as a defence against predators has been demonstrated for both prosobranch and pulmonate limpets (Branch 1981, Garrity & Levings 1983, Iwasaki 1993a). Garrity & Levings (1983), working on Panamanian shores, showed that when prevented from returning to their scars 26% of *S. gigas* were lost, compared with only 2% of animals that were allowed access to their scars. As limpets that were denied scars, but protected from predators by cages, all survived, Garrity & Levings (1983) suggested that predatory fishes were responsible for limpet mortality. Fishes were unable to remove those limpets that returned to their home scars. The home scar is also important for defence in the low shore species *S. sirius*, which retreats very rapidly to its scar when threatened by predatory starfish (Iwasaki 1993a). *S. sirius*, however, exhibits a very different response to the drilling predatory whelk, *Thais clavigera*. When threatened by this predator, *Siphonaria sirius* vacate their scars and rapidly flee (Iwasaki, 1993a). Although this behaviour is well documented for patellogastropods

(Branch 1981), this is the first report of such a response in a siphonariid limpet, and it is possible that the behaviour could be more widespread within this taxon. The direction of flight is not random, tending to be perpendicular to that of the attack. Having escaped the whelk, the limpets return to their home scars (Iwasaki 1993a).

Many species of *Siphonaria* are, however, avoided by predators because they probably have a chemical defence mechanism. The epidermis of siphonariids contains numerous multicellular glands (Fretter & Graham 1954, Marcus & Marcus 1960, de Villiers & Hodgson 1984) which will exude a sticky white mucus when the animal is irritated. The mucus is bitter to the taste (A.N.Hodgson, pers. experience). Studies on the chemistry of approximately 13 species of *Siphonaria* have revealed that they produce polypropionate metabolites (for reviews of literature see Branch 1988, Davies-Coleman & Garson 1998). It is thought that these metabolites, which are secreted as part of the mucus from the epidermal glands, are noxious. Some of the polypropionates are biologically active, being toxic to fish at levels as low as $10 \mu\text{g ml}^{-1}$ (Hochlowski et al. 1983), suppressing bacterial growth (Biskupiak & Ireland 1983) and the development of fertilized sea urchin eggs at $1 \mu\text{g ml}^{-1}$ (Hochlowski & Faulkner 1983). This chemical defence mechanism is very effective in some species. *S. capensis*, *S. serrata*, *S. concinna*, *S. thersites* and *Kerguelenella lateralis* suffer very little predation, and many predators that readily consume patellogastropods, refuse to eat these siphonariids when presented with them (Branch & Cherry 1985, Branch 1988, Davenport 1997, A.N.Hodgson unpubl. obs.). Other species (e.g. *Siphonaria hispidia*, *S. maura*, *S. denticulata*, *S. lessoni*, *S. normalis*, *S. gigas*, *S. sirius*, *S. japonica*, *S. diemenensis*, *S. atra*) can be eaten (Marcus & Marcus 1960, Menge 1973, Cook 1976, Paine & Palmer 1978, Moreno & Zamorano 1980, Underwood & Jernakoff 1981, Jara & Moreno 1984, Ortega 1986, Quinn 1988a, Navarrete & Castilla 1993, Iwasaki 1993a, Liu 1994). Most, however, only form a small or occasional part of the diet of the predator. A notable exception to this has been reported from Eniwetok Atoll (Marshall islands), where 99% of *Thais armigera* were found feeding on *Siphonaria normalis* (Menge 1973). Menge (1973) suggested that the size frequency and patchy distribution of *S. normalis* on the island was a result of the predatory activities of the whelk, which preferentially selected larger limpets (Fig. 12). Further selection pressure may be placed on these limpets by predatory fishes which also consume the larger limpets (Cook 1976, 1980).

The only siphonariid that has been found to lack polypropionates (D.J.Faulkner pers. comm. to Ortega 1986 and Branch & Moreno 1994) is *S. gigas*. Despite an apparent lack of a chemical defence, it appears to suffer very little fish predation (Garrity & Levings 1983, Ortega 1986). This is possibly due to the large size of this species and/or the substratum it occupies. *S. gigas* is more common on irregular substrata and in wave-exposed areas where predators may find it more difficult to feed (Branch 1986). *S. gigas* is the only species of *Siphonaria* to be exploited by man (Ortega 1987a). Although exploitation of this limpet in Costa Rica does not appear to be threatening populations, because of continued high recruitment, the population size structure has been affected. At sites where animals were exploited the mean shell length of *S. gigas* was 25 mm to 28 mm, whereas in a nearby protected reserve, animals were significantly larger (32 mm to 34 mm shell length) (Ortega 1987a).

The only other group of marine pulmonate limpets, the Trimusculidae, also produce sticky milky-white mucus (Rice 1985, A.N.Hodgson pers. obs.). As in siphonariids the mucus will deter predators, but the chemicals produced in the mucus by trimusculids are labdane diterpenes (see Gray et al. 1998 for literature). This chemical difference between siphonariids and trimusculids is perhaps further evidence that although these two taxa have much in common, phylogenetically they are not closely related.

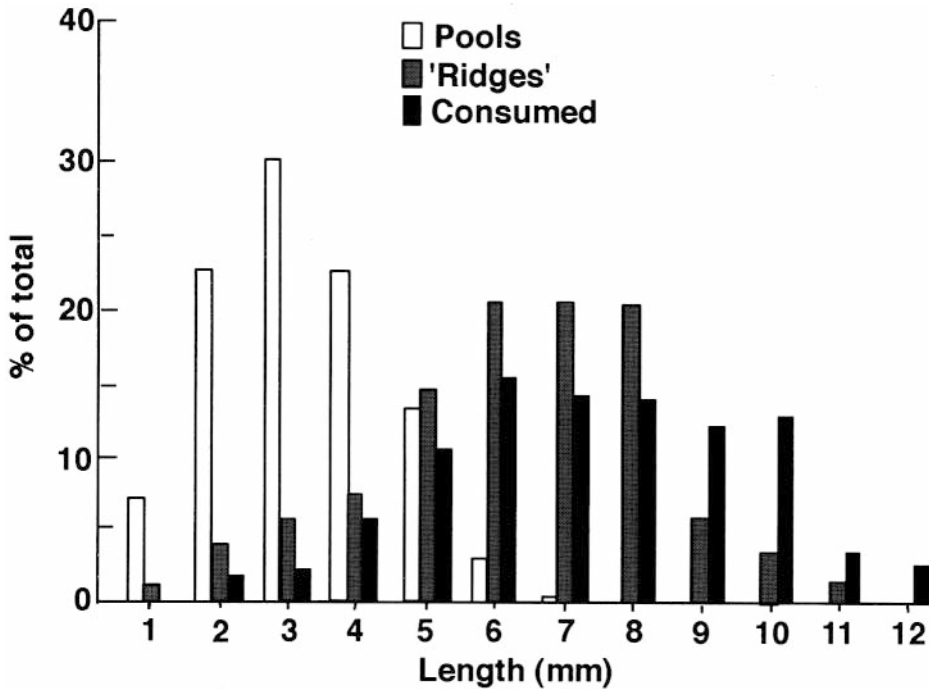


Figure 12 Size frequency histogram comparing the sizes of *Siphonaria normalis* in pools and on "ridges" to the size eaten by *Thais armigera*. (Redrawn from Menge 1973).

Branch (1981) speculated that the unpalatability of most siphonariids may be responsible for the success of this genus in tropical waters. This is an attractive hypothesis which I would support, but one which is very difficult to test.

Anthropogenic effects

As well as affecting populations by exploitation, numerous other human activities can impact on marine intertidal invertebrates. Such activities include pollution, habitat destruction and other more subtle effects such as trampling and rock disturbance associated with tourism, general leisure activities, and bait exploitation. As far as I am aware, there are no studies on siphonariids that have examined their tolerances to, or sublethal effects of, pollutants. Tablado et al. (1994) found that the growth rate of *S. lessoni* was 30% greater in the vicinity of a sewage outfall when compared with a clean site. Mortality, however, was higher. The increased growth rate at the organically polluted (and enriched) site was probably due to a combination of an increase in food availability and space. The authors were not able to explain the increased mortality at the polluted site, but suggested that increased predation by fishes and birds may have played a role.

Siphonariids are probably very resilient to habitat disturbances. In a study examining the effects of trampling on rocky shore organisms in southeastern Australia, Keough & Quinn (1998) found that trampling had no negative effects on *S. diemenensis* and *S. zelandica*. At some sites these limpets benefited from trampling, their densities increasing, a result of an alteration in macroalgal composition and abundance.

Parasitism

Two species of *Siphonaria* from southern Africa, *S. capensis* and *S. concinna*, are important intermediate hosts of trematode parasites (Hodgson et al. 1993). It is highly likely that siphonariids from other geographical regions are also host to such parasites, infestations being either overlooked or ignored. In their survey of 26 sites around the southern African coast, Hodgson et al. (1993) found *S. capensis* and *S. concinna* to have sporocysts (containing cercariae) of at least three species of trematode. Two species were found in *S. capensis* and one in *S. concinna*. The larvae infected the digestive gland of the limpets, and in about 30% of parasitized *S. capensis* and 10% of parasitized *S. concinna*, the digestive gland was destroyed completely. Considerable spatial and temporal variability in parasite prevalence was found. At several locations up to 40% of *S. capensis* were infected whereas at other locations parasites were absent. Over the three year study, parasite prevalence increased at some sites, whereas at others it declined. Hodgson et al. (1993) were unable to explain this variability but there was some correlation between parasite prevalence and limpet density, prevalence always being high where limpet density was $>90\text{ m}^{-2}$. At sites where a large percentage of the population were infected, parasite prevalence was size related, with more of the larger limpets bearing parasites (Fig. 13).

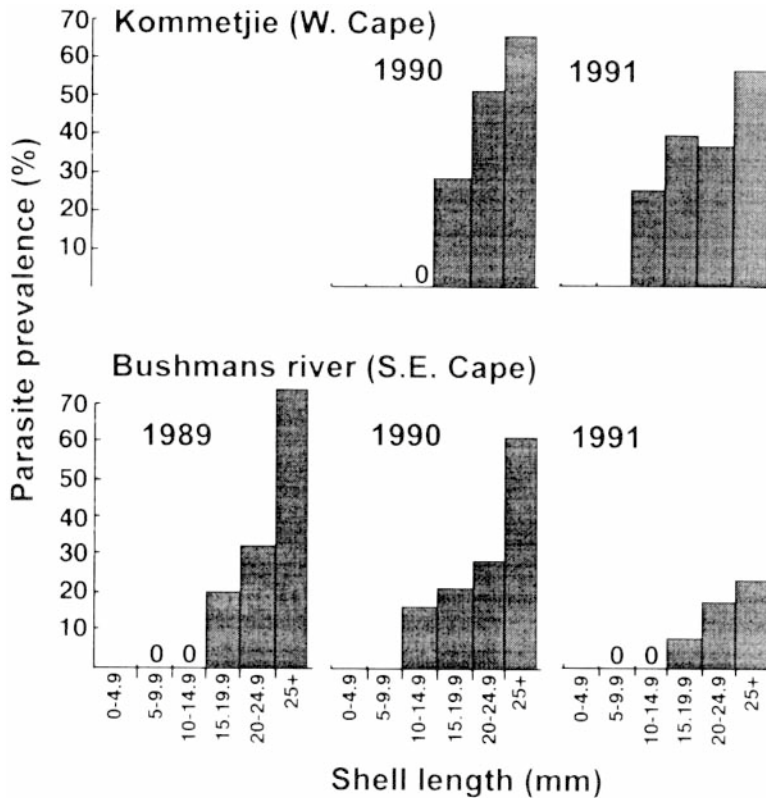


Figure 13 Prevalence of parasitic trematodes in different size classes of *Siphonaria capensis* from two sites in South Africa. (Redrawn from Hodgson et al. 1993).

Hodgson et al. (1993) were unable to observe any apparent effect of the parasite on the limpet hosts such as gigantism, colour change of tissues or behavioural aberrations. Nor did the parasite invade the gonad and castrate the host. It appeared that the parasites had little impact on the population dynamics of *S. capensis* and *S. concinna*. The final hosts of the parasites have still to be determined, but they are probably vertebrates (e.g. sea bird or fish).

Behavioural adaptations—homing and foraging activity

Activity patterns

Nearly all littoral gastropods studied to date have a distinct rhythm of activity, with foraging being confined to a particular phase of the tidal cycle and time of day (see Branch 1981, Hawkins & Hartnoll 1983, Little 1989 for reviews). The siphonariid limpets are no exception in this regard. Activity patterns of some 22 species have been studied, with observations from most of the geographic localities and tidal heights where these limpets can be found. Activity studies have varied in their objectives and detail, ranging from: anecdotal to more detailed qualitative observations of when limpets are active; more extensive quantitative monitoring of foraging during different phases of the moon and different seasons; and experiments to try to explain how these animals find home scars. Information on siphonariid activity rhythms have appeared in reviews by Branch (1981), Hawkins & Hartnoll (1983), Little (1989) and Iwasaki (1995a), but not all studies on these limpets were included.

Activity of intertidal gastropods is usually correlated to tides and the day/night cycle. Branch (1981, his Table IV) proposed that there were five patterns of gastropod activity within the intertidal zone, although the labile nature of these patterns makes rigid classification difficult (Hawkins & Hartnoll 1983, Little 1989). Activity patterns of siphonariids are equally diverse and there is some correlation between the timing of activity and position on the shore (Table 3, p. 261). High-shore species are active mainly when exposed, e.g. *S. thersites* (which inhabits the high intertidal in the northwest of North America), *Benhamina obliquata* (from New Zealand), *Siphonaria capensis*, *S. concinna* and *S. serrata* (from the southern and western Cape of South Africa) (Borland 1950, Branch & Cherry 1985, Branch 1988, Gray & Hodgson 1997, A.N.Hodgson unpubl. data). Mid- to low-shore species are more active when awash during the ebb and/or flood tide, ceasing all movement when completely submerged or shortly after emersion. *Kerguelenella lateralis*, which is common in mid-tide pools on sub-Antarctic islands (e.g. South Georgia), can be active during all phases of the tide (Davenport 1997). *Siphonaria sirius*, which inhabits the lower intertidal zone (Iwasaki 1993a, 1995a) is a species that has been found to be active during the daytime only and exclusively when awash and completely submerged.

Superimposed on the tidal cycle may be a daily cycle of activity. Siphonariids which forage while awash or submerged, are active during the day (some exclusively) and night (Tables 3, 5). Of those species that are active by day and night, nocturnal foraging excursions are usually longer in duration and distance (Table 5). This is a result of daytime activity ceasing when the rocks dry out (Abe 1941, Bertness et al. 1981, López Gappa et al. 1996). Of those species that are active at low tide only (e.g. *S. capensis* and *S. concinna*) foraging is restricted to night (e.g. Fig. 14B), although some activity can occur during early morning low tides in those animals which are shaded or in pools (Branch & Cherry 1985, Gray & Hodgson

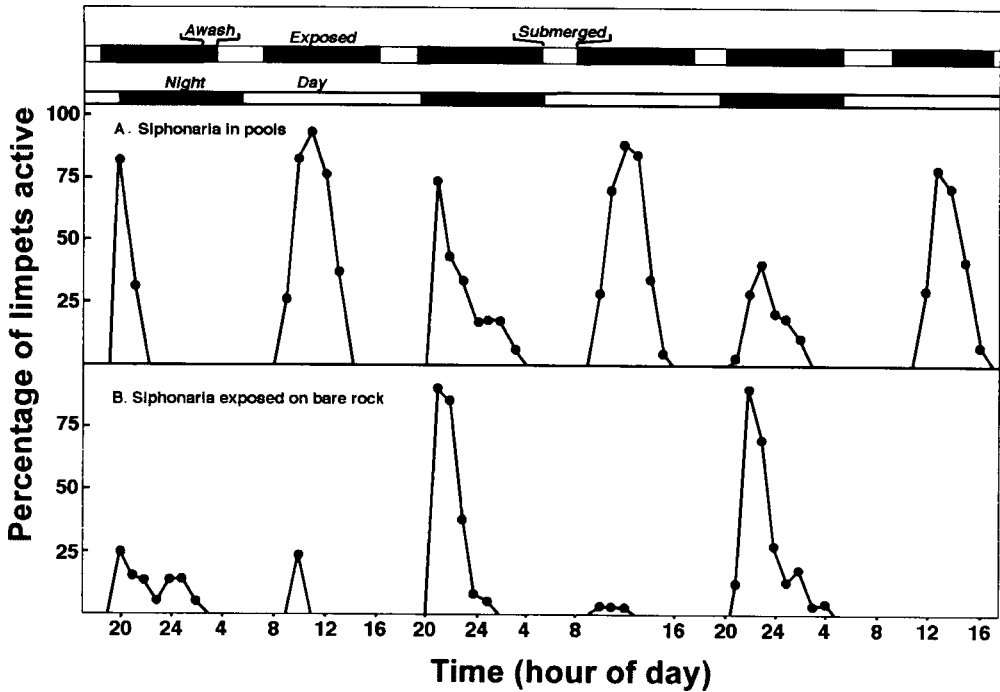


Figure 14 Activity, rhythms of *Siphonaria capensis* in pools (A) and on bare rock exposed to the air at low tide (B). Also shown at the top of the diagram is the state of the tide—whether the limpets were submerged (white bar), awash (black bar) or exposed to air (gray bar); immediately below the dark and light bars indicate night and day respectively. (Redrawn from Branch & Cherry 1985).

1997) (Fig. 14A). The daily cycle of activity in *S. thersites* alters with season. During summer it is active during the morning low tides, whereas in autumn activity shifts to the evening low tides (Branch 1988). Branch determined that this was a result of activity being regulated by tidal amplitude, as *S. thersites* is only active during the lower of the two low tides. In summer these are in the morning whereas in autumn they are at night.

A number of adaptive reasons for the timing of foraging activity of siphonariids have been proposed. These include avoidance of: osmotic stress (McAlister & Fisher 1968, Branch & Cherry 1985); desiccation and high temperatures (Verderber et al. 1983, Garrity 1984, Iwasaki 1995a, Gray & Hodgson 1997); wave action (Branch & Cherry 1985, Branch 1988, Gray & Hodgson 1997); and predation (Bertness et al. 1981, Garrity & Levings 1983, Levings & Garrity 1984, Iwasaki 1995a). However, it is unlikely that these selection pressures have acted in isolation, and the timing of activity is rather a result of a combination of factors which may be hierarchical and different for limpets at different tidal heights or geographic localities. It is important that activity secures enough time for foraging, while minimizing the threat of desiccation, and in some species wave activity and predation. For a high shore species, being active at high tide or when awash would present a small window for foraging only. A far greater window is available for low tide foraging, but this can only be at night as desiccation is clearly a threat during the day. High-shore species also tend to have a lower tenacity and therefore wave activity must be avoided (see discussion on tenacity). By contrast for mid- to low-shore species there is a good window of activity while the animals are awash and there is no threat of desiccation. Ceasing activity when

Table 5 Duration (\pm SD) for foraging excursions and distances (\pm SD) moved by *Siphonaria*.

Species	Time spent foraging (min)	Distances moved (mm)	Conditions	References
<i>S. alternata</i>	44.68 \pm 21	47 \pm 22.5	Ebb tide	Verderber et al. 1983
	39.52 \pm 35	35.4 \pm 14.6	Flood tide	
	20–55	25–45	Neap	Cook & Cook 1978
	0–90	35–50	Spring	
<i>S. capensis</i>	120 \pm 20	11 \pm 8	Neap tide	Branch & Cherry 1985
	270 \pm 62	62 \pm 3.9	Spring tide	
<i>S. concinna</i>	540	1790 \pm 319	Spring full moon	Gray & Hodgson 1997
	480	810 \pm 294	Neap quarter moon	
	480	1060 \pm 291	Spring new moon	
<i>S. japonica</i>	298 \pm 64	361 \pm 224	Neap half moon, night	Hirano & Inaba 1980
	163 \pm 44	286 \pm 115	Neap half moon, day	
	188 \pm 42	163 \pm 90	Spring new moon, night	
	29 \pm 17	87 \pm 73	Spring new moon, day	
	157 \pm 65	163 \pm 78	Neap half moon, night	
	101 \pm 64	204 \pm 193	Neap half moon, day	
	158 \pm 61	135 \pm 71	Spring full moon, night	
	41 \pm 13	115 \pm 49	Spring full moon, day	
<i>S. normalis</i>	90–190	380–1150	Neap	Cook & Cook 1978
	0–35	0–250	Spring	
<i>S. atra</i>	20–60	130–300	Day	Abe 1935, 1941
	(longer at night)	340–650	Night	
<i>S. sirius</i>	160–280	750–1200	No s.f. difference between neap and spring tides	Iwasaki 1995a
<i>S. laciniosa</i>	54 (25–100)	Up to 200	Night	Hulings 1985
<i>S. pectinata</i>	60–90	150–750	No data	Thomas 1973
<i>S. lessoni</i>	480	No data	Night, low shore	López Gappa et al. 1996
	180	No data	Day, low shore	
	180	No data	Day, high shore	
	300	No data	Night, harbour population	
	120	No data	Day, harbour population	
<i>S. thersites</i>	240	No data	Winter and Summer	Branch 1988
<i>S. gigas</i>		Can be >3000		Levings & Garrity 1984
<i>B. obliquata</i>		About 2000		Borland 1950

exposed reduces desiccation, and in tropical species at least, not being active at high tide reduces the threat of predation (see previous discussion on predation).

Although the bouts of foraging activity of siphonariids are relatively fixed with respect to the day/night and tidal cycles, the time spent foraging, and distance moved can vary

with phase of the moon (Table 5). Studies on *S. normalis* and *S. alternata* (Cook & Cook 1978) and *S. japonica* (Hirano & Inaba 1980), species that are active when awash, revealed that limpets are usually active for longer and travel greater distances on a neap tide than on a spring tide (Table 5). This can be attributed to the longer period limpets spend awash during neap tides, i.e. their foraging window is greater. However, Cook & Cook (1978) found that at one of their study sites, where there was minimal difference in tidal amplitude, *S. normalis* exhibited no difference in foraging activities on a spring and neap tide. Similarly, *S. alternata* that were in pools were equally active on tides of different magnitudes. These findings suggest that moisture is an important factor in controlling the amount of time available for activity in limpets which forage when awash (Cook & Cook 1978). These authors also found some differences in activity on ebbing and rising tides. During neap and middle amplitude tides and all tides at more protected sites where water did not drain rapidly, the percentage of animals active was about the same on the ebb and flood. Towards spring tides, a greater percentage (40–80% more) of *S. normalis* were active on a rising tide, than an ebb. This is thought to be a response by the limpets to reduce exposure to dry conditions (Cook & Cook 1978). At yet another site where predation was more intense, the number of limpets active was greater on the ebb tide. Several other species show differences in activity patterns on ebb and flood tides (Table 3). Thus for limpets that are active while awash, the degree of activity on ebbing and rising tides within a species is labile, being controlled by both physical and biological factors. Patterns of activity can therefore be adjusted to suit local conditions.

By contrast, studies on *S. capensis* (Branch & Cherry 1985) and *S. concinna* (Gray & Hodgson 1997) revealed that these nocturnal, low tide, foragers travel further (often twice as far in *S. concinna*) and are active longer on a spring tide than on a neap (Table 5). Again this difference in activity can be linked to the time available for foraging. For low tide foragers it is the time exposed to air which dictates this, exposure being longer on a spring tide than a neap (Gray & Hodgson 1997). Due to their low tenacity, both *S. capensis* and *S. concinna* are limited to foraging while exposed. Thus, foraging excursions will be both shorter in time and distance on neap tides. However, not every siphonariid shows variation in time spent foraging and distance moved with the phase of the moon. No such relationship was found in *S. sirius* (Iwasaki 1995a). This is a low shore species that is active while submerged and awash and therefore there is probably very little difference in the time available for foraging between spring and neaps.

Limpet foraging can be regarded as a four phase cycle, beginning and ending with an inactive phase, with three phases of activity in between (for literature see Gray & Hodgson 1997). Activity commences with an outward phase during which the limpet moves away from the home scar/site relatively rapidly. This is followed by a slower foraging phase and a rapid homeward phase. In some patellogastropods feeding has been observed to be most intense during the middle phase of the cycle (Little & Stirling 1985, Evans & Williams 1991). There has been very little analysis of siphonariid activity to determine whether they behave in this way. Cook & Cook (1978) reported that during grazing, *S. alternata* and *S. normalis* move away from their home scars slowly, but return rapidly. Analysis of activity of *S. concinna* (Gray & Hodgson 1997) revealed that this species, like other limpets, had a four phase activity cycle (Fig. 15), although these authors were unable to determine whether feeding was more intense during the middle phases. Such behaviour may well be found in other siphonariids.

There have been very few studies that have made detailed investigations on the directionality of siphonariid foraging. Abe (1935, 1940) observed that *S. atra* and *S. japonica* did

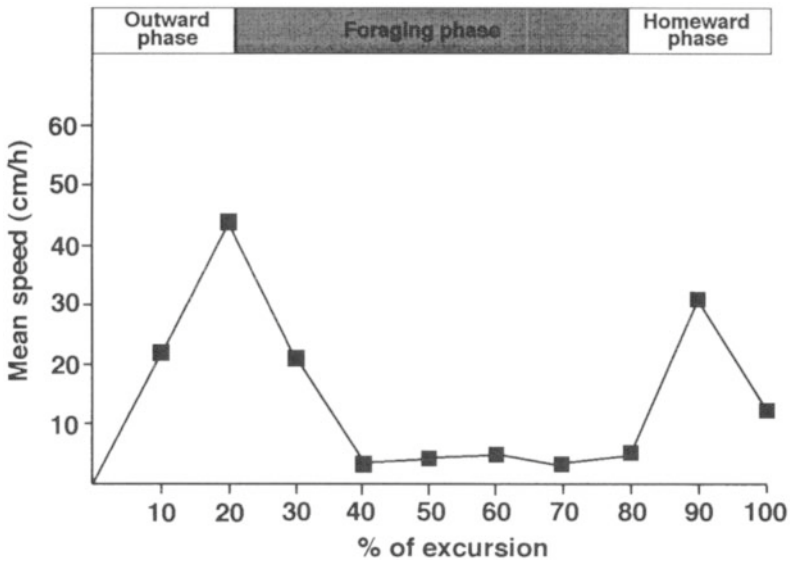


Figure 15 Mean speed of *S. concinna* ($n=20$) plotted against percentage of excursion period. (Redrawn from Gray & Hodgson 1997).

not forage in the same direction every day. Cook & Cook (1981) using circular statistical methods, determined that if *S. alternata* and *S. normalis* carried out two foraging excursions within four hours of each other, limpets would avoid moving in the same direction twice. If, however, foraging excursions were separated by more than four hours, the heading choice was random. These authors also analyzed statistically the data presented by Abe (1940) and found that in *S. japonica*, although movements appeared to be bipolar, foraging was uniformly distributed. More recently, Gray & Hodgson (1997) showed that foraging in *S. concinna* was highly directional, limpets having a mean upshore vector on spring and neap tides (Fig. 16). Furthermore, during the three months of the study, foraging direction did not alter significantly. Unfortunately these authors could not determine the reasons for this directionality although it was suggested that the foraging vector took limpets to an area of high food availability.

The rhythms of activity, while undoubtedly strongly influenced by exogenous factors, most probably have an endogenous component. Endogenous rhythms are a well established fact in many marine organisms (Palmer 1995), but such rhythms have only been demonstrated recently in patellogastropods (Della Santina & Naylor 1993, Gray & Hodgson 1999) and they remain to be proven in siphonariid limpets. There is some circumstantial evidence that endogenous rhythms may exist in siphonariids. In Bermuda, *S. alternata* occasionally anticipate the ebbing tide and begin to move while still covered by 10–15 cm of water (Cook 1976, Cook & Cook 1978). Such anticipation of the state of the tide is also seen in species that are active at low tide (*S. thersites*, *S. concinna*, *S. capensis*), which all return to their home sites or scars before being inundated by the rising tide. Although it has been suggested that such anticipation of the state of the tide is due to the detection of changes in hydrostatic pressure (*S. alternata*) or vibrations from wave activity (*S. concinna* and *S. capensis* and other limpets), an endogenous clock cannot be dismissed. Studies on endogenous rhythms in siphonariids clearly need to be undertaken and could prove rewarding.

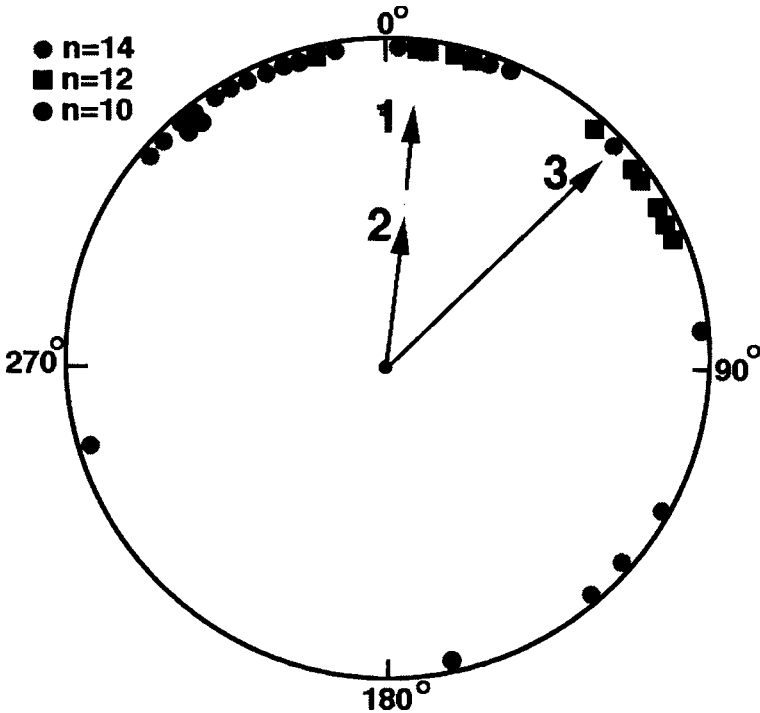


Figure 16 Foraging directions shown by *Siphonaria concinna* on a spring full moon (arrow 1; $\bar{x}=6.4^\circ$, $r=0.477$, $p < 0.05$), spring new moon (arrow 2; $\bar{x}=3.44^\circ$, $r=0.575$, $p < 0.05$) and neap quarter moon (arrow 3; $\bar{x}=48.6^\circ$, $r=0.894$, $p < 0.001$). Each point represents one excursion (gray circles—spring full moon; black squares—neap quarter moon; black circles—spring new moon); n , the number of excursions, r , is an estimate of the non-uniformity of the circular distributions given as mean vector lengths by the Raleigh test. (Redrawn from Gray & Hodgson 1997).

Homing

An integral facet of the activity rhythms of siphonariid limpets is their homing abilities. With the exception of *S. virgulata*, which tends to lack a scar particularly when it co-occurs with *Cellana* (Creese & Underwood 1982), *Siphonaria lessoni* (López Gappa et al. 1996) and *Kerguelenella lateralis* (Davenport & MacAlister 1996), all species studied home to either a fixed scar or site (such as a crevice) (Table 4, p.267). At the home scar the shell contours precisely match those of the rock. Site fidelity can be very high. Borland (1950) recorded *Benhamina obliquata* living in the mid-intertidal occupying the same scar for 3 yr (but note that high shore individuals homed to a crevice with no scar and there was no strong site fidelity). *Siphonaria concinna* can remain faithful to their home scars for at least 1 yr (A.N.Hodgson, pers. obs) and Garrity & Levings (1983) recorded that >90% of *S. gigas* remaining on the same scars over a 7-month period.

As well as the adaptive significance of homing (previously discussed), the mechanism of homing has intrigued researchers. How animals find their way back to these scars, even when artificially transplanted (Abe 1941, Cook 1969), is still equivocal. Cook (1969, 1971)

suggested four possible mechanisms for homing: (a) navigating by distance cues such as the position of the sun or moon, polarized light, coastal landmarks, sky brightness, or gravity; (b) dead-reckoning and retracing their outward trail (= reverse displacement); (c) topographical clues from the rock (= topographic memory); (d) chemical clues from mucous trails. While some species have been observed to retrace the outward mucous trails (e.g. *S. japonica*, *S. atra*, *S. siphonaria*, Abe 1935, 1940, 1941; *S. normalis*, *S. alternata*, Cook 1969; *S. capensis*, Branch 1981) some of these species and many others do not always do so. Nevertheless a series of experiments with *S. alternata* and *S. normalis* (Cook 1969, 1971, Cook & Cook 1975) provided strong evidence that limpets home using information from mucous trails. The limpets can not only detect their own trails but those of other conspecifics, and they can tell the polarity of the trail. Thomas (1973) found that *S. pectinata* can home using information from old trails. The information can be detected for 48–49 h after the trails have been laid down, but by 68–76 h limpets are unable to follow trail clues (Cook & Cook 1975). How individuals recognize their own trail from that of conspecifics, what chemicals are involved and how they are detected is not known. Although trail following is important for finding the home scar it cannot be the only mechanism, as many limpets can still home when trails have been physically or chemically removed (Branch 1981).

Interactions with other intertidal organisms—the role of siphonariids in intertidal communities

The interactions between marine organisms are varied, often complex and of major importance in any intertidal ecosystem. Because grazers play a pivotal role in structuring rocky shore communities, the interactions between these animals, their food, and predators, have received a great deal of attention (see Branch 1981, 1985, 1986, Lubchenco & Gaines 1981, Hawkins & Hartnoll 1983 for reviews). Studies on patellogastropods have been particularly noteworthy. Up until the late 1970s ecological information on siphonariid limpets was often incidental to the study in question. Furthermore, the majority of ecological investigations were from the northern hemisphere, particularly the north Atlantic, ecosystems where siphonariids are not common. In the northeast Atlantic siphonariids are only numerous as far north as Portugal (S.J.Hawkins, pers. comm.). More recently, there have been a greater number of ecological studies of rocky shores where siphonariids are abundant. Researchers have therefore sought to understand the role of these limpets.

Limpet—algal interactions

The radula of prosobranch limpets consists of a few large, highly mineralized teeth, which enable them to scrape and even excavate rocks for surface and endolithic microflora (Hawkins & Hartnoll 1983, Hawkins et al. 1989). Such grazing activity scrapes the rock clean. By contrast, the radula of siphonariids consist of rows (formula given as $-Y+R+-Y$) of small teeth (Fig. 17) which are all of a similar size (cusp length is usually $<35\ \mu\text{m}$) (e.g. Hubendick 1946, Allanson 1958, Jenkins 1981, Black et al. 1988, Iwasaki 1993b). Because the radular teeth of *Siphonaria* are relatively weak, it has been suggested that this restricts these limpets to feeding on foliose macroalgae (e.g. Underwood & Jernakoff 1981, Creese & Underwood 1982). Most studies on the diet of siphonariids report that they are indeed macroalgal grazers, although lichens, blue-green algae, microalgae and diatoms are often

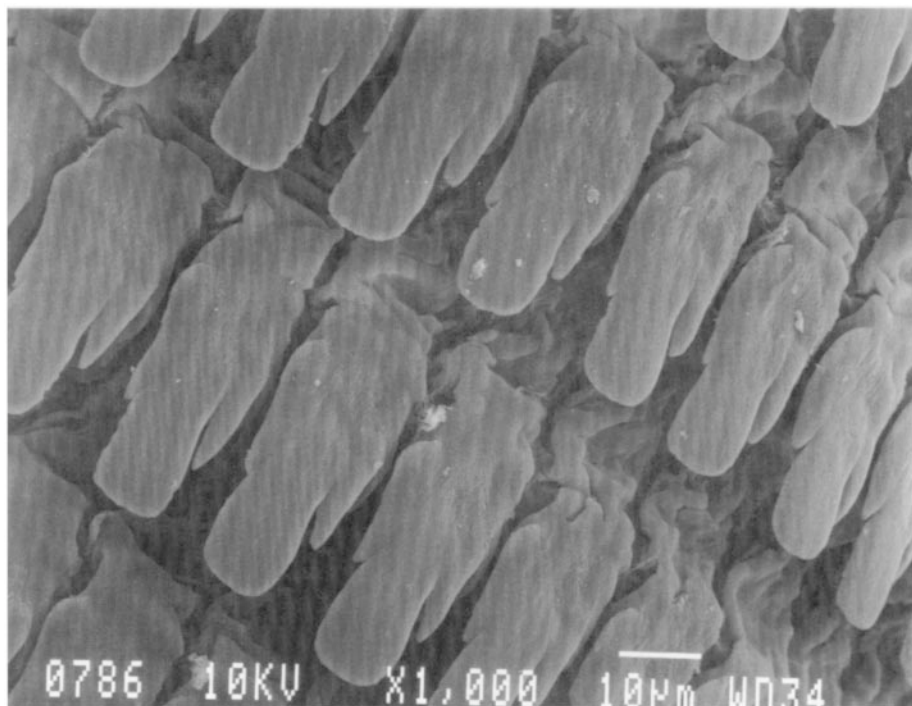


Figure 17 Scanning electron micrograph of the radula of *Siphonaria capensis*.

found in gut contents (Abe 1940, Allanson 1958, Borland 1950, Bastida et al. 1971, Simpson 1976, Underwood & Jernakoff 1981, Jara & Moreno 1984, Santilices & Correa 1985, Branch 1988, Quinn 1988a, Prasad et al. 1988, Iwasaki 1993b,c, Davenport 1997). Further evidence that siphonariids do not scrape the rock surface while feeding comes from estimates of the amount of inorganic material in the diet of these limpets. In a study of grazing in seven species of mollusc on Rottneest island, Black et al. (1979) found that *S. kurracheensis* has the lowest rate of egestion and smallest proportion of inorganic material (68.9%) in its faeces and unlike other grazers did not leave obvious signs of grazing activity. Iwasaki (1993c) also found that *S. sirius* had a significantly lower percentage of rock particles in the gut (0–3.6%) than *Cellana toreuma* (1.4–7.9%). Siphonariids can, however, excavate algae from softer rocks. The grazing activities of *Siphonaria pectinata* contribute to the erosion of calcarenite rock outcrops, the radula removing rock in places where rock-penetrating blue-green algae have softened the aragonite cementing material (Craig et al. 1969). It is probable, therefore, that the grazing activities of species such as *S. capensis*, which occurs in large densities on soft aeolian sandstone shores along the southeast coast of South Africa (A.N.Hodgson pers. obs.), also contributes to beach rock erosion.

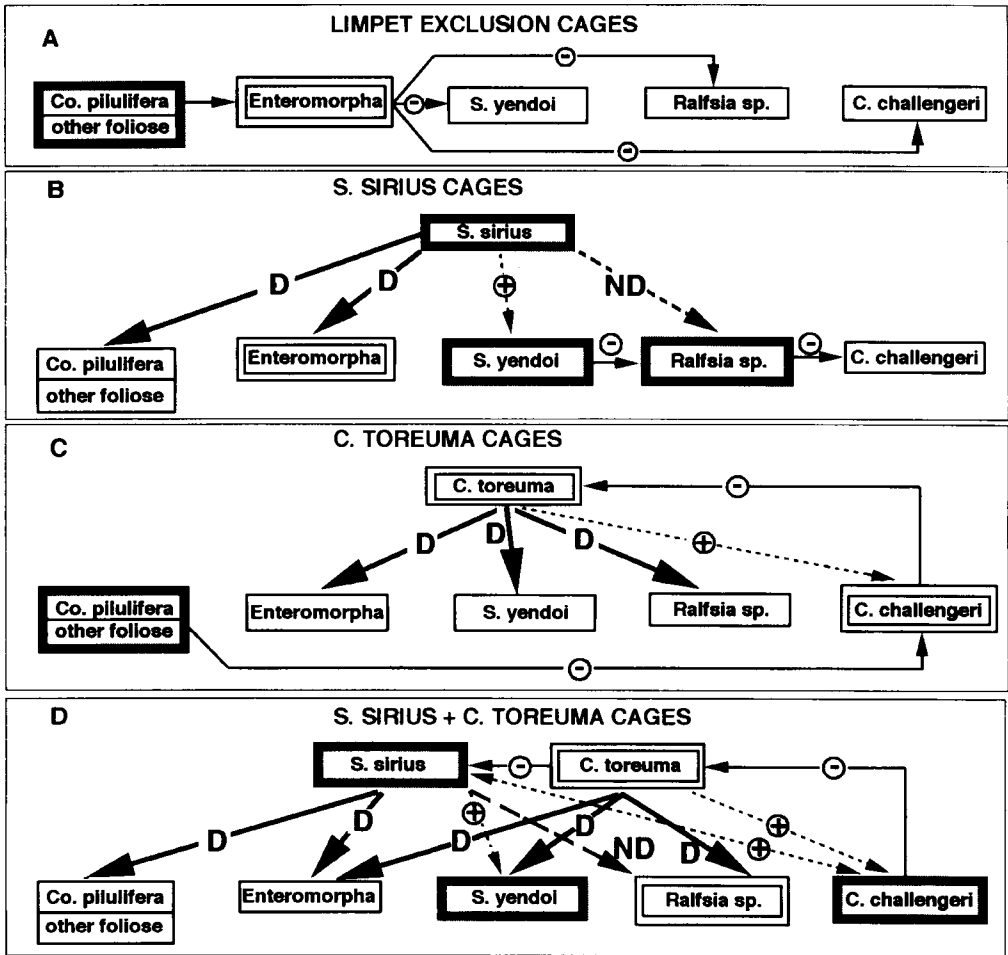
On some rocky shores, siphonariids appear to have very little impact on the structure of macroalgal densities or assemblages. Underwood & Jernakoff (1981) found that *S. denticulata* had no effect on reducing algal cover, even when limpet density was experimentally increased to five to ten times natural density. Algal cover was maintained because of the rapid regrowth of the thalli. These findings led to the suggestion that, unlike patellogastropods, siphonariids can only graze back existing macroalgae, which does not influence abundance (Branch 1986). While siphonariids may not be able to affect algae in the same way as patellogastropods,

they can interact with algae in other important ways. *S. lessoni* is important in the structuring of the macroalgal community on Chilean rocky shores. Limpets feed on the fronds of the red algae *Iridaea boryana* and in the presence of limpets the crustal form of the alga dominates. Grazing activity weakens the fronds which are then eliminated by wave action. This in turn permits the growth of the competitively inferior algae *Porphyra* and *Ulva* as well as the establishment of some ephemeral algae (*Petalonia* and *Scytosiphori*). Exclusion of *Siphonaria lessoni* from the shore results in *Iridaea boryana* retaining its fronds even during the winter storms (Jara & Moreno 1984). An algal canopy (>80% cover) of *I. boryana* develops with the result that other algae are excluded. Similarly the grazing activity of *Siphonaria thersites* damages the fronds of *Iridaea cornucopiae* and in summer nearly all blades of the alga are damaged (Branch 1988). Neither *Siphonaria lessoni* nor *S. thersites* graze at random; whereas the former species feeds preferentially on the reproductive structures (Jara & Moreno 1984), the latter has a preference for the infertile apical portions of the fronds where the cuticle is weakest (Branch 1988). The difference in feeding preference is probably a result of limpets feeding on the most palatable part of each species of alga.

The large tropical siphonariid, *S. gigas*, can influence the growth of encrusting algae (Levings & Garrity 1984). On the Pacific shores of Panama, the blue-green algal crust (*Schizothrix calcicoid*) is inversely related to the density of *Siphonaria gigas*. Experimental removal of this limpet resulted in an increase in blue-green algae on the shore and a decrease in the other encrusting alga *Ralfsia*, which is presumably out-competed by *Schizothrix* (Levings & Garrity 1984). A further effect of removing *Siphonaria gigas* is a decrease in the calcified morph of the blue-green alga and an increase in the fleshy-green morph. Levings & Garrity (1984) suggest that limpet grazing results in a phenotypic defensive response by *Schizothrix* in the form of calcification.

Some siphonariids are thought to promote the settlement, growth and survival of algae. Experiments by Iwasaki (1993b,d) indicated that *Siphonaria sirius* promotes settlement and growth in *Ralfsia*, and that the limpet might maintain *Ralfsia* crusts. When limpets were completely excluded from experimental quadrats, the development of coralline algae and then *Enteromorpha*, had a negative influence on the encrusting *Spongites yendoi* and *Ralfsia* (Fig. 18A). When *Siphonaria sirius* was present, although it was not able to prevent the seasonal growth of the algae *Spongites yendoi*, *Ralfsia* was able to become established (Fig. 18B). The limpet also contributed to the survival of algal crusts by removing the young thalli of foliose algae from the crusts. Mucous trails laid down by *Siphonaria* spp. also benefit algae, the trails trapping macroalgal propagules which therefore promotes their attachment and recruitment (Santelices & Bobadilla 1996, Davies & Hawkins 1998). The mucous trails probably also trap organic material and therefore act as a "fertilizer", promoting microbial growth (Davies & Hawkins 1998).

Algal abundance can in turn affect the growth rate and mortality of siphonariids. Voss (1959) noted that *S. pectinata* were larger at sites where *Enteromorpha* and *Ulva* were present. Similar findings were reported by Tablado et al. (1994) for *Siphonaria lessoni*, which were larger and grew 9.7 mm in 1 yr at a site where organic pollution had increased the amount of cyanophytes, diatoms and green algae. At an unpolluted site, the growth rate was only 6.2 mm in 2 yr. In an examination of population size structure, growth and mortality of *S. diemenensis*, Quinn (1988a) showed that higher shore limpets had a slower growth rate (summer to winter range 0.04–0.19 mm month⁻¹, 10mm animal) and higher mortality (39.59–53.40%) than animals living lower down the shore (growth=0.56–0.64 mm month⁻¹, 10 mm animals; mortality=33.64–39.16%). Quinn attributed the slower growth of high shore animals to food availability, which was very seasonal on the upper-shore.



Present in >30% cover at end of expt.
 Present in <30% cover or disappeared at end of expt.
 Absent on the substratum

← D Destructive grazing
- - - ND Non-destructive grazing
⊖ Negative effect
⊕ Positive effect

Figure 18 Diagrammatic representation of results of direct and indirect interactions between algae (*Corallina pilulifera*, *Enteromorpha* sp., *Spongites yendoii*, *Ralfsia* sp.), limpets (*Siphonaria sirius*, *Cellana toreuma*) and the barnacle (*Chthamalus challengeri*) from enclosure experiments. (Redrawn from Iwasaki 1993a, 1993d).

Mortality of upper-shore limpets (which was highest in summer) was thought to be caused by starvation, very little algae being present in summer. Seasonal differences in food abundance affecting growth rates of *Siphonaria* have also been reported by Creese (1981, *S. denticulata* and *S. virgulata*, maximum growth in autumn) and Liu (1994, *S. japonica*, maximum growth in winter). In *S. lessoni* macroalgal growth has been found to set the lower limit of zonation of this limpet. Bastida et al. (1971) observed that the limpets were unable to move lower than the edge of the algae. Despite intense grazing, algal growth and

re-population were of a rate high enough to keep the limpets at bay. When the algal zone was lowered experimentally, the limpets were able to migrate further down.

The presence of algae can promote the recruitment of *Siphonaria* to some shores. One week after flooding of the Orange river on the west coast of South Africa, mats of *Ulva* and *Enteromorpha* proliferated in the lower and mid-intertidal, a result of the death of grazers. Two months later massive recruitment of *Siphonaria serrata* (= *aspera*) was recorded, presumably stimulated by the presence of these algae. Shortly after recruitment, however, numbers of *S. serrata* were reduced, thought to be a result of the algae trapping sediment which smothered many of the limpets (Branch et al. 1990). Branch et al. (1990) concluded that there were some interactions between the algal mats and *Siphonaria*.

Intra- and inter-specific interactions

A number of authors have shown that there is a negative correlation between growth rate, size or body weight, and density in *Siphonaria* spp. (Olivier & Penchaszadeh 1968, Ortega 1985, Iwasaki 1993b, Lasiak & White 1993) (Fig. 19). As might be expected, high densities of conspecifics lead to competition for food and/or space. A possible consequence of competition would be the evolution of territoriality. A number of species of patellogastropod are territorial, defending a garden of algae against conspecifics and other grazers (Branch 1981). Such strict territoriality has not been observed in siphonariids although aggressive competition for food resources has been reported recently in *S. sirius* (Iwasaki 1993c, 1995b). Iwasaki observed that during foraging excursions these low shore limpets can enter into pushing competitions and that a dominance hierarchy existed between limpets. Lower dominance limpets generally lost pushing contests and as a consequence tended to shift resting

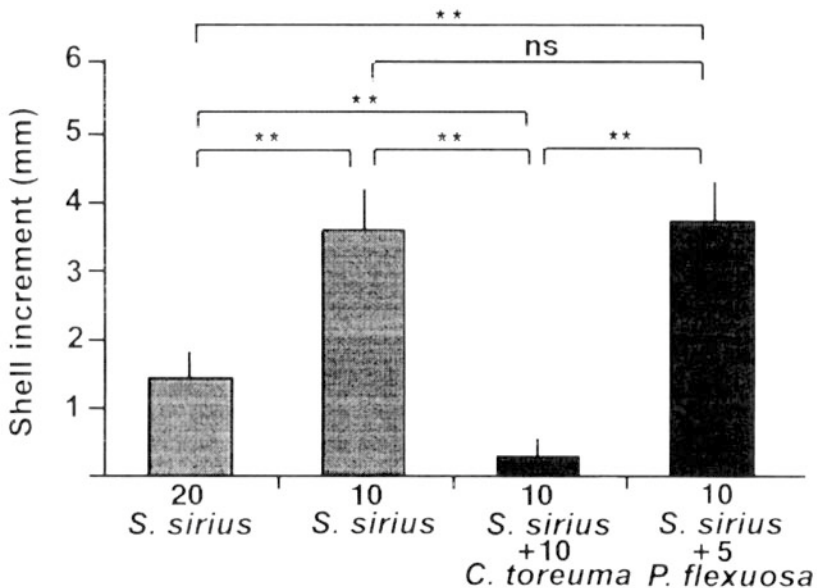


Figure 19 Comparisons of the growth rate (expressed as mean shell increment \pm so) of *Siphonaria sirius* from April to August 1983 when caged in different densities and with *Cellana toreuma* and *Patella flexuosa*. **=significantly different at 1%; ns=not significant at 5%. (Redrawn from Iwasaki 1993a).

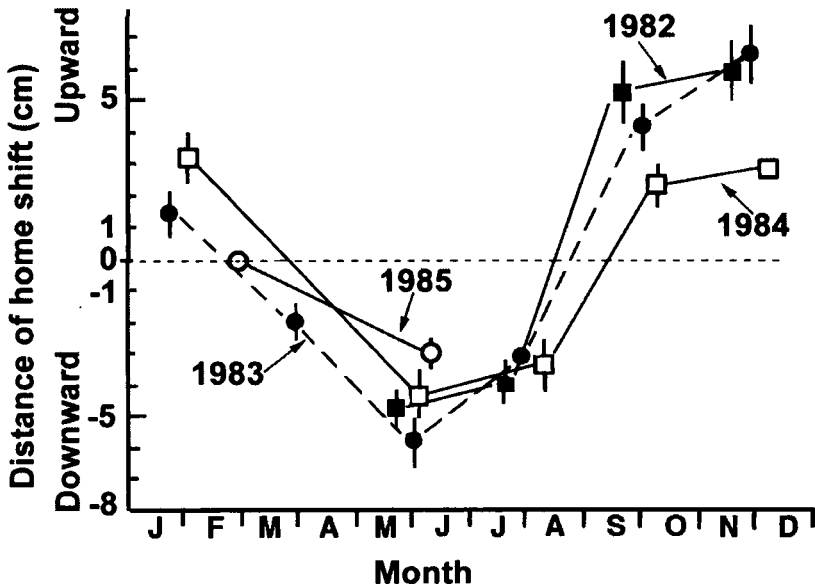


Figure 20 Bimonthly change in mean distance (in vertical direction) of home shift by *Siphonaria sirius*. Distance of upward home shift is expressed as a plus value, and that of downward shift as a minus value. Vertical bars indicate standard errors. (Redrawn from Iwasaki 1995b).

sites. The direction of shift varied with season, limpets moving in an upshore direction in winter and downshore in summer (Fig. 20).

On many shores, species of *Siphonaria* co-occur with other grazing gastropods, including patellogastropods and keyhole limpets (Fissurellidae). Although the food of siphonariids may be different to these other grazers, competitive interactions still occur. Black (1979) found that on Rottneest Island, *S. kurracheensis* had a bimodal distribution up the shore, with high densities towards the top and bottom of the intertidal and lower densities in the middle of the shore. Allozyme electrophoresis revealed that the high and low populations of this limpet were conspecific (Black & Johnson 1981). By contrast, the patellogastropod *Collisella* (= *Notoacmaea*) *onychitis*, was most abundant in the middle of the shore. Removal of *C. onychitis* resulted in the establishment of large numbers of *Siphonaria kurracheensis* suggesting that the former species was excluding the latter. *Collisella* later became reestablished after recruitment (Black et al. 1988). The inferior competitive ability of *Siphonaria* spp. has also been demonstrated on the southeast coast of Australia (*S. denticulata* and *S. virgulata*, Creese & Underwood 1982), in Japan (*S. sirius*, Iwasaki 1993b) and South Africa (*S. concinna*, Lasiak & White 1993) which are all out-competed by cellanid limpets. When enclosed with *Cellana* spp. all the above species had a reduced growth rate (e.g. Fig. 19) and increased mortality (except for *Siphonaria concinna*), but *Siphonaria* never had any negative effects on *Cellana* spp. Creese & Underwood (1982) concluded that the competitive superiority of *Cellana* was a result of its ability to exploit food before it became available to *Siphonaria*. Lasiak & White (1993) also found that *Cellana capensis* could seriously deplete, but not completely eliminate, food resources for *Siphonaria concinna*. Thus in the presence of *C. capensis* there was enough food for the survival of *S. concinna* but not enough for growth. Despite the competitive inferiority of *Siphonaria*,

Creese & Underwood (1982) found that *Cellana* was never able to completely eliminate *Siphonaria* from experimental enclosures. Possible explanations for this is the ability of *Siphonaria* to feed on the foliose algae on the shells of the cellanid limpets, and to feed opportunistically moving into areas where foliose algae have become more abundant. A further reason, however, is that intraspecific competition within *Cellana* is more intense than interspecific competition. Because of the intraspecific effects, *Cellana* never reaches large enough densities to eliminate *Siphonaria*. Siphonariids can also be out-competed for food by keyhole limpets, e.g. on some rocky shores in southern Chile where *S. lessoni* is out-competed by *Fissurella picta* (Moreno et al. 1984). Removal of keyhole limpets (by humans for food) results in an increase in the abundance of the algae *Iridaea boryana*, which in turn increases the growth rate, size and reproductive output of *Siphonaria lessoni*, but not density (Moreno et al. 1984, Godoy & Moreno 1989).

The competitive inferiority of *Siphonaria* is not always as marked and in some cases *Siphonaria* can exhibit dominance. Iwasaki (1993b), for example, found no evidence (i.e. increased mortality or reduction in growth rate) for interspecific competition between *Patella flexuosa* and *Siphonaria sirius* (Fig. 19). Ortega (1985) suggested that *S. gigas* was competitively inferior to *Fissurella virescens*, as in the presence of the keyhole limpet the body weight of *Siphonaria gigas* was usually lower, but there was no reciprocal effect. Garrity & Levings (1985), however, noted that Ortega's results also revealed that under some conditions *S. gigas* negatively affected the abundance of the fissurellid and vice versa. Because the interspecific effects of the fissurellid on the weight of *S. gigas* were less than the intraspecific effect of *S. gigas* on itself, interspecific interactions were thought to be small. Finally, a study of the interactions between *Lottia stipulata* and *Siphonaria gigas* on andesite and basalt shores of Panama revealed that the siphonarian negatively affected recruitment, abundance and growth of the prosobranch limpet (Garrity & Levings 1985). The interaction is one way as *Lottia* had no apparent effect on *Siphonaria gigas*.

In most of the above studies competitive inferiority or superiority has been attributed to the structure of the radula, the prosobranch radula with its large mineralized teeth being competitively superior to that of the fine-toothed pulmonate radula (Creese & Underwood 1982, Black et al. 1988). Where the excavating ability of the cusps are close (e.g. *Siphonaria* and *Fissurella*), or the rock type is such that it is not easy for prosobranchs to excavate (e.g. the andesite and basalt shores of Panama), the outcome of the interactions may be unpredictable or the pulmonate might be superior (Black et al. 1988). It has been suggested also that the outcomes observed are size related (Garrity & Levings 1985, Branch & Moreno 1994). Because *Siphonaria gigas* is a very large limpet, it has the ability to interfere with feeding by *Lottia* and/or bulldozes or consumes newly settled individuals. Thus an explanation based on competition need not be invoked (Garrity & Levings 1985). When limpets are of a similar size the outcome of the interaction would be more unpredictable.

Siphonaria has also been shown to interact with barnacles. Voss (1959) noted that although *S. pectinata* has a wide intertidal distribution it was most abundant above and below the barnacles, suggesting that there is some competition for space. The potential impact of barnacles on *Siphonaria* spp. was demonstrated by Sutherland & Ortega (1986) when they were able to observe a massive recruitment of *Chthamalus fissus* to their study site in Costa Rica in November and December 1983. *Siphonaria gigas* which were surrounded by barnacles were about 29% lighter, most probably a result of the barnacles effectively imprisoning limpets, which restricted their foraging. Limpets recovered weight after barnacle density had been reduced by the predator *Acanthina brevidentata*. The limpets were found to have very little effect on the barnacles. Thus in Costa Rica, *Siphonaria gigas*

was negatively affected by large numbers of barnacles, but benefited indirectly from predation by *Acanthina brevidentata* on barnacles. Using shell microgrowth banding, Crisp et al. (1990), confirmed the reduced growth rate of *Siphonaria gigas* in the presence of barnacles, calculating a reduction of about 24%. The interaction between *S. gigas* and barnacles is not necessarily one way, Levings & Garrity (1984) showing that on Panamanian shores, recruitment of barnacles is less in areas or rock subjected to limpet grazing.

Barnacle recruitment and survival may be promoted by the grazing activities of siphonariids. Bastida et al. (1971) found that the barnacle *Balanus amphitrite* only became established on experimental fouling plates once they have been grazed by *Siphonaria lessoni*. These findings have implications for the control of marine fouling as, although *S. lessoni* does not damage marine structures directly, it promotes growth of barnacles, which are destructive (Bastida et al. 1971). Work by Iwasaki (1993b,d) has shown that the survival of the barnacle *Chthamalus challengerii* requires the presence of at least two limpet grazers. When caged on its own, *Cellana toreuma* scraped the rocks clean of algae, which in turn allowed the settlement of the barnacle *Chthamalus challengerii*. The development of barnacles in turn restricted the feeding of the cellanid limpets within 4 months (Fig. 18C, p.281). Algae then became re-established which smothered and killed the barnacles (Fig. 18C). However, when cages contained both *Cellana toreuma* and *Siphonaria sirius*, the barnacles were able to survive to maturity. The grazing of the cellanid provided the barnacle with settlement space and the siphonariid consumed the foliose algae growing on or among the barnacles (Fig. 18D). Iwasaki (1993b,d) therefore explained the survival of the barnacle as being brought about by "synergism of the double indirect positive effects of two limpet species on the barnacle". Other grazers can also benefit from the grazing activities of siphonariids. Exclusion of *S. diemenensis* from experimental cages in winter/spring had a negative effect on the body weights of the trochid, *Austrocochlea constricta* (Quinn & Ryan 1989). This result is explained by the fact that the trochid requires another grazer, such as a siphonariid, to remove foliose algae so that it can obtain suitable microalgal food.

Reproduction and life histories

Siphonariid limpets are all hermaphrodites and monaulic (common opening to male and female reproductive tracts). The gross anatomy of their reproductive system has been described in detail by a number of workers (e.g. Hutton 1882, Köhler 1893, Cottrell 1910, Hubendick 1946, 1947, 1978, McAlpine 1952, Allanson 1959, Marcus & Marcus 1960, Simpson 1977, Berry 1977, Jenkins 1981, 1983, 1984). Although there are some anatomical differences between species (see Hubendick 1947, McAlpine 1952, Allanson 1959, Jenkins, 1981, 1983, 1984 for examples), the reproductive system of all siphonariids is essentially similar. There is a discrete apically located ovotestis which contains a number of acini in which gametes develop. The gonad is connected to the spermooviduct by a hermaphrodite duct, anterior to which is a seminal vesicle. Anteriorly, the hermaphrodite duct is joined by a duct from a glandular region which contains the albumen gland. These then join the spermooviduct, which has a simple lumen without separate male and female tracts. The spermooviduct opens into a genital atrium which has a single common genital opening on the right side of the body. Also opening into the atrium next to the spermooviduct is the duct of the bursa copulatrix. Finally, leading from the genital atrium are organs that are associated with spermatophore production and mating. These organs consist of an epiphallus duct, the male copulatory organ and a glandular region which secretes the material to form the spermatophores. The simplest terminal

copulatory organ is found in *Siphonaria lessoni* and *Williamia vernalis*. In other species there may be a stylet (e.g. *Siphonaria laeviuscula*) or a flagellum (e.g. *S. atra*, *S. cookiana*, *S. gigas*) which may bear a simple penis (Berry 1977).

Gametogenesis

A number of authors have suggested that siphonariids are protandrous hermaphrodites (e.g. Creese 1980a, citing Hubendick 1947). Protandric development has, however, only been observed in two species *S. hispida* and *S. pectinata* (Marcus & Marcus 1960, Zischke 1974). In the former species, spermatozoa are first produced in individuals with a shell height of 5 mm, oocytes developing when animals reach a shell height of 7 mm (Marcus & Marcus 1960). Similarly, in *S. pectinata*, animals become males at about 110 days old, only producing eggs at 140–170 days old. Most of the large limpets (20mm shell length) are female (Zischke 1974). Thus, whether protandric development is typical for *Siphonaria* remains to be established but it is likely that most species become reproductively active in their first or second year (e.g. *S. pectinata* and *S. alternata* sexual maturity is reached within the first year, Zischke 1974; *S. denticulata* and *S. gigas* begin to reproduce in their second, Creese 1980a, Levings & Garrity 1986).

As there are no published studies on seasonality of gametogenesis of any species of *Siphonaria* it is not possible to comment on seasonality of protandry. Eggs and sperm have been observed to be present simultaneously within the acini of the gonad of some species (Marcus & Marcus 1960, Berry 1977, Simpson 1977, Hodgson et al. 1991) (Fig. 21). In *S. hispida* and *S. exigua* the oocytes occur more to the periphery of the gonad and spermatozoa nearer the centre (Marcus & Marcus 1960, Berry 1977).

Gametogenesis may be seasonal in species that have annual spawning rhythms (Table 6), although Creese (1980a) found that *S. denticulata* and *S. virgulata* had mature eggs at most

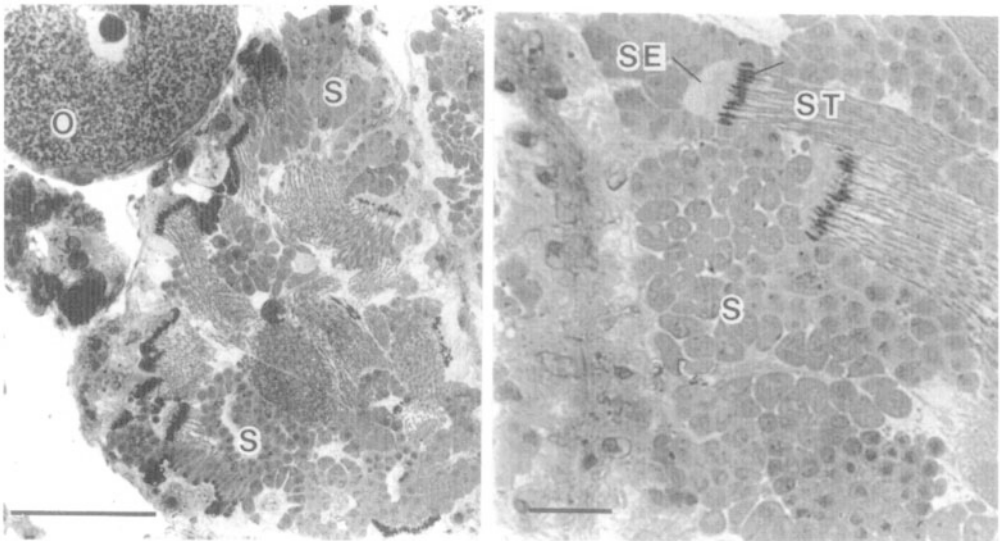


Figure 21 Light micrograph sections through the gonad of *Siphonaria capensis* showing some stages of spermatogenesis (S, spermatocytes and early spermatids; SE, Sertoli cell; ST, late spermatids with developed tails and mid-pieces) and an oocyte (O). Scale bars=0.1 mm. (From Hodgson et al. 1991).

Table 6 Period of spawning of *Siphonaria* spp.

Species	Locality	Spawning period	References
NORTHERN HEMISPHERE			
<i>S. thersites</i>	NW USA (48°30'N)	Spring	Strathmann 1987
<i>S. japonica</i>	Japan (40°54'N)	April to July (spring-early summer)	Abe 1940
	Japan (34°22'N)	Mid-March to July	Hirano 1980
<i>S. sirius</i>	Japan (33°42'N)	May-August (spring-summer)	Iwasaki 1993a
<i>S. alternata</i>	Florida, USA (25°02'N)	All year, peak in February, March	Zischke 1974
<i>S. pectinata</i>	Florida, USA (25°N)	December to March (winter)	Voss 1959
		September to May (autumn to spring), peaking December/January	Zischke 1974
<i>S. gigas</i>	Algeria (36°N)	October to June (autumn to early summer)	Dieuzeide 1935
<i>S. atra</i>	Panama (8°N)	All year	Levings & Garrity 1986
	Palau (7°N)	September to February?	Abe 1941
SOUTHERN HEMISPHERE			
<i>S. hispida</i>	Brazil (23°27'S)	All year	Marcus & Marcus 1960
<i>S. lessoni</i>	Argentina (38°03'S)	June to March (winter to summer)	Olivier & Penchaszadeh 1968
<i>S. denticulata</i>	Sydney, Australia (34°S)	November/December to April/May (summer to autumn)	Creese 1980a
<i>S. diemenensis</i>	Victoria, Australia (38°S)	September to April (spring to autumn)	Quinn 1988b
<i>S. tasmanica</i>	Victoria, Australia (38°S)	January and February (summer)	Quinn 1983
<i>S. jeanae</i>	S.W. Australia (32°S)	Onset of reproduction in late autumn	Johnson & Black 1984a, b
<i>S. concinna</i>	South Africa (35°S)	All year, peaks September to January (summer)	Chambers 1994
<i>S. serrata</i>	South Africa (35°S)	All year, peaks November to February (summer)	Chambers 1994
<i>Benhamina obliquata</i>	Otago, New Zealand (45°S)	Late October to early March (spring to summer)	Borland 1950
<i>Kerguelnella. lateralis</i>	Macquarie Island (54°38'S)	All year, possible increase frequency in summer	Simpson 1977

times of the year even though they spawn from summer to autumn only. In those tropical and sub-Antarctic species where spawning occurs all year round (Table 6), sperm and eggs are probably produced continuously or at frequent intervals. Marcus & Marcus (1960) observed that whereas spermatogenesis was continuous in the year round breeder *S. hispida*, oocyte production was more intermittent.

Spermatozoon morphology and spermatogenesis

Siphonariids have internal fertilization, and the spermatozoa (Figs 22, 23) are of the intro-sperm type (Healy 1983, Sumikawa & Funakoshi 1984, Azevedo & Corral 1985, Hodgson et al. 1991). The spermatozoa of the seven species described to date are structurally very similar, although Hodgson et al. (1991) showed that there were morphometric differences between species. Depending on the species, spermatozoa are 500–800 μm long and consist of a head region, mid-piece and tail. The head, which is about 6 μm long, contains a short nucleus (4–6 μm long) which is capped by a small acrosome (about 1 μm long). The

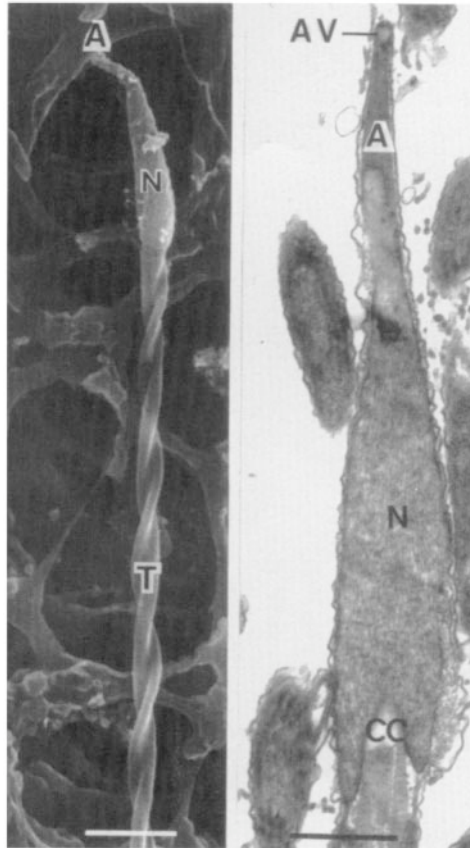


Figure 22 Scanning (left) and transmission (right) electron micrographs of longitudinal sections through the sperm head and mid-piece/tail (T) of *Siphonaria capensis* (left) and *S. serrata* (right). A, acrosome; AV, acrosomal vesicle; CC, centriolar complex; N, nucleus. Scale bars: left=2 μm ; right=1 μm . (TEM from Hodgson et al. 1991).

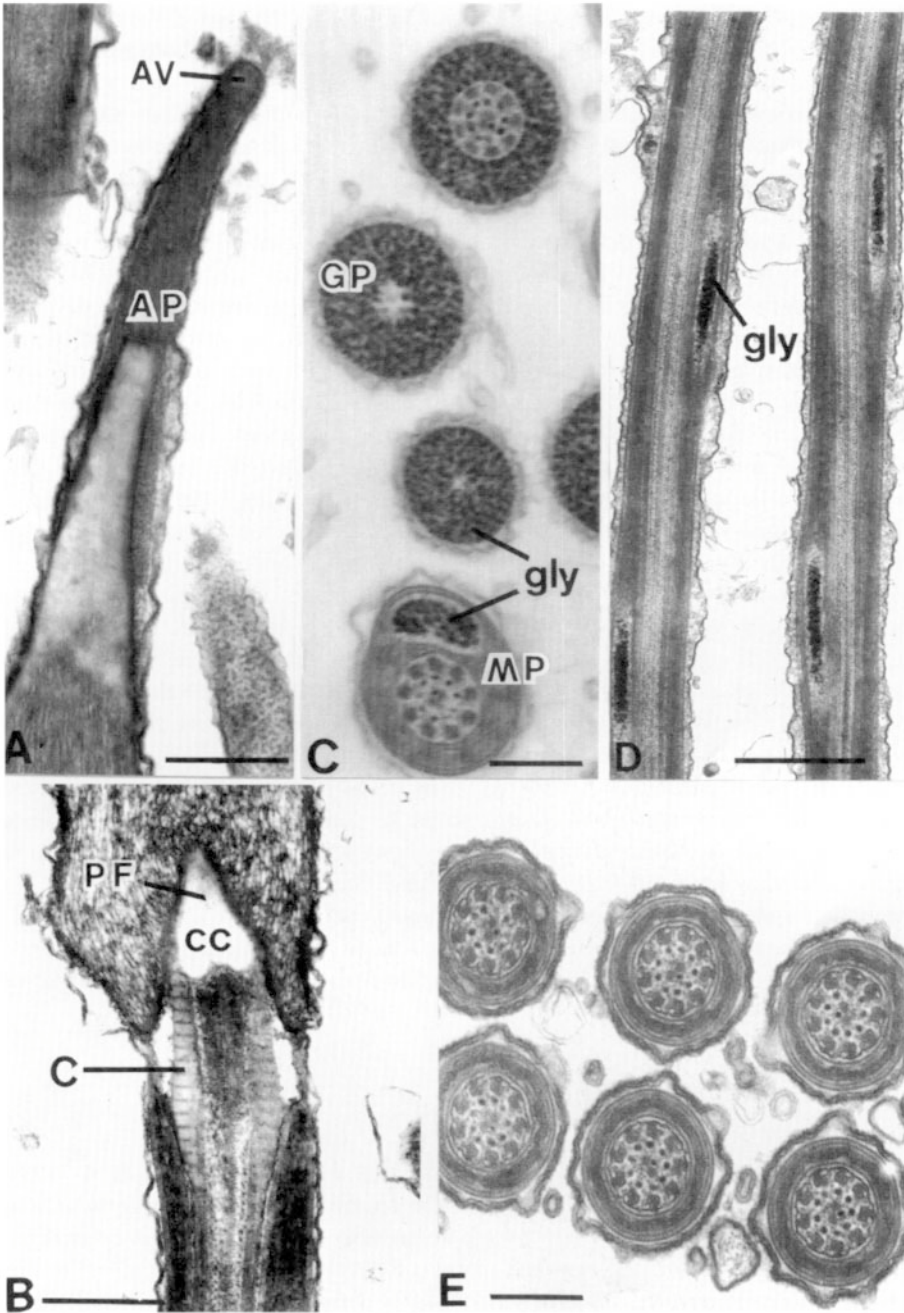


Figure 23 Transmission electron micrographs of longitudinal and transverse sections through the spermatozoa of *Siphonaria capensis*. A, longitudinal section of the acrosome showing acrosomal vesicle (AV) and pedestal (AP). B, base of the nucleus showing centriolar complex (cc) housed within the nuclear fossa (PF). Note also the striated columns (C). Transverse (C) and longitudinal (D) sections of a portion of the mid-piece (MP) and glycogen (GP) stained to show distribution of glycogen (gly). E, sections cut towards the end of mid-pieces. Scale bars: a=0.5 μm ; b-d, e=0.25 μm ; d=1 μm . (From Hodgson et al. 1991).

acrosome comprises an acrosomal pedestal which ensheathes the apex of the nucleus, and an apical vesicle. The nucleus is invaginated posteriorly, the invagination housing the centriolar apparatus. In addition to the 9+2 axoneme, nine periodically banded coarse fibres, which ensheath the axoneme, emerge from the centriolar plug. The mid-piece has a mitochondrial derivative that surrounds a single glycogen helix (which spirals along the axoneme), coarse fibres and axoneme (Fig. 23). Posterior to the mid-piece is a glycogen piece (about 60 μm long) and at the junction of the two a dense ring structure.

Spermatogenesis has been described in detail for four species of *Siphonaria* by Hodgson et al. (1991), the process being similar to that of other pulmonates (see Maxwell 1983, Geraerts & loose 1984 for reviews). A brief description only is given here. Spermatogonia develop next to the wall of the gonadal acini. As spermatogenesis proceeds spermatocytes and spermatids are gradually displaced towards the centre of the lumen of each acinus. Spermiogenesis involves a radical morphological transformation of spermatids. Early spermatids are characterized by a spheroidal nucleus with chromatin scattered throughout. The cytoplasm possesses numerous small mitochondria with lamellar cristae, well developed smooth endoplasmic reticulum and a large Golgi body with up to 19 cisternae. This latter organelle produces small proacrosomal vesicles which eventually form the acrosome. As maturation proceeds, the nucleus gradually assumes its more elongate shape, and the chromatin begins to condense, first becoming granular then fibrous and finally lamellar in appearance before condensing completely. Within the cytoplasm the mitochondria accumulate at the presumptive posterior of the cell where they fuse to form a mitochondrial derivative. The mitochondrial derivative as it develops encircles a small region of cytoplasm around the elongating axoneme. As the axoneme elongates cytoplasm along with the mitochondrial derivative migrates along it. Cytoplasmic migration halts at the junction of the mid-piece and glycogen piece, a region demarcated by a distinct annulus. Anteriorly, the proacrosomal vesicles coalesce and the single resultant vesicle become positioned anterior to the nucleus. Although the glycogen piece of the tail forms in the ovotestis, glycogen is only deposited in the glycogen compartment of the sperm after they have left the gonad and reached the hermaphrodite duct.

Throughout spermatogenesis, groups of developing spermatids are closely associated with Sertoli cells. The function of the Sertoli cells has still to be determined in these pulmonates but it is assumed that they play a similar role to that found in other animals (Hodgson et al. 1991).

Oogenesis

There are no published descriptions of oogenesis in *Siphonaria*. Hodgson et al. (1991), in a study of spermatogenesis of four South African species, noted that the gonadal acini, in addition to containing stages of sperm development, also contained some oocytes (Fig. 21). Therefore like other pulmonates, eggs and sperm can develop in the same acinus. Presumably aspects of siphonariid oogenesis is very similar to that described for other basommatophorans (see Berry 1977, Maxwell 1983, Geraerts & Joose 1984 for reviews). However, in some species large eggs (>300 μm in diameter) are formed that hatch into crawling larvae, whereas in others the eggs are small (70–100 μm in diameter) and develop into planktotrophic veliger larvae (Table 7). Oogenesis and vitellogenesis can be very different in closely related marine invertebrates with different life history strategies (see Eckelbarger 1994 for review). It is therefore possible that there are different mechanisms of egg development in siphonariid limpets with different life history strategies.

Table 7 Summary of the vertical distribution and developmental characteristics of some species of *Siphonaria*, *Kerguelenella* and *Benhamina*. nd, no data.

Species	Locality	Intertidal range	Egg size (µm)	Egg capsule size (µm)	Egg mass form	Fecundity (eggs/egg case)	Hatching time (days)	References
DIRECT DEVELOPMENT								
<i>S. annea</i>	South Africa	Mid-high	nd	433 × 307	Collar	350–450	15–20	Chambers & McQuaid 1994a,b
<i>S. serrata</i>	South Africa	Mid	nd	484 × 348	Collar	1000–2500	20–28	Chambers & McQuaid 1994a,b
<i>S. compressa</i>	South Africa	Mid	nd	nd	Capsule	25–50	nd	Chambers & McQuaid 1994a,b
<i>S. dayi</i>	South Africa	Mid-high	nd	472 × 349	Collar	400–500	15–20	Chambers & McQuaid 1994a,b
<i>S. nigerrima</i>	South Africa	High	nd	440 × 304	Collar	200–300	15–20	Chambers & McQuaid 1994a,b
<i>S. tenuicostulata</i>	South Africa	High	nd	474 × 346	Collar	250–350	15–20	Chambers & McQuaid 1994a,b
<i>S. karracheensis</i>	Persian Gulf	High	nd	500 × 380	Collar	Hundreds	nd	Thorson 1940
<i>S. thersites</i>	NW USA	High	150–162	1650 × 1200	Low cone	nd	34	Strathmann 1987
<i>K. lateralis</i>	Maquarie Is.	High	1260	1350 × 2000	Small egg mass	13–55	nd	Simpson 1977, Simpson & Harrington 1985
<i>K. stewartiana</i>	Stewart Is.	Supra-littoral	nd	1260 × ?	Small egg mass	9–35	nd	Knox 1955
PLANKTONIC DEVELOPMENT								
<i>S. capensis</i>	South Africa	Mid-high	nd	200 × 150	Ribbon	20 000	4–5	Chambers & McQuaid 1994a,b
<i>S. concinna</i>	South Africa	Mid	nd	265 × 198	Coil	>30 000	5–6	Chambers & McQuaid 1994a,b
<i>S. oculus</i>	South Africa	Mid	nd	259 × 187	Coil	>30 000	5–6	Chambers & McQuaid 1994a,b
<i>S. atra</i>	Palao	Mid	65–85	190 × 160	Coil	9000–20 500	4–5	Abe 1940, 1941

Table 7 continued

Species	Locality	Intertidal range	Egg size (μm)	Egg capsule size (μm)	Egg mass form	Fecundity (eggs/egg case)	Hatching time (days)	References
<i>S. baconi</i>	Australia	Mid	96	206 \times 156	Collar	nd	13–16	Mapstone 1978, Jenkins 1981
<i>S. denticulata</i>	Australia	Low-mid	100	200 \times 160	Coil	12 000–26 800	6	Anderson 1965, Creese 1980a
<i>S. diemenensis</i>	Australia	Mid-high	86	159 \times 125	Collar-Coil	nd	7–10	Mapstone 1978
<i>S. gigas</i>	Panama	Mid	nd	nd	Coil	75 000	7	Levings & Garrity 1986
<i>S. japonica</i>	N Japan	Mid	87–91	273 \times 154	Coil	Thousands	15–20	Abe 1940, Simpson & Harrington 1985
<i>S. lessoni</i>	Argentina	Mid-high	nd	216 \times 175	Coil	20 000–80 000	8–9	Olivier & Penchaszadeh 1968, Berry 1977
<i>S. pectinata</i>	USA Algeria	Mid Mid	100 nd	190 \times 150 nd	Collar nd	1680–8400 nd	17 20	Voss 1959, Zischke 1974 Voss 1959
<i>S. sipho</i>	Persian Gulf	Low-mid	95	250 \times 170	Coil	Thousands	14	Thorson 1940
<i>S. tasmanica</i>	Australia	High	95	159 \times 130	Collar	Thousands	6	Quinn 1983, Simpson & Harrington 1985
<i>S. virgulata</i>	Australia	High	100	200 \times 160	Ribbon	9200	6	Creese 1980a
<i>S. laciniosa</i>	Gulf of Aqaba	Mid	nd	nd	Ribbon	nd	nd	Hulings 1985
<i>S. sirius</i>	Japan	Low	nd	nd	Ribbon	nd	6–7	Iwasaki 1994
<i>B. obliquata</i>	New Zealand	Throughout but > mid-high littoral	nd	nd	Coil	45 000–190 000	nd	Cottrell 1910, Borland 1950, Mestayer 1920
SWIMMING/CRAWLING								
<i>S. alternata</i>	USA	Mid	150	150 \times ?	nd	280–760	15	Zischke 1974
<i>S. hispida</i>	Brazil	Mid	150	500 \times 300	Collar-Coil	2000	nd	Marcus & Marcus 1960

Note: Abe (1940) gives egg size of *S. australis* (= zelandica) and *S. lepida* as 67 & 100 μm respectively and egg capsules of *S. australis* of 180 \times 100 μm .

Copulatory behaviour

For copulation to occur, animals must first find a mate and this is probably facilitated in a number of ways. Some species naturally occur in high densities on the shore (e.g. *S. lessoni* can reach densities of 3676 m⁻², Olivier & Penchaszadeh 1968; *S. normalis* >3000 m⁻², Menge 1973) and in these conditions mate encounters are presumably high. Other species often have a clumped distribution (e.g. *S. concinna*, *S. capensis*, *S. serrata* on South African shores, Allanson 1958, Gray & Hodgson 1997, A.N.Hodgson pers. obs.), which again could increase the probability of finding a mate. *Benhamina obliquata* congregates in large groups in sheltered rock crevices at the onset of the breeding season, animals remaining congregated during the summer, after which they disperse (Borland 1950). Creese (1980a) has also observed *Siphonaria denticulata* aggregating in groups of up to 20 individuals during the reproductive season, some animals within the group copulating. Trail following may also be important in mate finding in a number of species. Hirano & Inaba (1980) have shown that in *S. japonica* some limpets upon crossing the trail of another will actively pursue it to initiate copulation. Whether siphonariids have any form of mate selection is not known. The observation that *S. gigas* mates with its nearest neighbour (Levings & Garrity 1986) suggests that in this species at least, there is no mate choice, it is simply a case of proximity.

Once a mate has been found, the two animals become orientated so that their heads are facing and the genital apertures are in contact (Abe 1940, 1941, Borland 1950, Hirano & Inaba 1980). In *S. japonica*, the "pursuer" also pushes its body underneath the shell of the "leader" (Hirano & Inaba 1980). Sperm transfer occurs by eversion of the copulatory organ, which becomes enlarged (Marcus & Marcus 1960), and insertion of the copulatory organ, or penis, into the genital pouch of the mate (Abe 1940). The secretion of mucus may also facilitate mating (Abe 1940). The stylets of the copulatory apparatus of *S. laevivscula* and *S. cookiana* presumably play an important role during copulation (Berry 1977). Spermatozoa are transferred in spermatophores which are variable in shape and produced by epiphallus gland secretions. In some species they are droplet-shaped, about 4 mm long × 2 mm diameter (Berry 1977, Jenkins 1981, 1983, 1984). In others the spermatophores are elongate (20mm long in *S. gigas*) and thread-like often bearing hooks and spines (Abe 1940, Berry 1977, Jenkins 1981, 1983, 1984) (Fig. 24). Both reciprocal and non-reciprocal copulations have been observed (Abe 1940, 1941). Copulation lasts for about 40 min. in *S. japonica* (Hirano & Inaba 1980) but may be up to several hours in *Benhamina obliquata* (Borland 1950). Most limpets copulate once only, but some pairs may take part in multiple copulations. Hirano & Inaba (1980) have observed some individuals copulating with more than one partner which raises the intriguing possibility that sperm competition may occur in some siphonariids as has recently been shown for other pulmonates (Baur 1998).

In some species (e.g. *Siphonaria atra*, *S. siphonaria*, *S. sirius*, *S. japonica*) copulation can occur during certain phases of the moon and/or specific times of the day (Table 8). Abe (1940) showed that spawning in *S. japonica* occurred on a full moon spring tide, 7 days after copulation. This enabled the larvae to develop and hatch on the following new moon spring tide (see discussion on spawning below). Thus copulation, spawning and development are timed to facilitate larval survival. In a more recent study of the reproductive behaviour of *S. japonica*, Hirano & Inaba (1980) found no relationship between mating and exogenous factors, 60% of the population copulating regardless of the lunar phase (Table 8). However, it is perhaps worth noting that most copulations observed (85%) were on a full moon spring

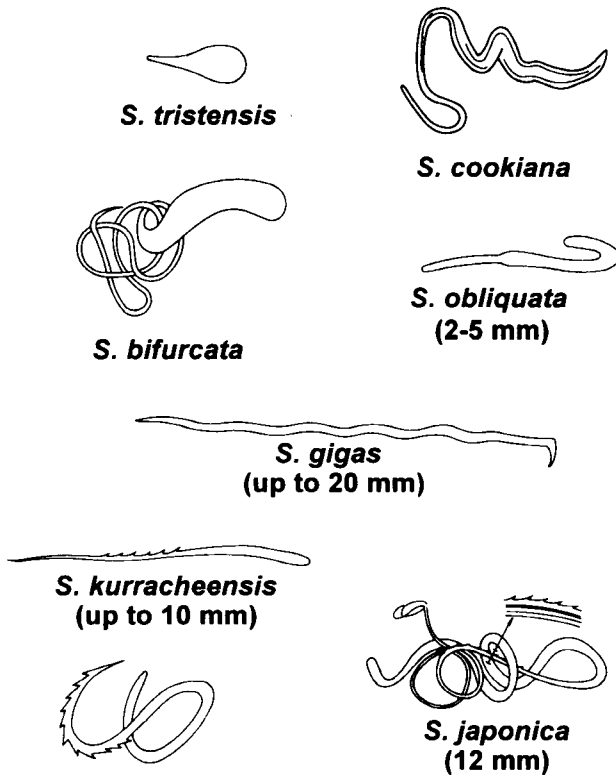


Figure 24 Some spermatophores of *Siphonaria* species.
(After Berry 1977).

tide. These differing results suggest that mating (and spawning?) in *Siphonaria* is not simply controlled by lunar rhythms but that other environmental factors are as important.

Spawning

Of the 29 species of *Siphonaria* for which there are data, 27 deposit benthic egg masses in a gelatinous ribbon which is cemented to the rock (Fig. 25). Two species (*S. tasmanica* and *S. virgulata*) release pelagic egg masses (Creese 1980a, Quinn 1988b, Chambers & McQuaid 1994a). In most species, each egg is housed in its own egg case, but Borland (1950) reports that in *Benhamina obliquata* each case can contain 20 to 30 eggs. The egg ribbons may take the form of; a simple egg mass, a straight, a collar-shaped, or a spiral-shaped ribbon (Fig. 25; Table 7). On some shores where more than one species of *Siphonaria* is found, it is possible to identify the egg masses of different species by their shape (Borland 1950, Mapstone 1978, Chambers & McQuaid 1994a). Spiral-shaped egg ribbons are formed by the animal moving in a circular pattern (usually backwards and anti-clockwise) during egg laying (Abe 1940, Borland 1950), a process which may take up to 8 h (Borland 1950). In some species the eggs ribbons may not be deposited at the same tidal height as that occupied by adult, *S. japonica* moving downshore and *S. atra* upshore (Abe 1940, 1941). *S. pectinata*, which has a wide intertidal distribution, also moves away from its home site to lay its eggs between the mean low water mark and mid-tide (Voss 1959).

Table 8 Timing of copulation and spawning by nine species of *Siphonaria*. "Yes" indicates a correlation, but no specific details provided by source. "No" indicates that no periodicity was found in relation to the day/night cycle and lunar phase. N, new moon; F, full moon; H, half moon; Wax H, waxing half moon, nd, indicates no data available. Table modified from Iwasaki (1995a).

Species	Height on shore	Copulation			Spawning			References
		Day/Night	Lunar phase	Day/Night	Lunar phase	Day/Night	Lunar phase	
<i>S. sirius</i>	Low	Early morning	Wax H	Early morning	1-2 days after Wax H	Early morning	Wax H	Iwasaki 1995a
<i>S. alternata</i>	Mid	nd	nd	No	No	No	No	Zischke 1974
<i>S. atra</i>	Mid	Early morning Late afternoon	N and F	nd	H	nd	H	Abe 1935, 1940, 1941
<i>S. japonica</i>	Mid	Early morning	Wax H	Low tide	F	Low tide	F	Abe 1940
<i>S. japonica</i>	Mid	No	No	Night common	Wax H	Night common	Wax H	Hirano 1980, Hirano & Inaba 1980
<i>S. laciniosa</i>	Mid	Night?	nd	Night	nd	Night	nd	Hulings 1985
<i>S. pectinata</i>	Mid	nd	nd	nd	N and F	nd	N and F	Zischke 1974
<i>S. denticulata</i>	nd	nd	Spring tides	nd	2-3 days after N and F	nd	2-3 days after N and F	Creese 1980a
<i>S. gigas</i>	Mid	Falling tides	nd	nd	N and F	nd	N and F	Levings & Garrity 1986
<i>S. sipho</i>	Mid-upper	N > D	N and F	nd	H	nd	H	Abe 1935, 1940, 1941
<i>S. diemenensis</i>	Mid-upper	nd	nd	nd	Yes	nd	Yes	Quinn 1988b
<i>S. tasmanica</i>	High	nd	nd	Low tide	No	Low tide	No	Quinn 1983
<i>S. thersites</i>	High	nd	nd	No	No	No	No	Strathmann 1987

Borland (1950) suggests that in *B. obliquata* there is no correlation between egg laying and phases of the moon; as eggs are deposited at night copulation is presumably at night when animals are active (see Table 3). Mapstone (1978) suggests that *S. diemenensis* spawns during spring tides and *S. baconi* neaps. Lopez Gappa et al. (1996) suggest that *S. lessona* spawns during submerision.

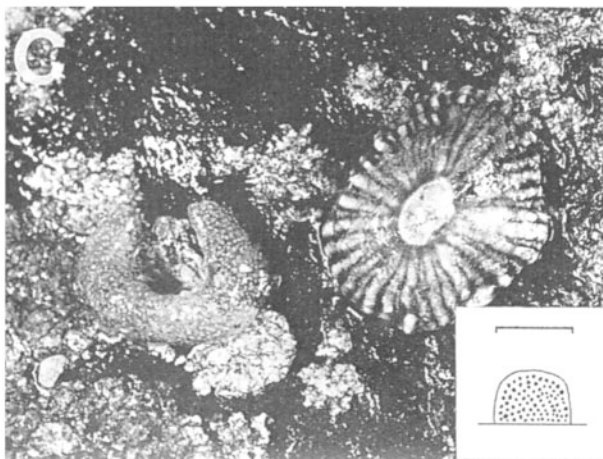
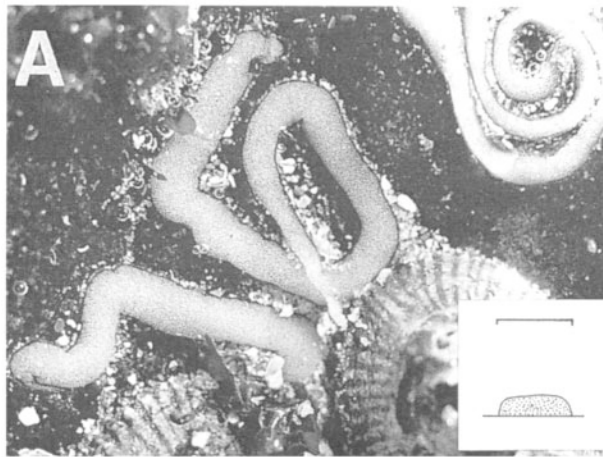


Figure 25 Egg masses, and diagrammatic cross-sections of an egg mass, of *Siphonaria* sp. A, egg ribbon of *S. capensis*. B, egg coil of *S. concinna*. C, egg collar of *S. annea*. Scale bars=5 mm. (From Chambers & McQuaid 1994a).

Trimusculids also produce gelatinous egg ribbons, each egg also surrounded by an egg case. Unlike the siphonariids, however, the egg ribbons lie as two collars, either side of the foot and extending up into the pallial groove (Haven 1974, A.N.Hodgson pers. obs.). Unlike siphonariids, trimusculids therefore brood their eggs, which is possibly a consequence of their sedentary lifestyle. Haven (1974) reports that each collar contains about 900 eggs.

Egg production in siphonariids is controlled by endocrine secretions of the dorsal bodies (Saleuddin et al. 1997). The dorsal body cells are concentrated as two distinct groups of cells on the dorsal surface of the cerebral ganglia. In a study of *S. pectinata*, Saleuddin et al. (1997) found that the dorsal body cells of reproductively active limpets were filled with lipid and mitochondria. By contrast in the dorsal body cells of non-egg-laying animals there was a significant reduction in the number of lipid droplets and evidence of reduced synthetic activity. Studies on other pulmonates (e.g. *Helisoma*, Saleuddin, et al. 1983) have shown that mating is a prerequisite for egg laying, and in virgin snails the dorsal bodies are synthetically inactive (Saleuddin et al. 1989, Kahn et al. 1990). It is possible that, like such pulmonates, copulation in *Siphonaria* activates the dorsal bodies as animals kept in isolation cease to produce eggs (Saleuddin et al. 1997).

Seasonality of spawning

There is some correlation between latitude and seasonality of spawning. In more temperate habitats spawning tends to be seasonal (e.g. *S. denticulata*, Fig. 26), whereas species from the more tropical regions and the sub-Antarctic are reproductively active throughout the year

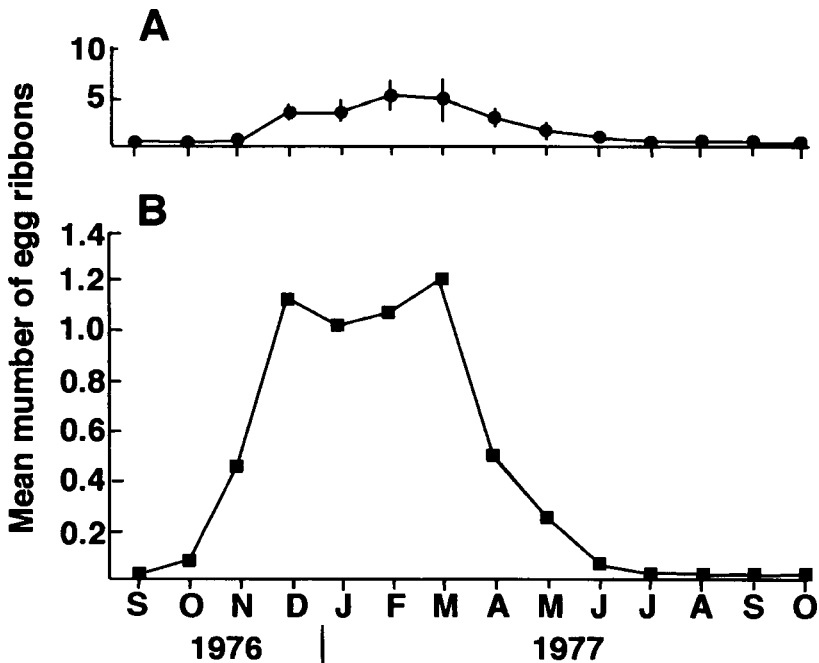


Figure 26 Densities of egg ribbons of *Siphonaria denticulata* at Cape Banks (nr Sydney, NSW). A, mean number (\pm SE) eggs per quadrat (0.0625 m²) (n=10). B, mean number per adult limpet (>12 mm shell length). (Redrawn from Creese 1980a).

(Table 6, p. 287), although some may show peaks of spawning activity. Some differences in spawning period have been reported within a species and Hirano (1980) has suggested that this is linked to temperature. In Japan, *S. japonica* has a 4-month spawning period at 40°N, but at 34°N where water temperatures are warmer, spawning occurs over 5 months (Hirano 1980). Similarly, in regions where water temperature was 21–23°C, *S. pectinata* spawns from December to March, but in warmer waters (24–28°C) spawning is extended from September to May (Table 6). Of those species that are more seasonal in their reproductive activity, spawning tends to be from spring through summer, with the greatest activity in the summer months (Table 6).

Rhythms and frequency of spawning

Branch (1981), suggested that in *Siphonaria* egg laying was very rhythmical and correlated to the lunar cycle. By contrast, Iwasaki (1995a) concluded that there was no consistent relationship between the timing of reproductive activity and exogenous factors. While there are some exceptions (e.g. *S. sirius* which spawns on a neap tide, Iwasaki 1995a) spawning in many species is correlated with phases of the moon (Table 8; Fig. 27). For example, *S. denticulata* and *S. diemenensis* both spawn at approximately fortnightly intervals (Creese 1980a, Quinn 1988b). There are a number of possible adaptive reasons for the timing of spawning activity which are not necessarily mutually exclusive. Spawning can be a lengthy process, and as limpets are more vulnerable while active (see earlier discussions) egg laying is timed to coincide with the greatest window of opportunity for this process. Alternatively,

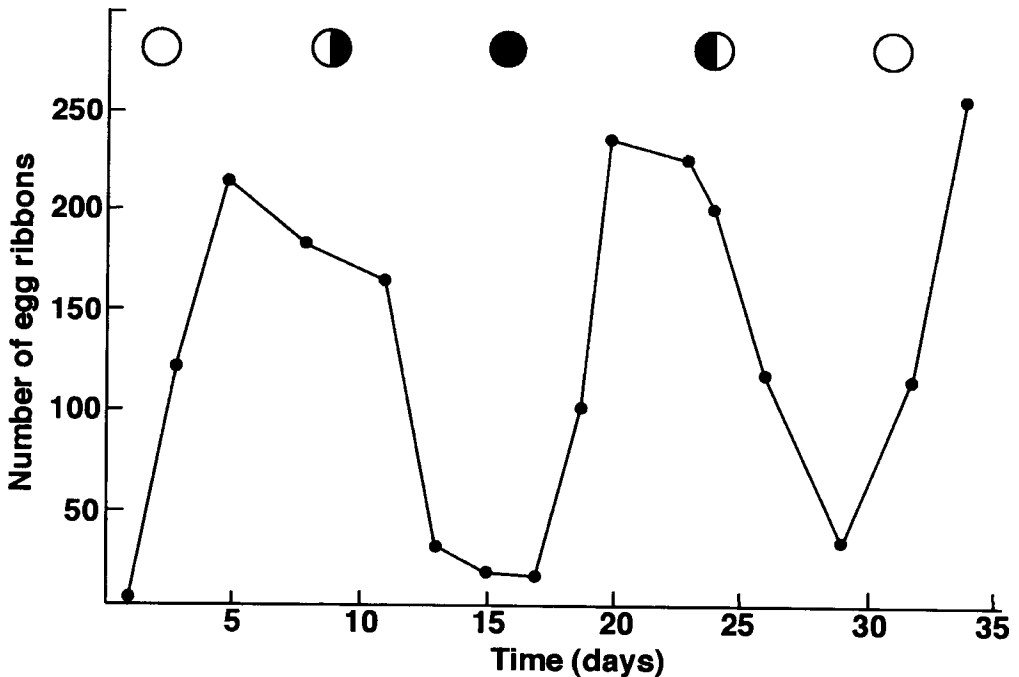


Figure 27 Total numbers of egg ribbons of *Siphonaria denticulata* present on an isolated rock at Bradley's head (nr. Sydney, NSW) between 11 November 1977 and 14 December 1977. (Redrawn from Creese 1980a).

spawning may be timed to ensure that the eggs have the greatest chance of survival. Finally, spawning may be timed to ensure that the larvae hatch when conditions are most favourable for their survival.

Fecundity and energetics of reproduction

Siphonariids are iteroparous. Depending on the species, longevities reported range between 1 to 6 yr (e.g. Creese 1981, Quinn 1988a, Liu 1994, Tablado et al. 1994), and *Benhamina obliquata* has been reported to live for 10 yr (Borland 1950). It is highly likely, therefore, that individuals of most species have more than one breeding season. Furthermore, a number of studies have shown that limpets lay more than one egg ribbon during the breeding season. *Siphonaria pectinata* lays 12–15 ribbons in 4–5 days (Dieuzeide 1935, Voss 1959), *Benhamina obliquata* 2–3 coils per summer (Borland 1950), *Siphonaria gigas* >1 ring per spawning period (Levings & Garrity 1986) and *S. concinna* and *S. serrata* >4 coils per spawning season (Chambers 1994). Reproductive output, in terms of the size of the egg ribbon and number of ribbons laid (and therefore number of eggs), however, is linked to both the size of the animal and availability of food (Abe 1941, Borland 1950, Creese 1980a, Quinn 1988b, Chambers 1994). The first detailed quantitative study of fecundity was by Creese (1980a) who carried out a number of field observations and experiments on *S. denticulata*. Creese found that large (20 mm shell length) and medium (16 mm shell length) individuals laid about one egg ribbon per fortnight whereas small limpets (12 mm shell length) only laid 0.5 egg ribbons in the same time period. The effect of food abundance, density and height on the shore on fecundity in *S. diemenensis* was demonstrated by the field work of Quinn (1998b). Fewer egg masses were produced when animal density was increased (Fig. 28), food abundance reduced, and by high shore limpets when there was a seasonal reduction in the supply of food. This reduction in fecundity was reflected in the energy spawned as egg masses which was calculated to be 62.48 kJ m⁻² yr⁻¹ to 74.89 kJ m⁻² yr⁻¹ for higher shore animals and 240.76 kJ m⁻² yr⁻¹ to 338.69 kJ m⁻² yr⁻¹ for those limpets living lower down. Parry (1977, cited by Branch 1981) determined that the reproductive effort (calculated as a fraction of assimilated energy) for *S. diemenensis* was 5.7–14.3%, values which were similar to that of prosobranch limpets. Working on the same species, Quinn (1988b) showed that like many other marine invertebrates, reproductive effort (= proportion of assimilated energy allocated to reproduction) increased with size and age. However, in both these studies the energy budgets were incomplete and such data should be treated cautiously.

The numbers of eggs contained within an egg ribbon not only varies with the size of the ribbon (which is linked to animal size as discussed above) but also with mode of larval development. Some species produce eggs that hatch as free-swimming veliger larvae whereas in others the entire larval development occurs within the egg from which a crawling juvenile emerges. Planktonic developers produce large numbers (often >20000 eggs egg case⁻¹) of relatively small eggs which are housed in a capsule <300 µm in diameter (Table 7, p. 291). The egg capsules of direct developers are >300 µm in diameter and egg cases contain <2500 eggs (Table 7). Thus, as would be expected, fecundity of planktonic developers is far higher than that of direct developers. Creese (1980a) used density and reproductive data to calculate and compare fecundities of *S. denticulata* and *S. virgulata* with the acmaeid limpets *Notoacmea petterdi* and *Patelloida alticostata*, all being sympatric in their distribution. Within a reproductive season the siphonariids (20mm individuals) were

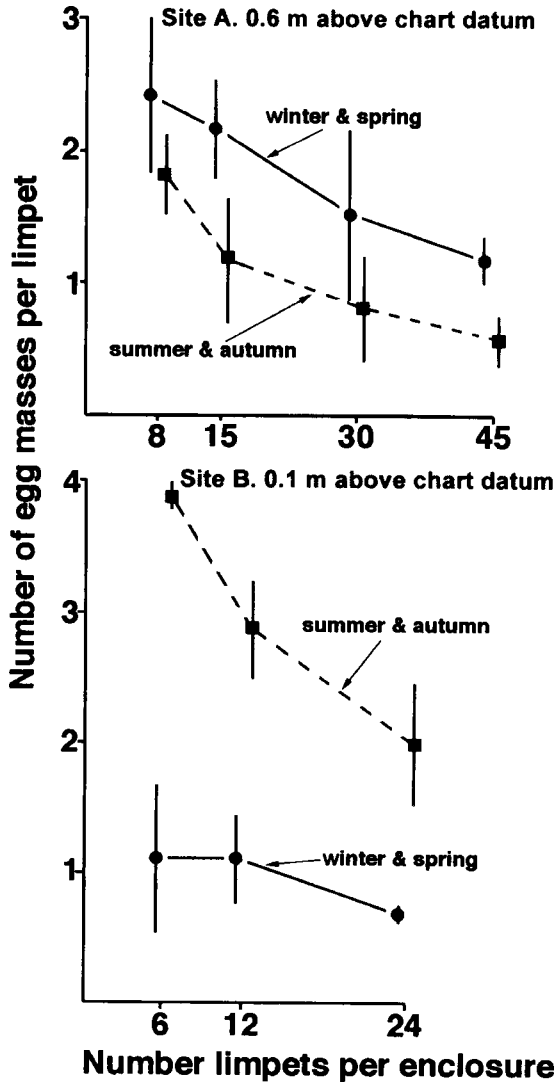


Figure 28 Mean number of egg masses (\pm SD) spawned per *Siphonaria diemenensis* during breeding seasons in experiments in which the densities of adults were manipulated. (Redrawn from Quinn 1988b).

estimated to produce 350000 eggs, approximately 10 times the number of the similar sized acmaeids (*Notoacmea petterdi*, 29700–44600; *Patelloida alticostata*, 30000–47100).

Embryonic and larval development

Embryonic development has been described at the light microscope level only (Fujita 1895 and 1904 cited in Abe 1940, Dieuzeide 1935, Abe 1940, 1941, Anderson 1965, Mapstone 1978). Egg cleavage is in the typical spiral manner, the first two divisions being equal and the third

unequal (Anderson 1965). In those species which release planktonic veligers, the blastula and gastrula phases are passed through in 24–48 h (but note: 5 days to blastula stage in *Siphonaria japonica* at 13–15°C, Abe 1940) and a simple yolky trochophore is formed within 48–72 h (Abe 1941, Anderson 1965, Mapstone 1978). By the third to fourth day (7 days in *S. japonica*) the larva has developed an operculate foot, a bilobed velum and a globular shell. The veliger is usually quite active, rotating within the capsule. Within an egg ribbon, larval development can proceed at different rates, Borland (1950) observing trochophores, young and old veligers in the same egg ribbon of *Benhamina obliquata*. By contrast, Simpson (1977) noted that in *Kerguelenella lateralis* development within an egg mass proceeded at the same rate.

The larvae which emerge from the egg cases are either free-swimming and planktonic or crawling larvae. The free-swimming veligers are about 130 µm to 180 µm long, have completed torsion and used most of the yolk, and have well developed organ systems (Abe 1940, Olivier & Penchaszadeh 1968, Mapstone 1978). They emerge from the egg usually within 7 days after the egg ribbons have been laid, whereas crawling larvae only emerge after spending 3–4 wk in the egg case (Table 7).

Although the egg ribbons of planktonic developers spend a short time only on the rocks, the position at which eggs are laid on the shore is probably critical for successful larval development. *Siphonaria japonica* and *S. lessoni* lay their eggs downshore, below the adult home site (Abe 1940, Olivier & Penchaszadeh 1968), which presumably reduces desiccation of the eggs. Creese (1980a) recorded a 70% mortality in eggs of *S. denticulata* which were transplanted upshore, a position where some adults could be found but rarely laid eggs. This compared to only 15% mortality in those eggs ribbons lower downshore. Laying eggs in rock pools also prevents desiccation. Creese (1980a) found that survival of the eggs of *S. denticulata* which were laid in both upshore and downshore pools was greater (>90% survival) than those laid on exposed rocks. *S. capensis* undoubtedly lay eggs in rock pools for the same reason (Chambers & McQuaid 1994a). When exposed to summer daytime conditions (35°C; 45% R.H.), when eggs ribbons would be present on the shore, egg masses of this species lose 50% of their water in 1.25 h, with 100% mortality of embryos occurring after 4h (Chambers 1994). Other species (e.g. *Kerguelenella lateralis*, *Siphonaria gigas*) lay their eggs in crevices (Simpson 1976, Levings & Garrity 1986) which are also humid environments. The shape of the egg ribbon also helps reduce desiccation. Chambers (1994) showed that the rate of water loss increased significantly (30–50%) in egg ribbons of *S. concinna* which were uncoiled experimentally. Chambers & McQuaid (1994a) suggested that egg ribbons which are laid in a coil reduce water loss by trapping water.

There are only a few experimental data comparing desiccation tolerances of siphonariid eggs within egg ribbons. Chambers (1994) found that the egg ribbons of the direct developer *S. serrata* had a greater resistance to water loss and lower embryonic mortality than those of the planktonic developers *S. capensis* and *S. concinna*. This is perhaps to be expected as the egg masses of direct developers spend up to 4 wk on the shore. Chambers & McQuaid (1994a) suggest that direct developers produce egg ribbons with a thick outer layer and low surface to volume ratio.

Microhabitat can also protect egg rings from predators. Levings & Garrity (1986) noted that 55% of egg ribbons of *S. gigas* laid on open rocks were damaged (probably by fishes during high tide), whereas very few ribbons (except for exposed portions) in crevices had any damage. Very little damage was found to egg ribbons that were laid on exposed rocks but protected by cages.

A review of larval development of 29 species of *Siphonaria*, reveals that planktonic development is most common, being found in 17 species. Ten species have direct

development, producing crawling juveniles and two species produce pediveligers (i.e. swimming-crawling larvae) (Table 7). The reasons for different developmental strategies in marine invertebrates continues to intrigue biologists. Some authors have suggested that mode of development is an optimal solution to the ecology of the animal, i.e. the strategy is adaptive. More recent studies propose that development reflects the phylogenetic history of the animal and that adaptive significance must be considered in an historical perspective and not just related to the current ecology of the animal (see Chambers & McQuaid 1994a,b for literature).

A number of studies have explored possible adaptive reasons for the mode of larval development in siphonariids, examining the relationship of development to position on the shore, latitude and animal size. Knox (1955) proposed that developmental mode would be related to position within the intertidal zone. The trend would be for high shore species to have direct development and for low shore species, to have planktonic development. Chambers & McQuaid (1994b) found some support for this proposal, determining that most direct-developing species are indeed found high on the shore, while planktonic species are commoner in the mid- to low intertidal. However they found a number of notable exceptions. *S. serrata*, which is more abundant in the mid-intertidal zone of South African rocky shores, has direct development. There are three high shore species with planktonic development; two, *S. tasmanica* and *S. virgulata*, release pelagic egg masses. The third species, *S. capensis*, according to Chambers & McQuaid (1994b) is found mainly in high shore pools where it deposits its eggs. However, this species and its egg masses are also very common out of pools in the high intertidal, particularly on rock faces that are shaded and remain moist (A.N.Hodgson pers obs.).

Thorson (1950) proposed that in marine invertebrates, direct development would increase in frequency towards the poles, whereas Clark & Goetzfried (1978), using data from nudibranch development, proposed a trend towards direct development in tropical waters. Chambers & McQuaid (1994b) in their review of larval development of *Siphonaria* examined the possible correlations of development and latitude. They concluded that although most direct developers are found within a narrow range of lower latitudes (34°S–30°N), when compared with planktonic developers (48°S–45°N, Fig. 29), and therefore seemingly favouring the hypothesis of Clark & Goetzfried, worldwide there was support for Thorson's hypothesis. Only siphonariids with planktonic development are found in the tropics and the only three species living at high latitudes (>45°) have direct development. Chambers & McQuaid (1994b) did suggest that direct development in *Kerguelenella lateralis* and *K. stewartiana* might be an adaptation to island conditions, not high latitudes, and that these species should not be included in any analysis. Both species are common to sub-Antarctic islands. It was argued that if they had planktonic development, the larvae would be swept away from the oceanic islands resulting in a failure to maintain the adult population. It is difficult to accept this argument as there is no evidence to suggest that *Kerguelenella* spp. evolved on islands. They have a wide circumpolar distribution and *K. lateralis* is found in the southern parts of South America (Hubendick 1946). Davenport (1997) points out that its presence on South Georgia Island, at least, is relatively recent, as this island had an extensive ice cap until ~10000 yr ago. After the icecap receded *K. lateralis* presumably reached the island by rafting from either the Falklands (1300 km away) or Tierra del Fuego (2000 km away). *Siphonaria thersites* is also not exclusively found on islands and it has direct development. Direct development, however, may be one reason for the persistence of these species on islands. At present it can only be concluded that the relationship between mode of larval development and latitude is equivocal.

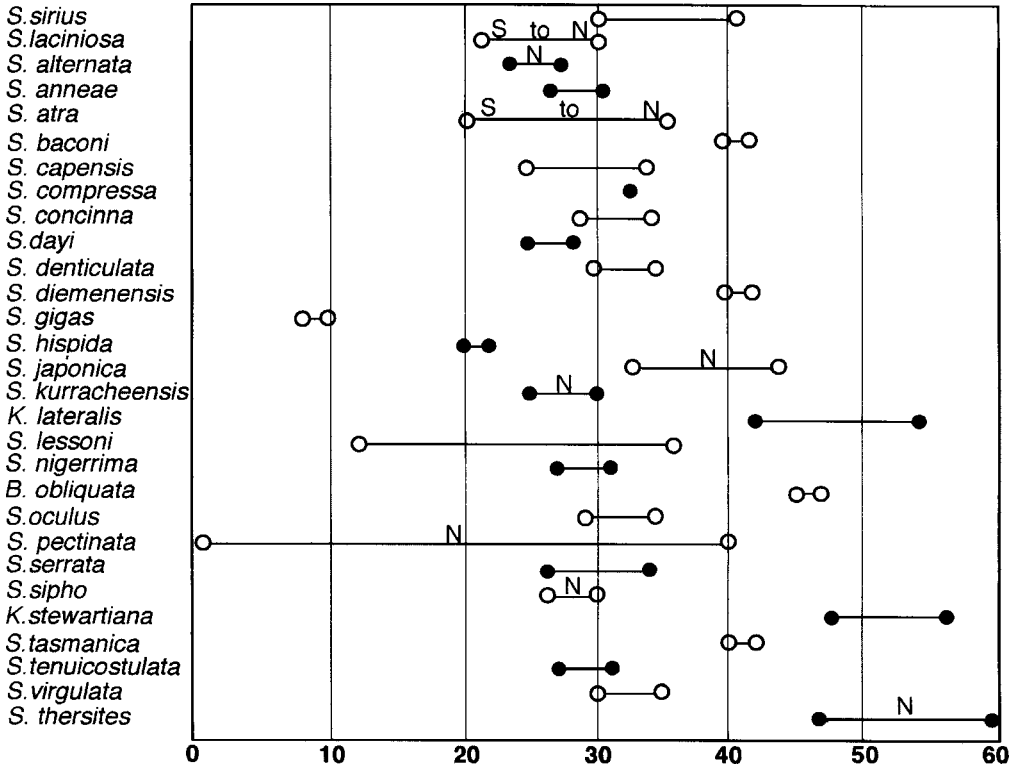


Figure 29 Worldwide latitudinal ranges of 26 species of *Siphonaria*, two species of *Kerguelenella* and one species of *Benhamina*. Open circles indicate planktonic development, closed circles indicate direct development (and include species with pediveligers). Northern hemisphere species are indicated by 'N'. (Redrawn and modified from Chambers & McQuaid 1994b).

Chambers & McQuaid (1994b) did find that there was a weak correlation between body size (as represented by shell length) and mode of development, the body size of planktonic species being just significantly larger than direct developers.

More recently Chambers et al. (1996, 1998) have used both polyacrylamide gel electrophoresis of total soluble proteins and RAPD techniques to explore phylogenetic explanations for larval strategies in South African species of *Siphonaria*. Although they found some support for a systematic basis to mode of larval development, the findings at present are equivocal as some clades (e.g. *Patellopsis* and *Siphonaria* clades) contain both planktonic and direct developers (Note: Chambers et al. 1998, have *S. atra* incorrectly given as a direct developing species whereas it is planktonic). One possible explanation for this is that these subgenera are not monophyletic. The earlier branching of planktonic developers in this subgenus, however, does suggest that planktonic species are primitive. This would add further support to hypotheses that the Siphonariidae are truly marine and not a terrestrial group which have re-invaded the marine environment. At present no one model (adaptive or phylogenetic) can explain the larval strategies of siphonariids.

It is generally thought that the production of planktotrophic larvae results in higher dispersal rates and gene flow. Consequently, species with a wide dispersal would have high genetic variability within local populations and homogeneity among neighbouring

populations (see Johnson & Black 1984a,b, Chambers et al. 1996 for examples of literature). In some species of *Siphonaria* the situation may not be this simple as Johnson & Black (1982, 1984a,b) found that in *S. jeanae* there were differences in allelic frequencies between high and low shore populations, animals from different sites along the shore, adults and recruits, and between recruits in two different years. These patterns were not consistent in space or time and resulted in chaotic genetic patchiness. The electrophoretic results of Chambers et al. (1996) on South African species of *Siphonaria* gave higher levels of genetic variability in planktonic developers when compared with direct developers, which would be expected due to the resulting greater gene flow. By contrast RAPD results indicated greater genetic variability in the direct developers (Chambers et al. 1998). Chambers et al. suggested that a possible reason for this was that “the low levels of gene flow between the direct-developers cause small-scale founder effects in sub-populations which increases the overall genetic diversity of the whole population”.

Very little is known about the biology and ecology of siphonariid veliger larvae. Bastida et al. (1971) suggested that the veligers of *S. lessoni* were confined to the upper 0.5 m of the water column. Creese (1980a) estimated that the veligers of *S. denticulata* could spend up to 10 wk in the plankton. This estimate was based on the lag period between first observed spawnings and time of recorded juvenile settlement. However, Creese does note that this time lag could be due to greater mortality of early settling larvae. Zischke (1974) was able to maintain the veligers of *S. pectinata* for 11 days in the laboratory, but the larvae did not feed nor settle. *S. lessoni* are estimated to spend about 9 days in the plankton (Olivier & Penchaszadeh 1968). The pediveligers of *S. hispida* and *S. alternata* lose their velum after 3 days after which time they presumably lose their pelagic capability.

Settlement of pelagic larvae is influenced by a number of factors including the presence of adults and of algae. Whereas Creese (1981) demonstrated that there was a correlation between successful recruitment of *S. denticulata* and *S. virgulata* and the presence of adults, Quinn (1988c) could find no such relationship for *S. diemenensis*. Recruitment by this species was very successful in areas with macroalgae. A positive relationships between the presence of macroalgae and recruitment has been noted for other species (Bastida et al. 1971, Branch et al. 1990). Quinn (1988c), however, has pointed out that successful recruitment in areas with macroalgae could be due to differential survival rather than preferential settlement. The algae could provide a food supply or a heterogeneous substratum with more microhabitats.

The timing of larval settlement is also crucial to successful recruitment, and whether planktonic larvae can delay settlement until a suitable habitat is found is not known. In some species settlement occurs at the most favourable time of year, e.g. in winter in *S. japonica* and *S. diemenensis* (Quinn 1988b, Liu 1994). In both these species winter recruitment is advantageous because temperatures are not only lower (desiccation is therefore less of a threat), but food availability and algal cover higher (Quinn 1988b,c, Liu 1994).

Conclusions and possible future work

The Siphonariidae are undoubtedly successful intertidal invertebrates. The weight of evidence points to these pulmonates having a marine ancestry, rather than terrestrial origins with a re-invasion of the marine environment. Particularly compelling is the fact that planktonic larval development is viewed as being plesiomorphic (primitive). Terrestrial origins would have required planktonic larvae to be re-evolved, which seems highly improbable. Although they are a particular

success in lower latitudes, siphonariids have a wide geographic distribution. They are abundant on many shores, where their densities often exceed 1000 m⁻². The number of species (at least 60) rivals that of intertidal patellogastropod families. The success of the siphonariids as intertidal gastropods, particularly in warmer latitudes, is probably due to a combination of physiological and behavioural adaptations, some of which may be more important than others. Physiological adaptations include: an ability to respire efficiently in air and water; facultative metabolic rate depression; tolerance of low oxygen levels; possible anaerobiosis; an ability to re-hydrate rapidly after desiccation. They are also tolerant of a range of salinities, which has not only enabled several species to inhabit rock pools and estuaries, but also gives them greater tolerance (when compared with patellogastropods) of elevated internal osmolarities, which can be a result of desiccation. Behaviourally siphonariids from different tidal heights have adapted activity patterns to allow the maximum time for foraging while minimizing the chances of desiccation, predation (in some species) and effects of wave activity. In addition, with very few exceptions, siphonariids all make use of refuges (e.g. home scars or crevices) during periods of inactivity. Finally, siphonariids are not palatable to predators, a distinct advantage in lower latitudes where predation pressure is particularly high.

There is still a great deal to be learned about the physiology of the Siphonariidae, information on tropical species being particularly scarce. Current understanding of their respiratory physiology is based on one or two experiments on a few species only. Data on tolerances and sublethal effects of temperature and desiccation are severely lacking. Nevertheless, those results obtained to date have raised a number of important questions which should be addressed. Is metabolic rate depression and non-acclimation to temperature ubiquitous within the family and therefore a phylogenetic trait? Under what physiological conditions is metabolic rate depression triggered? How well developed is anaerobic metabolism?

Any attempt to explain the success of an organism in its habitat must consider the adaptations and survival of the larvae and/or juveniles. Whereas there is a great deal of information on many aspects of the reproductive biology (except seasonally of gametogenesis and details on oogenesis and vitellogenesis), the biology of their larvae is largely unknown. A number of workers have successfully hatched larvae under laboratory conditions, and larval studies would therefore seem feasible. Investigations on larval physiology, behaviour, longevity, and whether larvae can delay settlement, would provide a greater understanding of population dynamics of species, dispersal, gene flow, as well as aspects of intertidal community structure.

A number of ecological and behavioural studies have provided a good understanding of the grazing habits of siphonariids, as well as the interactions of these limpets with plants and other intertidal animals. As energy budgets have not been determined for siphonariids, it is not possible to assess their importance in energy flow within intertidal ecosystems. Many important components of energy budgets are lacking and in terms of grazing no study to date has determined the proportion of algal productivity that is utilized by siphonariids, and what proportion goes into other food chains. The fact that siphonariid limpets can occur in large densities would suggest that their role in energy transfer could be of considerable importance.

Siphonariids adapt well to laboratory conditions. This makes them ideal intertidal molluscs with which to explore many aspects of gastropod physiology, behaviour and development. In addition, the laboratory manipulations could be used in concert with field experiments on these hardy organisms to investigate ecological phenomena. The biology of the Siphonariidae does warrant more attention. Hopefully this review will stimulate further research.

Acknowledgements

This review was completed as a visiting research scholar at Darling Marine Center (DMC), University of Maine. It is my great pleasure to thank Professor Kevin Eckelbarger and the staff of the DMC for their warm hospitality and use of facilities. My stay in Maine was made possible by a University of Maine (DMC) visiting scholarship and a sabbatical fellowship from the Foundation for Research Development (South Africa). I would also like to thank Dr Alan Ansell, Professor Alec Brown and Professor Steve Hawkins for valuable comments on the manuscript, and my wife Val, who has helped in numerous ways with the preparation of this review. Finally, it is a pleasure to acknowledge Professor George Branch who stimulated my interest in limpets, and Professor Brian Allanson who introduced me to *Siphonaria*.

References

- Abe, N. 1935. On the locomotion of a limpet-like pulmonate, *Siphonaria atra* Quoy et Gaimard [in Japanese with English summary]. *The Venus* **5**, 206–13.
- Abe, N. 1940. The homing, spawning and other habits of a limpet, *Siphonaria japonica* Donovan. *Tohoku University Science Reports* **15**, 59–95.
- Abe, N. 1941. Ecological observations on a limpet-like pulmonate, *Siphonaria atra* Quoy et Gaimard. *Palao Tropical Biological Station Studies* **2**, 239–78.
- Allanson, B.R. 1958. Some aspects of the ecology of the molluscan genus *Siphonaria* in South Africa. *Portugaliae Acta Biologica* **6**, 179–212.
- Allanson, B.R. 1959. On the systematics and distribution of the molluscan genus *Siphonaria* in South Africa. *Hydrobiologia* **12**, 149–80.
- Allanson, B.R. 1963. A systematic account of the Siphonariidae collected from South and West Africa and lodged in the Musée Royal, Tervuren, Belgium. *Revue de Zoologie et de Botanique Africaines*. **67**, 68–73.
- Anderson, D.T. 1965. Further observations on the life histories of littoral gastropods in New South Wales. *Proceedings of the Linnean Society of New South Wales* **90**, 242–51.
- Azevedo, C. & Corral, L. 1985. The fine structure of the spermatozoa of *Siphonaria algesirae* (Gastropoda, Pulmonata). *Journal of Morphology* **186**, 107–17.
- Bastida, R., Capezzani, A. & Torti, M.R. 1971. Fouling organisms in the port of Mar del Plata (Argentina). I. *Siphonaria lessoni*: ecological and biometric aspects. *Marine Biology* **10**, 297–307.
- Baur, B. 1998. Sperm competition in molluscs. In *Sperm competition and sexual selection*, T.R. Birkhead & A.P.Møller (eds). New York: Academic Press, 255–305.
- Bedford, J.J. 1969. The soluble amino acid pool in *Siphonaria zelandica*: its composition and the influence of salinity changes. *Comparative Biochemistry and Physiology* **29**, 1005–1014.
- Berry, A.J. 1977. Gastropoda: Pulmonata. In *Reproduction of marine invertebrates. IV*. A.C.Giese & J.S.Pearse (eds). New York: Academic Press, 181–226.
- Bertness, M.D., Garrity, S.D. & Levings, S.C. 1981. Predation pressure and gastropod foraging: a tropical-temperate comparison. *Evolution* **35**, 995–1007.
- Bieler, R. 1992. Gastropod phylogeny and systematics. *Annual Review of Ecology and Systematics* **23**, 311–38.
- Biskupiak, J.E. & Ireland, C.M. 1983. Pectinatone, a new antibiotic from the mollusc *Siphonaria pectinata*. *Tetrahedron Letters* **24**, 3055–8.
- Black, R. 1979. Competition between intertidal limpets: an intrusive niche on a steep resource gradient. *Journal of Animal Ecology* **48**, 401–11.
- Black, R. & Johnson, M.S. 1981. Genetic differentiation independent of intertidal gradients in the pulmonate limpet *Siphonaria kurracheensis*. *Marine Biology* **64**, 79–84.
- Black, R., Lymbery, A. & Hill, A. 1988. Form and function: size of radular teeth and inorganic content of faeces in a guild of grazing molluscs at Rottneest Island, Western Australia. *Journal of Experimental Marine Biology and Ecology* **121**, 23–35.
- Black, R., Fisher, K., Hill, A. & McShane, P. 1979. Physical and biological conditions on a steep intertidal gradient at Rottneest Island, Western Australia. *Australian Journal of Ecology* **4**, 67–74.
- Borland, C. 1950. Ecological study of *Benhamina obliquata* (Sowerby), a basommatophorous pulmonate in Otago Harbour. *Transactions of the Royal Society of New Zealand* **78**, 385–93.

- Boss, K.J. 1982. Mollusca. In *Synopsis and classification of living marine organisms 2*, S.C.Parker (ed. in chief). New York: McGraw-Hill, 945–1166.
- Branch, G.M. 1975. Ecology of *Patella* species from the Cape peninsula, South Africa. IV. Desiccation. *Marine Biology* **32**, 179–88.
- Branch, G.M. 1981. The biology of limpets: physical factors, energy flow, and ecological interactions. *Oceanography and Marine Biology: an Annual Review* **19**, 235–380.
- Branch, G.M. 1985. Limpets: evolution and adaptation. In *The Mollusca. 10*, E.R.Trueman & M.R. Clarke (eds). Orlando: Academic Press, 187–220.
- Branch, G.M. 1986. Limpets: their role in littoral and sublittoral community dynamics. In *The ecology of rocky coasts*, P.G.Moore & R.Seed (eds). New York: Columbia University Press, 97–116.
- Branch, G.M. 1988. Activity rhythms in *Siphonaria thersites*. In *Behavioural adaptation to intertidal life*, G.Chelazzi & M.Vannini (eds). New York: Plenum Press, 27–44.
- Branch, G.M. & Cherry, M.I. 1985. Activity rhythms of the pulmonate limpet *Siphonaria capensis* Q. & G. as an adaptation to osmotic stress, predation and wave action. *Journal of Experimental Marine Biology and Ecology* **87**, 153–68.
- Branch, G.M. & Marsh, A.C. 1978. Tenacity and shell shape in six *Patella* species: adaptive features. *Journal of Experimental Marine Biology and Ecology* **34**, 111–30.
- Branch, G.M. & Moreno, C.A. 1994. Intertidal and subtidal grazers. In *Rocky shores: exploitation in Chile and South Africa*, W.R.Siegfried (ed.). Berlin: Springer-Verlag, 75–100.
- Branch, G.M., Eekhout, S. & Bosman, A.L. 1990. Short-term effects of the 1988 Orange River floods on the intertidal rocky-shore communities of the open coast. *Transactions of the Royal Society of Southern Africa* **47**, 331–54.
- Chambers, R.J. 1994. The conflict between adaptation and constraint: the case of the siphonariid limpets. PhD thesis, Rhodes University.
- Chambers, R.J. & McQuaid, C.D. 1994a. Notes on the taxonomy, spawn and larval development of South African species of the intertidal limpet *Siphonaria* (Gastropoda: Pulmonata). *Journal of Molluscan Studies* **60**, 263–75.
- Chambers, R.J. & McQuaid, C.D. 1994b. A review of larval development in the intertidal limpet genus *Siphonaria* (Gastropoda: Pulmonata). *Journal of Molluscan Studies* **60**, 415–23.
- Chambers, R.J., McQuaid, C.D. & Kirby, R. 1996. Determination of genetic diversity of South African intertidal limpets (Gastropoda: *Siphonaria*) with different reproductive modes using polyacrylamide gel electrophoresis of total cellular proteins. *Journal of Experimental Marine Biology and Ecology* **201**, 1–11.
- Chambers, R.J., McQuaid, C.D. & Kirby, R. 1998. The use of randomly amplified polymorphic DNA to analyze the genetic diversity, the systematic relationships and the evolution of intertidal limpets, *Siphonaria* spp. (Pulmonata: Gastropoda), with different reproductive modes. *Journal of Experimental Marine Biology and Ecology* **227**, 49–66.
- Christiaens, J. 1973. La superfamille des Siphonarioidea. *Information Société Beige de Malacologie* **10–11**, 163–82.
- Christiaens, J. 1980. The limpets of Hong Kong with descriptions of seven new species and subspecies. In *The malacofauna of Hong Kong and Southern China. Proceedings of the First International Workshop on the Malacofauna of Hong Kong 1977*, B.Morton (ed.). Hong Kong: Hong Kong University Press, 61–84.
- Clark, K.B. & Goetzfried, A. 1978. Zoogeographic influences on development patterns of north Atlantic Ascoglossa and Nudibranchia, with a discussion of factors affecting egg size and number. *Journal of Molluscan Studies* **44**, 283–94.
- Cook, S.B. 1969. Experiments on homing in the limpet *Siphonaria normalis*. *Animal Behaviour* **17**, 679–82.
- Cook, S.B. 1971. A study of homing behavior in the limpet *Siphonaria alternata*. *Biological Bulletin* **141**, 449–57.
- Cook, S.B. 1976. The role of the “home scar” in pulmonate limpets. *Bulletin of the American Malacological Union* **42**, 34–7.
- Cook, S.B. 1979. Shell shape in a pulmonate limpet. *American Zoologist* **19**, 1007 only.
- Cook, S.B. 1980. Fish predation on pulmonate limpets. *The Veliger* **22**, 380–81.
- Cook, S.B. & Cook, C.B. 1975. Directionality in the trail-following response of the pulmonate limpet *Siphonaria alternata*. *Marine Behaviour and Physiology* **3**, 147–55.

- Cook, S.B. & Cook, C.B. 1978. Tidal amplitude and activity in the pulmonate limpets *Siphonaria normalis* (Gould) and *S. alternata* (Say). *Journal of Experimental Marine Biology and Ecology* **35**, 119–36.
- Cook, S.B. & Cook, C.B. 1981. Activity patterns in *Siphonaria* populations: heading choice and the effects of size and grazing interval. *Journal of Experimental Marine Biology and Ecology* **49**, 69–79.
- Cottrell, A.J. 1910. Anatomy of *Siphonaria obliquata*. *Transactions of the New Zealand Institute* **43**, 582–94.
- Cottrell, A.J. 1914. Vascular system of *Siphonaria obliquata*. *Transactions of the New Zealand Institute* **44**, 374–9.
- Craig, A.K., Dobkin, S., Grimm, R.B. & Davidson, J.B. 1969. The gastropod, *Siphonaria pectinata*: a factor in destruction of beach rock. *American Zoologist* **9**, 895–901.
- Creese, R.G. 1980a. Reproductive cycles and fecundities of two species of *Siphonaria* (Mollusca: Pulmonata) in South-eastern Australia. *Australian Journal of Marine and Freshwater Research* **31**, 37–47.
- Creese, R.G. 1980b. An analysis of distribution and abundance of populations of the high shore limpet, *Notoacmea petterdi* (Tenison-Woods). *Oecologia* **45**, 252–60.
- Creese, R.G. 1981. Patterns of growth, longevity and recruitment of intertidal limpets in New South Wales. *Journal of Experimental Marine Biology and Ecology* **51**, 145–71.
- Creese, R.G. & Underwood, A.J. 1982. Analysis of inter- and intra-specific competition among intertidal limpets with different methods of feeding. *Oecologia* **53**, 337–46.
- Crisp, D.J., Wieghell, J.G. & Richardson, C.A. 1990. Tidal microgrowth bands in *Siphonaria gigas* (Gastropoda, Pulmonata) from the coast of Costa Rica. *Malacologia* **31**, 229–36.
- Davenport, J. 1997. Comparisons of the biology of the intertidal sub-Antarctic limpets *Nacella concinna* and *Kerguelenella lateralis*. *Journal of Molluscan Studies* **63**, 39–48.
- Davenport, J. & MacAlister, H. 1996. Environmental conditions and physiological tolerances of intertidal fauna in relation to shore zonation at Husvik, South Georgia. *Journal of the Marine Biological Association of the United Kingdom* **76**, 985–1002.
- Davies, M.S. & Hawkins, S.J. 1998. Mucus from marine molluscs. *Advances in Marine Biology* **34**, 1–71.
- Davies, M.S. & Williams, G.A. 1995. Pedal mucus of a tropical limpet, *Cellana grata*: energetics, production and fate. *Journal of Experimental Marine Biology and Ecology* **187**, 77–87.
- Davies, M.S. & Williams, G.A. 1997. Mucus production by species of *Siphonaria* (Mollusca: Gastropoda: Pulmonata) in Hong Kong. In *The marine flora and fauna of Hong Kong and Southern China, IV. Proceedings of the Eighth International Marine Biological Workshop: The marine flora and fauna of Hong Kong and Southern China*, B.Morton (ed.). Hong Kong: Hong Kong University Press, 2–20.
- Davies, P.S. 1969. Physiological ecology of *Patella*. III. Desiccation effects. *Journal of the Marine Biological Association of the United Kingdom* **49**, 291–309.
- Davies-Coleman, M.T. & Garson, M.J. 1998. Marine polypropionates. *Natural Products Reports* **15**, 477–93.
- Della Santina, P. & Naylor, E. 1993. Endogenous rhythms in the homing behaviour of the limpet *Patella vulgata* Linnaeus. *Journal of Molluscan Studies* **59**, 87–91.
- De Villiers, C.J. & Hodgson, A.N. 1984. The structure of the epidermal glands of *Siphonaria capensis* (Gastropoda; Pulmonata). *Proceedings of the Electron Microscopy Society of Southern Africa* **14**, 93–4.
- De Villiers, C.J. & Hodgson, A.N. 1987. The structure of the secondary gills of *Siphonaria capensis* (Gastropoda: Pulmonata). *Journal of Molluscan Studies* **53**, 129–38.
- De Villiers, C.J., Grange, N. & Wise, D.L. 1985. A study of the alimentary tract of *Siphonaria capensis* (Mollusca: Gastropoda). *Proceedings of the Electron Microscopy Society of Southern Africa* **15**, 133–4.
- De Zwaan, A. 1977. Anaerobic energy metabolism in bivalve molluscs. *Oceanography and Marine Biology: An Annual Review* **15**, 103–87.
- Dieuzeide, R. 1935. Contribution à l'étude de deux types de gastéropode pulmonés marins: *Siphonaria algerirae* Q & G; *Gadinia garnotii* Payr. *Station d'aquiculture et de pêche de Castiglioni*, volume for 1934, 1–196.
- Dye, A.H. 1987. Aerial and aquatic oxygen consumption in two siphonariid limpets (Pulmonata: Siphonariidae). *Comparative Biochemistry and Physiology* **87A**, 695–8.

- Eckelbarger, K.J. 1994. Diversity of metazoan ovaries and vitellogenic mechanisms: implications of life history theory. *Proceedings of the Biological Society of Washington* **107**, 193–218.
- Evans, M.R. & Williams, G.A. 1991. Time partitioning of foraging in the limpet *Patella vulgata*. *Journal of Animal Ecology* **60**, 563–75.
- Frescura, M. 1991. Aspects of the structure and function of some gastropod columellar muscles (Mollusca). PhD thesis, Rhodes University.
- Frescura, M. & Hodgson, A.N. 1992. The fine structure of the columellar muscle of some gastropod mollusks. *The Veliger* **35**, 308–15.
- Fretter, V. & Graham, A. 1954. Observations on the opisthobranch mollusc *Acteon tornatilis* (L.). *Journal of the Marine Biological Association of the United Kingdom* **33**, 565–85.
- Garrity, S.D. 1984. Some adaptations of gastropods to physical stress on a tropical rocky shore. *Ecology* **65**, 559–74.
- Garrity, S.D. & Levings, S.C. 1983. Homing to scars as a defense against predators in the pulmonate limpet *Siphonaria gigas* (Gastropoda). *Marine Biology* **72**, 319–24.
- Garrity, S.D. & Levings, S.C. 1985. Interspecific interactions and scarcity of a tropical limpet. *Journal of Molluscan Studies* **51**, 297–308.
- Geraerts, W.P.M. & Joose, J. 1984. Freshwater snails (Basommatophora). In *The Mollusca. 7: Reproduction*. A.S.Tompa et al. (eds). Orlando: Academic Press, 142–207.
- Godoy, C. & Moreno, C.A. 1989. Indirect effects of human exclusion from the rocky intertidal in southern Chile: a case of cross-linkage between herbivores. *Oikos* **54**, 101–6.
- Gray, C.A., Davies-Coleman, M.T. & McQuaid, C. 1998. Labdane diterpenes from the South African marine pulmonate *Trimusculus costatus*. *Natural Product Letters* **12**, 47–53.
- Gray, D.R. & Hodgson, A.N. 1997. Temporal variation in foraging behaviour of *Patella granularis* (Patellogastropoda) and *Siphonaria concinna* (Basommatophora) on a South African shore. *Journal of Molluscan Studies* **63**, 121–30.
- Gray, D.R. & Hodgson, A.N. 1999. Endogenous rhythms of locomotor activity in the high shore limpet *Helcion pectunculus* (Patellogastropoda). A preliminary investigation. *Animal Behaviour* **57**, 387–91.
- Haszprunar, G. & Huber, G. 1990. On the central nervous system of Smeagolidae and Rhodopidae, two families questionably allied with the Gymnomorpha (Gastropoda: Euthyneura). *Journal of Zoology* **220**, 185–99.
- Haven, N. 1974. Reproduction, development, and feeding of the Australian marine pulmonate, *Trimusculus (Gadinia) conica*. *The Veliger* **16**, 61–5.
- Hawkins, S.J. & Hartnoll, R.G. 1983. Grazing of intertidal algae by marine invertebrates. *Oceanography and Marine Biology: an Annual Review* **21**, 195–282.
- Hawkins, S.J., Watson, D.C., Hill, A.S., Harding, S.P., Kyriakides, M.P., Hutchinson, S. & Norton, T.A. 1989. A comparison of feeding mechanisms in microphagous herbivorous intertidal prosobranchs in relation to resource partitioning. *Journal of Molluscan Studies* **55**, 151–65.
- Healy, J.M. 1983. An ultrastructural study of basommatophoran spermatozoa (Mollusca, Gastropoda). *Zoologica Scripta* **12**, 57–66.
- Hirano, Y. 1980. *Siphonaria* (pulmonate limpet) survey of Japan. II. Periodicity of spawning activity in *Siphonaria japonica*. *Publications of the Seto Marine Biological Laboratory* **25**, 335–42.
- Hirano, Y. 1981. Comparative ecological studies on the habitat and habits of intertidal limpets. *Journal of Science of Hiroshima University Series B* **29**, 1–45.
- Hirano, Y. & Inaba, A. 1980. *Siphonaria* (pulmonate limpet) survey of Japan. I. Observations on the behavior of *Siphonaria japonica* during breeding season. *Publications of the Seto Marine Biological Laboratory* **25**, 323–34.
- Hochlowski, J.E. & Faulkner, D.J. 1983. Antibiotics from the marine pulmonate *Siphonaria diemenensis*. *Tetrahedron Letters* **24**, 1917–20.
- Hochlowski, J.E., Faulkner, D.J., Matsumoto, G.K. & Clardy, J. 1983. The denticulatins, two polypropionate metabolites from the pulmonate *Siphonaria denticulata*. *Journal of the American Chemical Society* **105**, 7413–15.
- Hodgson, A.N. & Healy, J. 1998. Comparative sperm morphology of the pulmonate limpets *Trimusculus costatus*, *T. reticulatus* (Trimusculidae) and *Burnupia stenochorias* and *Ancylus fluviatilis* (Ancylidae). *Journal of Molluscan Studies* **64**, 447–60.
- Hodgson, A.N., Bernard, R.T.F. & Lindley, D.S. 1991. Comparative spermatology of four sympatric species of *Siphonaria* (Pulmonata: Basommatophora). *Journal of Molluscan Studies* **57**, 309–22.

- Hodgson, A.N., de Villiers, C.J. & Bojarski, C. 1990. A preliminary examination of the structure of the salivary gland of *Siphonaria capensis* (Gastropoda: Pulmonata). *Proceedings of the Electron Microscopy Society of Southern Africa* **20**, 193–4.
- Hodgson, A.N., Farquhar, M.R. & de Villiers, C.J. 1993. Variations in infestations of *Siphonaria capensis* and *S. concinna* (Pulmonata) by larval trematodes in southern Africa. *Journal of Molluscan Studies* **59**, 83–93.
- Houlihan, D.F. 1979. Respiration in air and water of three mangrove snails. *Journal of Experimental Marine Biology and Ecology* **41**, 143–61.
- Hubendick, B. 1946. Systematic monograph of the Patelliformia. *Kungliga Svenska Vetenshapsakademiens Handlingar Tredje Serien* **23**, 5–93.
- Hubendick, B. 1947. Phylogenie und Tiergeographie der Siphonariidae. Zur Kenntnis der Phylogenie in der Ordnung Basommatophora und des Ursprungs der Pulmonatengruppe. *Zoologiska Bidrag Från Uppsala* **24**, 1–216.
- Hubendick, B. 1978. Systematics and comparative morphology of the Basommatophora. In *Pulmonates* 2A, V.Fretter & J.Peake (eds). London: Academic Press, 1–47.
- Hulings, N.C. 1985. Activity patterns and homing in two intertidal limpets, Jordan Gulf of Aqaba. *The Nautilus* **99**, 75–80.
- Hutton, F.W. 1882. Notes on the structure and development of *Siphonaria australis*, Quoy and Gaimard. *Annals and Magazine of Natural History, Series 5*, **9**, 341–4.
- Hyman, L.H. 1967. *The invertebrates, Volume VI, Mollusca I*. New York: McGraw-Hill.
- Innes, A.J., Marsden, I.D. & Wong, P.P.S. 1984. Bimodal respiration of intertidal pulmonates. *Comparative Biochemistry and Physiology* **77A**, 441–5.
- Iwasaki, K. 1993a. Analyses of limpet defense and predator offense in the field. *Marine Biology* **116**, 277–89.
- Iwasaki, K. 1993b. Synergistic effects of mixed grazing by intertidal limpets on sessile organisms: consequences of differences in grazing ability and feeding habit. *Physiological Ecology of Japan* **30**, 1–30.
- Iwasaki, K. 1993c. The role of individual variability in limpet resting site fidelity and competitive ability in the organization of a local rocky intertidal community. *Physiological Ecology of Japan* **30**, 31–70.
- Iwasaki, K. 1993d. Individual variation, social structure, community organization and hierarchical views in the marine context. In *Mutualism and community organization: behavioural, theoretical and food-web approaches*, H.Kawanabe et al. (eds). Oxford: Oxford University Press, 13–36.
- Iwasaki, K. 1994. Intra- and interspecific variation in activity patterns of intertidal limpets. *Venus* **53**, 85–104.
- Iwasaki, K. 1995a. Foraging and spawning rhythms of the pulmonate limpet *Siphonaria sirius* (Pilsbry): switching of activity period by a diurnal forager. *Journal of Molluscan Studies* **61**, 275–88.
- Iwasaki, K. 1995b. Dominance order and resting site fidelity in the intertidal pulmonate limpet *Siphonaria sirius* (Pilsbry). *Ecological Research* **10**, 105–15.
- Jara, H.F. & Moreno, C.A. 1984. Herbivory and structure in a midlittoral rocky community: a case in southern Chile. *Ecology* **65**, 28–38.
- Jenkins, B.W. 1981. *Siphonaria funiculata* Reeve (Siphonariidae, Pulmonata): a redescription making *S. virgulata* Hedley a geographical variant of *S. funiculata*. *Journal of the Malacological Society of Australia* **5**, 1–15.
- Jenkins, B.W. 1983. Redescriptions and relationship of *Siphonaria zelandica* Quoy and Gaimard to *S. australis* Quoy and Gaimard with a description of *S. propria* sp. nov. (Mollusca: Pulmonata: Siphonariidae). *Journal of the Malacological Society of Australia* **6**, 1–35.
- Jenkins, B.W. 1984. A new siphonarid (Mollusca: Pulmonata) from southwestern Australia. *Journal of the Malacological Society of Australia* **6**, 113–23.
- Johnson, M.S. & Black, R. 1982. Chaotic genetic patchiness in an intertidal limpet, *Siphonaria* sp. *Marine Biology* **70**, 157–64.
- Johnson, M.S. & Black, R. 1984a. The Wahlund effect and the geographical scale of variation in the intertidal limpet *Siphonaria* sp. *Marine Biology* **79**, 295–302.
- Johnson, M.S. & Black, R. 1984b. Pattern beneath the chaos: the effect of recruitment on genetic patchiness in an intertidal limpet. *Evolution* **38**, 1371–82.
- Jones, H.D. & Trueman, E.R. 1970. Locomotion of the limpet, *Patella vulgata* L. *Journal of Experimental Biology* **52**, 201–17.

- Kahn, H.R., Ashton, M.L. & Saleuddin, A.S.M. 1990. Changes in the fine structure of the endocrine dorsal body cells of *Helisoma duryi* (Mollusca) induced by mating. *Journal of Morphology* **203**, 41–53.
- Keough, M.J. & Quinn, G.P. 1998. Effects of periodic disturbances from trampling on rocky intertidal algal beds. *Ecological Applications* **8**, 141–61.
- Kilburn, R. & Rippey, E. 1982. *Sea shells of southern Africa*. Johannesburg: Macmillan.
- Knox, G.A. 1955. The development of *Kerguelenella stewartiana* (Powell) (Gastropoda: Siphonariidae). *Pacific Science* **9**, 85–9.
- Köhler, A. 1893. Beiträge zur Anatomic der Gattung *Siphonaria*. *Zoologische Jahrbucher. Abtheilung für Anatomic und Ontogenie der Thiere* **7**, 1–85.
- Lasiak, T.A. & White, D.R.A. 1993. Microalgal food resources and competitive interactions among the intertidal limpets *Cellana capensis* (Gmelin 1791) and *Siphonaria concinna* Sowerby, 1824. *South African Journal of Marine Science* **13**, 97–108.
- Levings, S.C. & Garrity, S.D. 1984. Grazing patterns in *Siphonaria gigas* (Mollusca, Pulmonata) on the rocky Pacific coast of Panama. *Oecologia* **64**, 152–9.
- Levings, S.C. & Garrity, S.D. 1986. Notes on reproduction of a tropical pulmonate limpet, *Siphonaria gigas* (Sowerby). *The Veliger* **29**, 86–90.
- Lindberg, D.R. & Dwyer, K.R. 1983. The topography, formation and role of the home depression of *Collisella scabra* (Gould). *The Veliger* **25**, 229–34.
- Little, C. 1989. Factors governing patterns of activity in littoral marine herbivorous molluscs. *Journal of Molluscan Studies* **55**, 273–84.
- Little, C. & Stirling, P. 1985. Patterns of foraging activity in the limpet *Patella vulgata* L.—a preliminary study. *Journal of Experimental Marine Biology and Ecology* **89**, 283–96.
- Liu, J.H. 1994. Distribution and population dynamics of three populations of *Siphonaria* on rocky intertidal shores in Hong Kong. *Journal of Molluscan Studies* **60**, 431–43.
- López Gappa, L., Tablado, A. & Magaldi, N. 1996. Observations on activity pattern and resting site fidelity in the pulmonate limpet *Siphonaria lessoni*. *Thalassas* **12**, 27–36.
- Lubchenco, J. & Gaines, S.D. 1981. A unified approach to marine plant-herbivore interactions. 1. Populations and communities. *Annual Review of Ecology and Systematics* **12**, 405–37.
- Malli, P.C., Prasad, M.N. & Mansuri, A.P. 1982. The response of the limpets, *Cellana radiata* (Born) and *Siphonaria siphonaria* (Sowerby) of Saurashtra coast, to desiccation and waters of different salinity. *Journal of Animal Morphology and Physiology* **29**, 71–7.
- Mapstone, G.M. 1978. Egg capsules and early development in *Siphonaria diemenensis* (Quoy & Gaimard 1833) and *Siphonaria baconi* (Reeve 1856). *Journal of the Malacological Society of Australia* **4**, 85–92.
- Marcus, E. & Marcus, E. 1960. On *Siphonaria hispida*. *Universidade de Sao Paulo. Faculdade de Filosofia, Ciências e Letras. Boletim de Zoologia* **23** (nr. 23), 107–39.
- Marshall, B.A. 1981. The genus *Williamia* in the western Pacific (Mollusca: Siphonariidae). *New Zealand Journal of Zoology* **8**, 487–92.
- Marshall, D.J. & McQuaid, C.D. 1989. The influence of respiratory responses on the tolerance to sand inundation of the limpets *Patella granularis* L. (Prosobranchia) and *Siphonaria capensis* Q. et G. (Pulmonata). *Journal of Experimental Marine Biology and Ecology* **128**, 191–201.
- Marshall, D.J. & McQuaid, C.D. 1991. Metabolic rate depression in a marine pulmonate snail: pre-adaptation for a terrestrial existence? *Oecologia* **88**, 274–6.
- Marshall, D.J. & McQuaid, C.D. 1992a. Comparative aerial metabolism and water relations of the intertidal limpets *Patella granularis* L. (Mollusca: Prosobranchia) and *Siphonaria oculus* Kr. (Mollusca: Pulmonata). *Physiological Zoology* **65**, 1040–56.
- Marshall, D.J. & McQuaid, C.D. 1992b. Relationship between heart rate and oxygen consumption in the intertidal limpets *Patella granularis* and *Siphonaria oculus*. *Comparative Biochemistry and Physiology* **103A**, 297–300.
- Marshall, D.J. & McQuaid, C.D. 1993. Effects of hypoxia and hyposalinity on the heart beat of the intertidal limpets *Patella granularis* (Prosobranchia) and *Siphonaria capensis* (Pulmonata). *Comparative Biochemistry and Physiology* **106A**, 65–8.
- Marshall, D.J. & McQuaid, C.D. 1994. Seasonal and diel variations of in situ heart rate of the intertidal limpet *Siphonaria oculus* Kr. (Pulmonata). *Journal of Experimental Marine Biology and Ecology* **179**, 1–9.

- Maxwell, W.L. 1983. Mollusca. In *Reproductive biology of invertebrates, V.II: Spermatogenesis and sperm function*, K.G.Adiyodi & R.G.Adiyodi (eds). Chichester: John Wiley, 275–319.
- McAlister, R.O. & Fisher, R.M. 1968. Responses of the false limpet, *Siphonaria pectinata* Linnaeus (Gastropoda, Pulmonata) to osmotic stress. *Biological Bulletin* **134**, 96–117.
- McAlpine, D. 1952. Notes on some Siphonariidae. *Proceedings of the Royal Zoological Society of New South Wales* 36–42.
- McLean, J.H. 1998. Reinstatement of *Williamia subspiralis* (Carpenter 1864) (Gastropoda, Siphonariidae). *The Veliger* **41**, 243–8.
- McMahon, R.F. & Russell-Hunter, W.D. 1981. The effects of physical variables and acclimation on survival and oxygen consumption in the high littoral salt-marsh snail, *Melampus bidentatus* Say. *Biological Bulletin* **161**, 246–69.
- Menge, B.A. 1973. Effect of predation and environmental patchiness on the body size of a tropical pulmonate limpet. *The Veliger* **16**, 87–92.
- Mestayer, M.K. 1920. Notes on the spawn coils of *Kerguelenella obliquata*. *New Zealand Journal of Science and Technology* **3**, 171–2.
- Moreno, C.A. & Zamorano, J.H. 1980. Selectividad del alimento en dos peces bentófagos (*Mugiloides chilensis* y *Calliclinus geniguttatus*). *Boletim do Instituto Oceanográfico, São Paulo* **29**, 245–9.
- Moreno, C.A., Sutherland, J.P. & Jara, H.F. 1984. Man as a predator in the intertidal zone of southern Chile. *Oikos* **42**, 155–60.
- Morrison, J.P.E. 1963. Notes on American *Siphonaria*. *Bulletin of the American Malacological Union* **30**, 7–9.
- Morton, J.E. 1955. The evolution of the Ellobiidae with a discussion on the origin of the Pulmonata. *Proceedings of the Zoological Society of London* **125**, 127–68.
- Navarrete, S.A. & Castilla, J.C. 1993. Predation by Norway rats in the intertidal zone of central Chile. *Marine Ecology Progress Series* **92**, 187–99.
- Nordsieck, N. 1992. Phylogeny and system of the Pulmonata (Gastropoda). *Archiv für Molluskenkunde* **121**, 31–52.
- Ohgushi, R. 1954. Ethological studies on the intertidal limpets. I. On the tidal rhythmic activities of two species of limpets. [In Japanese with English summary]. *Japanese Journal of Ecology* **4**, 120–22.
- Ohgushi, R. 1955. Ethological studies on the intertidal limpets. II. Analytical studies on the homing behaviour of two species of limpets. [In Japanese with English summary]. *Japanese Journal of Ecology* **5**, 31–5.
- Ohgushi, R., Miura, T. & Kotani, M. 1953. Some observations on the homing behaviours of two species of limpets. *Venus* **17**, 219–23.
- Olivier, S.R. & Penchaszadeh, P.E. 1968. Observaciones sobre la ecología y biología de *Siphonaria (Pachysiphonaria) lessoni* (Blainville 1824) (Gastropoda, Siphonariidae) en el litoral rocoso de Mar del Plata (Buenos Aires). *Cahiers de Biologie Marine* **9**, 469–91.
- Ortega, S. 1985. Competitive interactions among tropical intertidal limpets. *Journal of Experimental Marine Biology and Ecology* **90**, 11–25.
- Ortega, S. 1986. Fish predation on gastropods on the Pacific coast of Costa Rica. *Journal of Experimental Marine Biology and Ecology* **97**, 181–91.
- Ortega, S. 1987a. The effect of human predation on the size distribution of *Siphonaria gigas* (Mollusca: Pulmonata) on the Pacific coast of Costa Rica. *The Veliger* **29**, 251–5.
- Ortega, S. 1987b. Habitat segregation and temporal variation in some tropical intertidal populations. *Journal of Experimental Marine Biology and Ecology* **113**, 247–65.
- Paine, R.T. & Palmer, A.R. 1978. *Sicyases sanguineus*: a unique trophic generalist from the Chilean intertidal zone. *Copeia* **1978**, 75–81.
- Palmer, A.R. 1979. Fish predation and the evolution of gastropod shell sculpture: experimental and geographic evidence. *Evolution* **33**, 697–713.
- Palmer, J.D. 1995. *The biological rhythms and clocks of intertidal animals*. New York: Oxford University Press.
- Prasad, M.N., Malli, P.C. & Mansuri, A.P. 1988. Adaptational strategies of two tropical intertidal limpets. *Comparative Physiology and Ecology* **13**, 135–9.
- Purchon, R.D. 1979. *The biology of the Mollusca*. Oxford: Pergamon Press.
- Quinn, G.P. 1983. Spawning and egg masses of *Siphonaria tasmanica* Tenison Woods, 1876 from Victoria. *Journal of the Malacological Society of Australia* **6**, 81–2.

- Quinn, G.P. 1988a. Ecology of the intertidal pulmonate limpet *Siphonaria diemenensis* Quoy et Gaimard. I. Population dynamics and availability of food. *Journal of Experimental Marine Biology and Ecology* **117**, 115–36.
- Quinn, G.P. 1988b. Ecology of the intertidal pulmonate limpet *Siphonaria diemenensis* Quoy et Gaimard. II. Reproductive patterns and energetics. *Journal of Experimental Marine Biology and Ecology* **117**, 137–56.
- Quinn, G.P. 1988c. Effects of conspecific adults, macroalgae and height on the shore on recruitment of an intertidal limpet. *Marine Ecology Progress Series* **48**, 305–8.
- Quinn, G.P. & Ryan, N.R. 1989. Competitive interactions between two species of intertidal herbivorous gastropods from Victoria, Australia. *Journal of Experimental Marine Biology and Ecology* **125**, 1–12.
- Rankin, J.C. & Davenport, J. 1981. *Animal osmoregulation*. New York: John Wiley.
- Read, K.R.H. 1968. The myoglobins of the gastropod molluscs *Busycon contrarium* Conrad, *Lunatia heros* Say, *Littorina littorea* L. and *Siphonaria gigas* Sowerby. *Comparative Biochemistry and Physiology* **25**, 81–94.
- Rice, S.H. 1985. An anti-predator chemical defense of the marine pulmonate gastropod *Trimusculus reticulatus* (Sowerby). *Journal of Experimental Marine Biology and Ecology* **93**, 83–9.
- Ridgway, S.A., Reid, D.G., Taylor, J.D., Branch, G.M. & Hodgson, A.N. 1998. A cladistic phylogeny of the family Patellidae (Mollusca, Gastropoda). *Philosophical Transactions of the Royal Society of London, Series B* **353**, 1645–71.
- Saleuddin, A.S.M., Ashton, M.L. & Kahn, H.R. 1989. Mating-induced release of granules by the endocrine dorsal body cells of the snail *Helisoma duryi* (Mollusca). *Journal of Experimental Zoology* **250**, 206–13.
- Saleuddin, A.S.M., Ashton, M.-L. & Kahn, H.R. 1997. An electron microscope study of the endocrine dorsal bodies in reproductively active and inactive *Siphonaria pectinata* (Pulmonata: Mollusca). *Tissue and Cell* **29**, 267–75.
- Saleuddin, A.S.M., Kunigelis, S.C., Schollen, L.M., Breckenridge, W.R. & Mykys, S.L. 1983. Studies on endocrine control of respiration in *Helisoma* and *Helix*. In *Molluscan neurobiology*, J.Lever & H.Boer (eds). Holland: Elsevier, 138–41.
- Salvini-Plawen, L.V. 1990. Origin, phylogeny and classification of the phylum Mollusca. *Iberus* **9**, 1–33.
- Salvini-Plawen, L.V. & Steiner, G. 1996. Synapomorphies and plesiomorphies in higher classification of Mollusca. In *Origin and evolutionary radiation of the Mollusca*, J.D.Taylor (ed.). Oxford: Oxford University Press, 29–51.
- Santelices, B. & Bobadilla, M. 1996. Gastropod pedal mucus retains seaweed propagules. *Journal of Experimental Marine Biology & Ecology* **197**, 251–61.
- Santelices, B. & Correa, J. 1985. Differential survival of macroalgae to digestion by intertidal herbivore molluscs. *Journal of Experimental Marine Biology and Ecology* **88**, 183–91.
- Scheltema, R.S. 1995. The relevance of passive dispersal for the biogeography of Caribbean molluscs. *American Malacological Bulletin* **11**, 99–115.
- Shumway, S.E. 1981. Factors affecting oxygen consumption in the marine pulmonate *Amphibola crenata* (Gmelin 1791). *Biological Bulletin* **160**, 332–47.
- Simpson, J.W., Allen, K. & Awapara, J. 1959. Free amino acids in some aquatic invertebrates. *Biological Bulletin* **117**, 371–81.
- Simpson, R.D. 1976. Physical and biotic factors limiting the distribution and abundance of littoral molluscs on Macquarie Island (Sub-Antarctic). *Journal of Experimental Marine Biology and Ecology* **21**, 11–49.
- Simpson, R.D. 1977. The reproduction of some littoral molluscs from Macquarie Island (Sub-Antarctic). *Marine Biology* **44**, 125–42.
- Simpson, R.D. & Harrington, S.A. 1985. Egg masses of three gastropods, *Kerguelenella lateralis* (Siphonariidae), *Laevittorina caliginosa* and *Macquariella hamiltoni* (Littorinidae), from Macquarie Island (sub-Antarctic). *Journal of the Malacological Society of Australia* **7**, 17–28.
- Strathmann, M.F. 1987. *Reproduction and development of marine invertebrates of the northern Pacific Coast*. Seattle: University of Washington Press.
- Sumikawa, S. & Funakoshi, C. 1984. The fine structure of mature spermatozoa in two species of the Siphonariidae (Pulmonata: Basommatophora). *Venus, Japanese Journal of Malacology* **43**, 143–55.

- Sutherland, J.P. & Ortega, S. 1986. Competition conditional on recruitment and temporary escape from predators on a tropical rocky shore. *Journal of Experimental Marine Biology and Ecology* **95**, 155–66.
- Tablado, A., López Gappa, J.J. & Magaldi, N.H. 1994. Growth of the pulmonate limpet *Siphonaria lessoni* (Blainville) in a rocky intertidal area affected by sewage pollution. *Journal of Experimental Marine Biology and Ecology* **175**, 211–26.
- Thiele, J. 1931. *Handbuch der systematischen Weichtierkunde*, Jena: P.Fischer.
- Thomas, R.F. 1973. Homing behavior and movement rhythms in the pulmonate limpet, *Siphonaria pectinata* Linnaeus. *Proceedings of the Malacological Society of London* **40**, 303–11.
- Thorson, G. 1940. Studies on the egg masses and larval development of gastropods from the Iranian Gulf. *Danish Scientific Investigations in Iran* **2**, 189–238.
- Thorson, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. *Biological Reviews* **25**, 1–45.
- Tillier, S. 1984. Relationships of gymnomorph gastropods (Mollusca, Gastropoda). *Zoological Journal of the Linnean Society* **82**, 345–62.
- Tillier, S. & Ponder, W.F. 1992. New species of *Smeagol* from Australia and New Zealand, with a discussion of the affinities of the genus (Gastropoda: Pulmonata). *Journal of Molluscan Studies* **58**, 135–55.
- Tillier, S., Masselot, M. & Tillier, A. 1996. Phylogenetic relationships of the pulmonate gastropods from rRNA sequences, and tempo and age of the stylomatophoran radiation. In *Origin and evolutionary radiation of the Mollusca*, J.Taylor (ed.). Oxford: Oxford University Press. 267–84.
- Underwood, A.J. & Jernakoff, P. 1981. Effects of interactions between algae and grazing gastropods on the structure of a low shore intertidal algal community. *Oecologia* **48**, 221–33.
- Verderber, G.W., Cook, S.B. & Cook, C.B. 1983. The role of the home scar in reducing water loss during aerial exposure of the pulmonate limpet, *Siphonaria alternata* (Say). *The Veliger* **25**, 235–43.
- Vermeij, G.J. 1971a. Temperature relationships of some tropical Pacific intertidal gastropods. *Marine Biology* **10**, 308–14.
- Vermeij, G.J. 1971b. Substratum relationships of some tropical Pacific intertidal gastropods. *Marine Biology* **10**, 315–20.
- Vermeij, G.J. 1973. Morphological patterns in high-intertidal gastropods: adaptive strategies and their limitations. *Marine Biology* **20**, 319–46.
- Vermeij, G.J. & Rosenberg, G. 1993. Giving and receiving: the tropical Atlantic as donor and recipient region for invading species. *American Malacological Bulletin* **10**, 181–93.
- Voss, N.A. 1959. Studies on the pulmonate gastropod *Siphonaria pectinata* (Linnaeus) from the southeast coast of Florida. *Bulletin of Marine Science of the Gulf and Caribbean*, **9**, 84–99.
- Wells, R.M.G. & Wong, P.P.S. 1978. Respiratory functions of the blood in the limpet *Siphonaria zelandica* (Gastropoda: Pulmonata). *New Zealand Journal of Zoology* **5**, 417–20.
- Williams, G.A. 1993. Seasonal variation in algal species richness and abundance in the presence of molluscan herbivores on a tropical rocky shore. *Journal of Experimental Marine Biology and Ecology* **167**, 261–75.
- Williams, J.P.F. 1964. A preliminary investigation into the osmoregulation of the pulmonate gastropod *Siphonaria aspera*. BSc (Hons) thesis, Rhodes University.
- Wolcott, T.G. 1973. Physiological ecology and intertidal zonation in limpets (*Acmaea*): a critical look at limiting factors. *Biological Bulletin* **145**, 389–422.
- Yonge, C.M. 1952. The mantle cavity of *Siphonaria alternata* Say. *Proceedings of the Malacological Society of London* **29**, 190–99.
- Zischke, J.A. 1974. Spawning, development and growth in the pulmonate limpets *Siphonaria pectinata* Linnaeus, 1758 and *Siphonaria alternata* Say, 1882. *The Veliger* **16**, 399–404.

AUTHOR INDEX

References to complete articles are given in **bold type**; references to page numbers are given in normal type; references to bibliographical lists are given in *italics*.

- Abe, N., 260, 261, 266, 272, 274, 275, 276,
277, 278, 279, 287, 291, 292, 293, 294, 295,
299, 300, 301; 306
- Abel, K.M. *See* Drew, E.A., 105; 124
- Abeloos, M., 130; 146
- Adey, W.H., 70, 71; 75
See Hackney, J.M., 79
- Admiraal, W., 48, 67, 71; 75
See Ludden, E., 81
- Ahmad, M. *See* Skibinski, D.O.F., 152
- Alaux, G. *See* Jean-Baptiste, P., 39
- Alberte, R.S. *See* Perry, M.J., 82
- Albritton, D. *See* Schimel, D.S., 43
- Alivon, E. *See* Barranguet, C., 76
- Allanson, B.R., 246, 249, 250, 257, 258, 259,
264, 265, 266, 278, 279, 285, 293; 306
- Allbut, C. *See* Lubbock, R., 130; 149
- Allcock, A.L., 130, 133; 146
- Allee, W.C., 226; 229
- Allen, K. *See* Simpson, J.W., 313
- Allen, M.R. *See* Watts, P.D., 45
- Aller, R.C. *See* Sun, M.-Y., 85
- Alliot, E. *See* Barranguet, C., 76
See Plante-Cuny, M.R., 83
- Alongi, D.M., 73; 75
- Alves, D. *See* Schimel, D.S., 43
- Ampoker, M.C. *See* McIntire, C.D., 57; 81
- Anderson, D.T., 292, 300, 301; 306
See Otway, N.M., 157; 239
- Anderson, J.G. *See* Meadows, P.S., 49; 81
- Anderson, J.R. *See* Burger, J.F., 230
- Anderson, M.L., 23; 35
- Anderson, R.J. *See* Oost, W.A., 42
See Smith, S.D., 43
- Andreae, M.O., 1; 35
See Bange, H.W., 35
See Charlson, R.J., 36
See Kim, K.H., 1; 39
See Uher, G., 1; 44
- Andres, A., 131; 146
- Andrews, D.L. *See* Mujer, C.V., 126
- Anger, K. *See* Harms, J., 165; 235
- Antezana, T. *See* Morales, C., 170; 238
- Antia, N.J., 71; 75
- Apts, C.W. *See* Hardy, J.T., 26; 38
- Araujo, M.E. *See* Solé-Cava, A.M., 152
- Arnold, J.M., 205; 229
- Arnold, K.O. *See* Arnold, J.M., 205; 229
- Arvidsson, J. *See* Feder, H.M., 206; 233
- Arvy, L., 154; 229
- Asher, W. *See* Wanninkhof, R., 44
- Asher, W.E., 7, 17, 23, 24, 25; 35
- Ashton, M.L. *See* Kahn, H.R., 311
See Saleuddin, A.S.M., 313
- Asmus, H., 73; 75
- Asmus, R., 49, 55; 75
See Asmus, H., 73; 75
- Ates, R.M.L., 129; 146
- Avelin, Sr M. *See* Vitalina, Sr M., 243
- Avise, J.C. *See* Karl, S.A., 145; 149
- Awapara, J. *See* Simpson, J.W., 313
- Ayre, D.J., 129, 130, 132, 135, 139, 142, 143,
144; 146
See Hunt, A., 130, 135; 149
- Azevedo, C., 288; 306
- Badgley, F. *See* Miyake, M., 41
- Bahls, H., 156; 229
- Baillie, P.W., 55, 70, 72; 75, 76
- Bainbridge, A.E. *See* Peng, T.-H., 42
- Baird, I.E. *See* Steele, J.H., 48, 59, 66; 85
- Bal, D.V. *See* Wagh, A.B., 165, 227; 243
- Balazs, G.H. *See* Losey, G.S., 237
- Balick, M. *See* Hadrys, H., 148
- Balls, P.W. *See* Liss, P.S., 40
- Bange, H.W., 1, 18, 23; 35
- Banks, R B., 32; 35
- Baptista, L.R.M. *See* Garcia-Baptista, M., 49;
79
- Barilotti, D.C. *See* Dawes, C.J., 104; 123
- Barnes, H., 154, 156, 157, 158, 162, 171, 173,
188, 199, 200, 201, 202, 204, 207, 225;
229
- Barnes, M., **158–244**; 169, 171, 188, 191, 209,
225, 226; 229
- Barnett, B.E., 189, 194; 229
- Barnier, B. *See* Boutin, J., 36
- Barranguet, C., 55, 64, 68; 76
See Plante-Cuny, M.R., 83
- Barreiro, M.T. *See* Day, J.W., 77

AUTHOR INDEX

- Barrett, J.C. *See* Iannuzzi, T.J., 80
 Barry, J.P. *See* Dayton, P.K., 78
 Bartell, U.H. *See* Bange, H.W., 35
 Barter, J.D. *See* Lee, P.H.Y., 40
 Bartrop, J. *See* Gallop, A., 124
 Bastida, R., 266, 279, 281, 285, 304; 306
 Bate, G.C. *See* du Preez, D.R., 78
 Bates, T.S. *See* Asher, W.E., 35
 See Johnson, J.E., 1; 39
 Bathmann, U.V. *See* Grant, J., 79
 Baur, B., 294; 306
 Bayliss, D.E., 181; 229
 Bayne, B.L., 193; 229
 Beach, K.L. *See* Lee, P.H.Y., 40
 Beardmore, J.A., 145; 146
 See Shaw, P.W., 151
 See Skibinski, D.O.F., 152
 Bebout, B.M., 72; 76
 Bedford, J.J., 264; 306
 Bejda, A.J. *See* Olla, B.L., 239
 Belanger, T.V., 32; 35
 Belviso, S. *See* Jean-Baptiste, P., 39
 Bender, J.A., 178; 229
 Bennett, J. *See* Farmanfarmaian, A., 233
 Beretich Jr, G.R., 62, 64; 76
 See Cahoon, L.B., 76
 Berger, R., 28; 35
 Bergeron, P., 160, 165; 229
 Berkshire, D.C. *See* Hoover, T.E., 27, 28, 31;
 38
 Berland, B.R. *See* Antia, N.J., 75
 Berman, T. *See* Megard, R.O., 69; 81
 Bermingham, E. *See* Coffroth, M.A., 148
 Bermudez, D. *See* Bertness, M.D., 229
 Bernard, F.R., 169, 171, 188, 191, 209; 229
 Bernard, R.T.F. *See* Hodgson, A.N., 309
 Berry, A.J., 285, 286, 290, 292, 293, 294; 306
 Berthon, J.-F. *See* Morel, A., 63; 82
 Bertness, M.D., 162, 190, 260, 261, 272, 273;
 229, 306
 Bertuzzi, A., 71; 76
 Bianchi, T.S. *See* Roller, R.A., 117; 126
 Bieler, R., 247; 306
 Bigelow, G.W., 55; 76
 Bigger, C.H., 129, 130; 146
 Billen, G. *See* Wollast, R., 50, 51; 86
 Billenand, T. *See* Jähne, B., 39
 Bird, J.L. *See* Kamykowski, D., 70; 80
 Birkeland, C., 206, 207; 229
 See Mauzey, K.P., 237
 Biron, R.W. *See* Pierce, S.K., 126
 Bishop, S. *See* Hanson, R.B., 79
 Biskupiak, J.E., 269; 306
 Blachier, J. *See* Meinesz, A., 125
 Black, R., 118, 121, 135, 137, 139, 259, 260,
 261, 278, 279, 282, 283, 284; 123, 146,
 306
 Black, R. *See* Johnson, M.S., 287, 304; 310
 Blair, S.M. *See* Littler, M., 81
 Blanc, T.V., 14; 35
 Blanchard, D.C., 27; 35
 Blanchard, G. *See* Gouleau, D., 79
 Blanchard, G.F., 67, 73; 76
 See Cariou-Le Gall, V., 49; 77
 See Guarini, J.-M., 79
 See Montagna, P.A., 82
 Blaxter, J.H.S., 213, 214; 229
 Bleakney, J.S. *See* Gibson, G.D., 124
 Bliven, L.F., 6, 32; 36
 See Ho, D.T., 38
 See Wanninkhof, R.H., 7, 8, 9, 11, 20, 22; 45
 Blower, J.G., 171; 229
 Bobadilla, M. *See* Santelices, B., 280; 313
 Bock, I.R., 143; 146
 Bodoy, A., 55, 64; 76
 See Plante-Cuny, M.R., 58, 66; 83
 Bojarski, C. *See* Hodgson, A.N., 310
 Bokenham, N.A.H., 162, 163; 229
 Bold, H.C., 49, 69, 70; 76
 Bolin, B., 28; 36
 Bomberger, D.C. *See* Smith, J.H., 43
 Boney, A.D. *See* Huang, R., 70; 80
 Bonin, D.J. *See* Antia, N.J., 75
 Bonnin, J.-P., 129, 130; 147
 Boolootian, R.A. *See* Farmanfarmaian, A., 233
 Boothe, P. *See* Bender, J.A., 229
 Bopp, R.F., 32; 36
 Borland, C., 246, 260, 262, 272, 274, 277, 279,
 287, 292, 293, 294, 295, 299, 301; 306
 Bosch, M., 164; 230
 Bosinger, R. *See* Jähne, B., 39
 Bosman, A.L. *See* Branch, G.M., 307
 Boss, K.J., 247; 307
 Boucher, G., 64; 76
 Boudouresque, C.F. *See* Lemée, R., 125
 Bourassa, M.A., 20, 34; 36
 Bourget, E., 156, 157, 158; 230
 See Bergeron, P., 160, 165; 229
 See Gosselin, L.A., 160, 195; 234
 Boutin, J., 21; 36
 Boutton, T.W. *See* Tieszen, L.L., 127
 Boyle, E. *See* Trench, R.K., 127
 Brace, R.C., 130, 133, 144; 147
 See Donoghue, A.M., 148
 See Quicke, D.L.J., 130, 135, 136, 144; 151
 Brambati, A. *See* Bertuzzi, A., 76
 Branch, G., 133; 147
 Branch, G.M., 162, 163, 166, 172, 186, 187,
 208, 246, 249, 250, 253, 255, 257, 259,
 260, 262, 263, 264, 265, 266, 267, 268,
 269, 270, 272, 273, 274, 275, 278, 279,
 280, 282, 298, 299, 304; 230, 307
 See Fielding, P.J., 78
 See Ridgway, S.A., 313

AUTHOR INDEX

- Branch, M. *See* Branch, G., 133; 147
 Brandley, B.K., 99, 106, 108, 112, 113, 117; 123
 Branger, H. *See* Bliven, L.F., 36
 Branscomb, E.S., 165, 168; 230
 See Rittschof, D., 241
 Brassington, R.A., 143; 147
 Brawley, S.H., 99; 123
 Braziunas, T.F., 2; 36
 Breckenridge, W.R. *See* Saleuddin, A.S.M., 313
 Brenowitz, A.H., 130; 147
 Bretherton, F. *See* McKeown, W., 41
 Brix, O. *See* Revsbech, N.P., 83
 Broadgate, W. *See* Nightingale, P., 41
 Broecker, H.-C., 14, 21, 25; 36
 Broecker, W.S., 13, 14, 15, 19, 20, 21, 28; 36
 See Emerson, S., 37
 See Peng, T.-H., 42
 See Torgersen, T., 44
 See Wanninkhof, R., 45
 Broecker, W. *See* Peng, T.-H., 13; 42
 Broenkow, W.W. *See* Martin, J.H., 81
 Brookfield, J.F.Y. *See* Bruford, M.W., 147
 Brosnan, D.M., 225, 226; 230
 Brotas, V., 49; 76
 Brown, B., 197; 230
 See Rittschof, D., 241
 See Williams, L.G., 243
 Brown, G.H. *See* Thompson, T.E., 154, 199, 200; 242
 Brown, R.H. *See* Upstill-Goddard, R.C., 34; 44
 Bruenn, J.A. *See* Coffroth, M.A., 148
 Bruford, M.W., 145; 147
 Bryce, C.W. *See* Wells, F.E., 88, 89, 90; 128
 Bucklin, A., 135, 138, 142, 143; 147
 Bufton, A.W.J. *See* Pike, E.B., 42
 Bunse, G. *See* Conrad, R., 37
 Bunt, J.S., 55, 64; 76
 Burckle, L.H. *See* Palmisano, A.C., 82
 Burger, J.F., 171, 172; 230
 Burke, T. *See* Bruford, M.W., 147
 Burkholder, P.R., 49; 76
 Burkill, P.H. *See* Owens, N.J.P., 42
 Burkovsky, I.V. *See* Epstein, S.S., 78
 Burn, R., 88, 90, 91, 92, 118; 123
 Burney, C.M. *See* Sieburth, J.M., 43
 Burrell Jr, V.G., 167; 230
 Burrows, M.T., 191, 193, 194; 230
 See Gibson, R.N., 234
 See Hughes, R.N., 193, 194; 236
 Busacca, M. *See* Clark, K.B., 99, 106, 107, 112, 113, 114, 115; 123
 Businger, J.A., 15; 36
 Butler, A.J., 188, 190; 230
 Butler, J.H., 1; 36
 See Lobert, J.M., 40
 Buyse, J.J. *See* Suijlen, J.M., 18; 44
 Bystrom, B.G. *See* Trench, R.K., 127
 Cadée, G.C., 55; 76
 Caffey, H.M., 182, 183, 185, 196, 227; 230
 Cahoon, L. *See* Posey, M., 83
 Cahoon, L.B., 47-86; 49, 50, 53, 55, 63, 64, 68, 70, 74; 76, 77
 See Sigmon, D.E., 71, 72; 84
 See Thomas, C.J., 73; 85
 Cain, A.J., 137; 147
 Cake Jr, E.W., 192; 230
 Caldwell, D.R., 32; 36
 Callander, B.A. *See* Houghton, J.T., 38
 Cameron, B.B. *See* McFadden, C.S., 150
 Campbell, E.E. *See* du Preez, D.R., 78
 Campbell, N.A. *See* Phillips, B.F., 196; 240
 Cancino, J.M., 217, 218, 219; 230
 Canfield, D.E., 72; 77
 Cao, M., 2; 36
 Capezzani, A. *See* Bastida, R., 306
 Carefoot, T.H. *See* Miller, K.M., 173, 174, 175; 238
 Cariou-Le Gall, V., 49; 77
 See Goulet, D., 79
 Carlgren, O., 130, 131; 147
 Carlson, L. *See* Wulff, A., 86
 Carlucci, A.F., 26; 36
 See Williams, P.M., 45
 Carman, K.R. *See* Dobbs, F.C., 78
 Caron, D.A. *See* Sieburth, J.M., 43
 Carpenter, R., 55, 64, 68; 77
 Carpenter, R.C. *See* Hackney, J.M., 79
 Carriker, M.R., 175, 198; 230
 See Rittschof, D., 241
 See Williams, L.G., 243
 Carter, M.A., 130, 132, 133, 134, 135, 137, 138, 139, 140, 141, 142, 143, 144; 147
 See Haylor, G.S., 148
 See Larkman, A.U., 138; 149
 See Orr, J., 150
 Carter, R.E. *See* Carvalho, G.R., 147
 Carvalho, G.R., 145; 147
 Castel, J. *See* Santos, P.J.P., 84
 Castenholz, R.W. *See* Decho, A.W., 73; 78
 Castilla, J.C., 205, 206, 207; 230
 See Cancino, J.M., 217, 218, 219; 230
 See Durán, L.R., 180, 226; 232
 See Guisado, C., 179; 235
 See Navarrete, S.A., 120; 239
 Castle, R.M. *See* Hadley, C.D., 224, 225; 235
 Caulliez, G. *See* Jähne, B., 39
 Caverhill, C. *See* Longhurst, A., 81
 Cember, R., 13, 19, 20; 36
 Chamberlain, C. *See* Hanson, R.B., 79
 Chambers, R.J., 247, 287, 291, 294, 296, 301, 302, 303, 304; 307

AUTHOR INDEX

- Chambers, R.M., 72; 77
 Chan, Y.-H. *See* Wong, C.S., 15; 45
 Chang, P. *See* Wilke, C.R., 5; 45
 Chao, L.N., 217, 219; 230
 Chapman, A.R.O. *See* McCook, L.J., 160; 237
 Chapron, B. *See* Bliven, L.F., 36
 Charlson, R.J., 1; 36
 Charlson, R. *See* Schimel, D.S., 43
 Charnock, H. *See* Robinson, I.S., 42
 Charpy, L., 65; 77
 Charpy-Roubaud, C., 51, 60; 77
 Charpy-Roubaud, C.J., 56, 65; 77
 See Charpy, L., 65; 77
 Charrier, S. *See* Meinesz, A., 125
 Chen, H. *See* Asher, W.E., 35
 See Wanninkhof, R., 44
 Cherry, M.I. *See* Branch, G.M., 260, 262, 263, 264, 265, 266, 267, 268, 272, 273, 274, 275; 307
 Chétail, M., 198; 230
 Chia, F.-S., 130, 137, 138, 140, 154, 204; 147, 230
 Chia, F.S. *See* Cowden, C., 231
 Chierigato, A.R. *See* Ferrari, L., 213, 214, 216; 234
 Child, A.R., 143; 147
 Chintiroglou, C.C., 130, 132; 148
 Chipman, D.W. *See* Smethie, W.M., 43
 Choat, J.H., 163; 231
 Chong, V.C. *See* Newell, R.I.E., 82
 Christensen, D.J., 168; 231
 Christensen, M.S., 213, 214; 231
 Christensen, P.B. *See* Rysgaard, S., 84
 Christiaens, J., 246; 307
 Christian, R.R. *See* Rizzo, W.M., 84
 Christiansen, M.B. *See* Jahnke, R.A., 53; 80
 Christie, A.O., 154; 231
 Clardy, J. *See* Hochlowski, J.E., 309
 Clark, J.F., 6, 8, 9, 11, 16; 36, 37
 Clark, K.B., 87, 88, 99, 103, 104, 105, 106, 107, 108, 109, 110, 111, 112, 113, 114, 115, 116, 121, 302; 123, 307
 See DeFreese, D.E., 102; 124
 See Stirts, H.M., 106, 114; 126
 See Waugh, G.R., 106, 110, 112; 127
 See Weaver, S., 100, 106, 118; 128
 Clarke, W.B. *See* Jenkins, W.J., 16; 39
 See Münnich, K.O., 41
 Clauss, E., 29, 30; 37
 Clavier, J. *See* Boucher, G., 64; 76
 Clayton, M.N., 104; 123
 Coantic, M., 9; 37
 See Jähne, B., 39
 See Liss, P.S., 40
 Cobb, A.H. *See* Williams, M.L., 87, 106; 128
 Cocks, W.P., 133; 148
 Coffroth, M.A., 145; 148
 Coker, R.D. *See* Nriagu, J.O., 41
 Colebrook, J.M., 138; 148
 Colijn, F., 56, 65; 77
 See Ludden, E., 81
 Collins, K.J., 217, 218; 231
 Connell, J.H., 154, 156, 158, 162, 163, 166, 169, 172, 176, 179, 187, 188, 190, 191, 193, 194, 204, 208, 209, 227, 228; 231
 Connor, M.S., 73, 74; 77
 Conover, D.O. *See* Edwards, D.C., 232
 Conover, J.T., 164; 231
 Conrad, R., 12, 33; 37
 Cook, C.B. *See* Cook, S.B., 261, 274, 275, 276; 307, 308
 See Verderber, G.W., 314
 Cook, S.B., 260, 261, 263, 269, 274, 275, 276, 277, 278; 307, 308
 See Verderber, G.W., 314
 Cooke, J.E. *See* Cahoon, L.B., 50, 55, 63, 64; 77
 Cornwall, J.C. *See* Stribling, J.M., 73; 85
 Corral, L. *See* Azevedo, C., 288; 306
 Correa, J. *See* Santelices, B., 279; 313
 Cory, R.L., 165, 168; 231
 Cosovic, B. *See* Vojvodic, V., 27; 44
 Costlow, J.D. *See* Rittschof, D., 241
 See Standing, J.D., 242
 Cottrell, A.J., 246, 250, 285, 292; 308
 Cowden, C., 154; 231
 Craig, A.K., 279; 308
 Craig, H. *See* Lupton, J.E., 40
 Crampton, D.M., 154, 201; 231
 Cranwell, L.M., 166, 181; 231
 Craven, D.B. *See* Carlucci, A.F., 36
 Creese, R.G., 182, 183, 262, 277, 278, 281, 283, 284, 286, 287, 292, 293, 294, 295, 297, 298, 299, 301, 304; 231, 308
 Crisp, D.J., 143, 157, 162, 165, 285; 148, 231, 308
 See Castilla, J.C., 205, 206, 207; 230
 See Yule, A.B., 162; 244
 Crocker, K.M. *See* Bebout, B.M., 76
 Croley, F.C., 104; 123
 Crucius, J., 22; 37
 Crumrine L.L. *See* Brosnan, D.M., 225, 226; 230
 Crutzen, P.J., 1; 37
 Cullen, J.J. *See* MacIntyre, H.L., 54, 57, 67; 81
 Currey, J.D. *See* Murdock, G.R., 157, 158; 239
 Currin, C.A., 73; 77
 Cushing, D.H., 50, 51; 77
 Daehnick, A.E. *See* Moncrieff, C.A., 82
 Daemen, E.A. M.J., 62; 77
 Daiber, F.C. *See* Gallagher, J.L., 56; 79

AUTHOR INDEX

- Dakin, W.J., 132; 148
 Dalley, R. *See* Christie, A.O., 154; 231
 Daly, M.A., 159; 231
 Dalyell, J.G., 133, 136; 148
 Damstra, K. St J. *See* Fielding, P.J., 78
 Danckwerts, P.V., 7; 37
 Daniel, T.L. *See* Denny, M.W., 232
 Darcy, G.H., 223; 231
 Darley, W.M., 53, 56, 71; 77
 See Whitney, D.E., 62, 64, 65, 67; 86
 Darwin, C., 153, 156; 231, 232
 Davenport, J., 257, 258, 260, 261, 264, 265,
 266, 267, 269, 272, 277, 279, 302; 308
 See Rankin, J.C., 264; 313
 Davidson, J.B. *See* Craig, A.K., 308
 Davies, J.T., 25; 37
 Davies, M.S., 267, 268, 280; 308
 Davies, P.S., 260; 308
 Davies-Coleman, M.T., 269; 308
 See Gray, C.A., 309
 Davis, L.H. *See* Stoecker, D.K., 126, 127
 Davis, M.W., 56; 77
 Davis, W.P. *See* Turner, B.J., 152
 Dawes, C.J., 104; 123
 See Croley, F.C., 104; 123
 Day, J.W., 56; 77
 Day, R.H. *See* Day, J.W., 77
 Dayton, P.K., 56, 65, 160, 162, 163, 166, 173,
 174, 188, 190, 193, 209, 211, 227; 78, 232
 See Mauzey, K.P., 237
 Deacon, E.L., 5, 7, 9, 10, 14, 18, 19, 23; 37
 Dean, J.M. *See* Holland, A.F., 79
 Dean, T.A., 165, 168; 232
 Decho, A.W., 69, 73; 78
 Deck, B.L. *See* Bopp, R.F., 36
 DeCosmo, J. *See* Oost, W.A., 42
 DeFreese, D. *See* Clark, K.B., 87, 88, 103, 104,
 105, 111, 112, 118, 121; 123
 DeFreese, D.E., 102; 124
 De Jonge, V.N., 70, 71; 78
 See Colijn, F., 56; 77
 See Delgado, M., 78
 DeLaca, T.E. *See* Rivkin, R.B., 73; 84
 Delgado, M., 65, 70; 78
 Della Santina, P., 276; 308
 Delle Chiaje, S., 131; 148
 Den Daas, J.H., 18; 37
 DeNiro, M.J., 100, 101, 102; 124
 Denley, E.J., 164, 169, 173, 174, 182, 183; 232
 See Underwood, A.J., 243
 Dennett, M.R. *See* Frew, N.M., 37
 See Goldman, J.C., 28; 38
 Denny, M.W., 158, 160; 232
 DeRiemer, K. *See* Bender, J.A., 229
 Derwent, R. *See* Schimel, D.S., 43
 Des Marais, D.J. *See* Canfield, D.E., 72; 77
 De Silva, S.S., 213, 214; 232
 Desjardins, R.L. *See* Pattey, E., 42
 See Smith, S.D., 43
 De Souza, E.C. P.M., 59; 78
 De Villiers, C.J., 247, 250, 251, 269; 308
 See Hodgson, A.N., 310
 De Winder, B. *See* Yallop, M.L., 86
 Dexter, R.W., 164, 195; 232
 Dexter, R.W.D., 195; 232
 De Zwaan, A., 257; 308
 Diamond, M.E. *See* Coffroth, M.A., 148
 Dickson, M.L. *See* Wanninkhof, R., 44
 Dietrich, W. *See* Jähne, B., 39
 Dieuzeide, R., 287, 299, 300; 308
 Dinat, A. *See* Montagna, P.A., 82
 Divanach, P. *See* Kentouri, M., 213; 237
 Dobbins, W.E. *See* Metzger, L., 9; 41
 Dobbs, F.C., 73; 78
 Dobkin, S. *See* Craig, A.K., 308
 Donelan, M. *See* Miyake, M., 41
 Doney, S.C., 30; 37
 Donoghue, A.M., 136, 145, 146; 148
 See Quicke, D.L.J., 151
 Donohoe, R.M. *See* Fong, P., 78
 Douchement, C. *See* Riaux-Gobin, C., 83
 Dougherty, W.J., 162; 232
 Downing, A.L., 9; 37
 Doyle, R.W. *See* Todd, C.D., 154, 202; 242
 Dragovich, A., 217, 223; 232
 Drew, E.A., 105; 124
 Drewett, D. *See* Hughes R.N., 194; 236
 Dubreuil, A. *See* Lemée, R., 125
 Duchemin, C. *See* Edean, R., 233
 Dugan, J.E. *See* Page, H.M., 82
 Duineveld, G.C.A. *See* Jenness, M. L., 65, 69; 80
 Dungan, M.L., 163, 166, 172, 176, 177; 232
 Dunkin, S. de B., 193, 194; 232
 See Hughes, R.N., 191, 193, 194, 227; 236
 Dunn, D.F., 137, 138; 148
 Dunn, E.L. *See* Darley, W.M., 77
 Dunne, J., 217, 222; 232
 Du Preez, D.R., 67; 78
 Dupuy, J.L. *See* Manziat, J.J., 40
 Durako, M.J., 70; 78
 Durán, L.R., 180, 226; 232
 Durand-Clément, M. *See* Lemée, R., 125
 Dutzi, A. *See* Jähne, B., 39
 Dwyer, K.R. *See* Lindberg, D.R., 263; 311
 Dye, A.H., 172, 251, 252, 253, 255; 232, 308
 Ebuchi, N., 21; 37
 Eckelbarger, K.J., 290; 309
 Eckman, J.E. *See* Jahnke, R.A., 80
 Edens, J.L. *See* Riznyk, R.Z., 84
 Edgar, R.K. *See* Connor, M.S., 73; 77
 Edgell, M.H. *See* Hutchison, C.A., 149
 Edson, J.B. *See* Oost, W.A., 42
 Edwards, D.C., 163, 195, 217, 219; 232

AUTHOR INDEX

- Eekhout, S. *See* Branch, G.M., 307
 Ehleringer, J.R. *See* Farquhar, G.D., 124
 Eisenhauer, A. *See* Harnisch, J., 16; 38
 Elder, J.F. *See* Turner, B.J., 152
 Eliot, C., 204; 232
 Elkins, J.W. *See* Lobert, J.M., 40
 Ellehauge, J.O., 154; 232
 Elliott, W.P. *See* Caldwell, D.R., 32; 36
 Ellis, D.V., 159, 160; 232
 Elmhirst, R., 145; 148
 Emerson, S., 14; 37
 Emery, W.J. *See* Schluessel, P., 43
 Emlen, J.M., 188, 227; 232
 Endean, R., 154, 182; 233
 Endler, J.A., 140; 148
 Engel, M.H. *See* Macko, S.A., 125
 Enhalt, D. *See* Schimel, D.S., 43
 Enoksson, V. *See* Sundbäck, K., 85
 Enting, I. *See* Schimel, D.S., 43
 Ephraim, J.J. *See* Houghton, J.T., 39
 Epstein, S. *See* DeNiro, M.J., 100, 101, 102; 124
 Epstein, S.S., 73; 78
 Erickson III, D.J., 6, 25, 30, 31; 37
 See Nevison, C.N., 41
 Espedal, H.A., 27; 37
 Estep, M.L.F. *See* Macko, S.A., 125
 Etcheto, J. *See* Boutin, J., 21; 36
 Etter, R.J., 162; 233
 Evans, M.R., 275; 309
 Ewing, G., 29, 30; 37
- Faganeli, J. *See* Bertuzzi, A., 76
 Fairall, C.W. *See* Oost, W.A., 42
 See Smith, S.D., 43
 Fairweather, P.G., 169, 182, 183, 184, 185, 186,
 196, 198, 227; 233
 See Jernakoff, P., 164, 182, 184; 236
 See Moran, M.J., 238
 See Underwood, A.J., 182, 196, 228; 243
 Falkowski, P.G., 68; 78
 Fallen, R.D. *See* Hopkinson Jr, C.S., 80
 Fanning, K. *See* Wanninkhof, R., 44
 Fanuko, N. *See* Herndl, G.J., 79
 Farley, P.J. *See* Asher, W.E., 23, 24; 35
 Farmanfarmaian, A., 208, 210; 233
 Farmer, D.M., 11, 23; 37
 See Vagle, S., 24; 44
 Farquhar, G.D., 102; 124
 Farquhar, M.R. *See* Hodgson, A.N., 310
 Farran, G.P., 154, 199; 233
 Farrell, T.M., 162, 164, 172; 233
 Faulkner, D.J. *See* Hochlowski, J.E., 269; 309
 Fautin, D.G., 130; 148
 Feare, C.J., 193, 223; 233
 Feder, H.M., 171, 206, 208, 210, 211; 233, 234
 See Paul, A.J., 240
 See Jewett, S. C., 171; 236
- Fenical, W. *See* Paul, V.J., 119, 122; 126
 Fenical, W.F. *See* Hay, M.E., 94, 121; 124
 Fenner, R.B. *See* McKechnie, R.J., 217, 220;
 238
 Ferek, R.J. *See* Andreae, M.O., 1; 35
 Ferguson, A. *See* Brassington, R.A., 143; 147
 Fermin, C. *See* Clark, K.B., 123
 Ferrari, L., 213, 214, 216; 234
 Fielding, P.J., 56; 78
 Filho, L.G. M. *See* Houghton, J.T., 38
 Fingerman, M. *See* Thompson, M.-F., 242
 Fischer, K.H. *See* Jähne, B., 39
 See Münnich, K.O., 41
 Fischer, R. *See* Jähne, B., 39
 Fischer-Piette, E., 193; 234
 Fisher, K. *See* Black, R., 306
 Fisher, R.M. *See* McAlister, R.O., 258, 260,
 264, 265, 273; 312
 Fitzpatrick, M. *See* Pinckney, J., 82
 Fitzwater, S.E., 53; 78
 Fives, J.M., 217, 222, 223; 234
 Fleegeer, J.W. *See* Decho, A.W., 73; 78
 Fleming, R.H. *See* Sverdrup, H.U., 85
 Flothman, A.M. *See* Münnich, A.S., 7, 9; 41
 Flothmann, D. *See* Münnich, K.O., 41
 Fong, P., 71; 78
 Foster, B.A., 153; 234
 Fouquart, Y. *See* Schimel, D.S., 43
 Fournié, J. *See* Chétail, M., 198; 230
 Franz, D., 199; 234
 Fraser, E.H. *See* Endean, R., 233
 Fraser, P. *See* Schimel, D.S., 43
 Freilich, M.H. *See* Bourassa, M.A., 36
 French III, F.W. *See* Sieburth, J.M., 43
 Frescura, M., 247, 266; 309
 Fretter, V., 217, 219, 269; 234, 309
 Frew, N.M., 25, 26, 27; 37
 Friedmann, D., 29; 37
 Friehe, C.A. *See* Schmitt, K.F., 43
 Frost, T., 1-45
 Fry, B., 73; 78
 Fuchs, G., 16; 37
 Fuentes, H.R., 217, 219; 234
 Fuhrman, F.A. *See* Bender, J.A., 229
 Fuji, A., 56; 78
 Fujii, H., 144; 148
 Fujitani, T., 15; 37
 Funakoshi, C. *See* Sumikawa, S., 288; 313
 Fung, I.Y. *See* Braziunas, T.F., 36
 See Tans, P.P., 44
 Funnell, N. *See* Carter, M.A., 137; 147
- Gabrielson, J.O., 70; 78
 Gaines, S.D., 213, 215, 217; 234
 See Bertness, M.D., 229
 See Lubchenco, J., 118, 278; 125, 311
 Gallagher, D.L. *See* Reay, W.G., 83

AUTHOR INDEX

- Gallagher, E.D. *See* Gould, D.M., 56, 74; 79
 Gallagher, J.L., 56; 79
 Gallop, A., 106, 107, 108, 117; 124
 Galtsoff, P.S., 206; 234
 Gameson, A.H.L., 17; 37
 Garabétian, F., 26, 33; 38
 Garcia-Baptista, M., 49; 79
 Gardiner, W.W. *See* Asher, W.E., 35
 Gargas, E., 56; 79
 Garrity, S.D., 196, 227, 259, 260, 261, 263, 264, 268, 269, 273, 277, 284; 234, 309
 See Bertness, M.D., 306
See Levings, S.C., 196, 259, 261, 273, 274, 280, 285, 286, 287, 292, 293, 295, 299, 301; 237, 311
 Garson, M.J. *See* Davies-Coleman, M.T., 269; 308
 Gascoigne, T., 88, 90; 124
 Gashout, S.E., 130, 137, 138; 148
 Gat, J.R., 25; 38
 Gee, J.M. *See* Joint, I.R., 80
 Geernaert, G.L. *See* Smith, S.D., 43
 Geider, R.J. *See* Miller, D.C., 82
 See MacIntyre, H.L., 81
 Geller, L.S. *See* Lobert, J.M., 40
 Geraerts, W.P.M., 290; 309
 Gerhart, D.J., 154; 234
 GESAMP, 12, 27, 32, 33; 38
 Gibson, C.H. *See* Schmitt, K.F., 43
 Gibson, G.D., 106; 113; 124
 Gibson, R.N., 217, 220, 221, 223; 234
 Giehl, H. *See* Conrad, R., 37
 Giese, A.C. *See* Farmanfarmaian, A., 233
 Gilbert, N.S., 56, 65; 79
 Giovanangeli, J.P. *See* Bliven, L.F., 36
 Glover, D.M., 14, 20; 38
 Gobert, J. *See* Lemée, R., 125
 Goddard, R.H. *See* Dawes, C.J., 104; 123
 Godin, J.-G. J., 213, 214; 234
 Godoy, C., 284; 309
 Goetzfried, A. *See* Clark, K.B., 302; 307
 Goldman, J.C., 28; 38
 See Frew, N.M., 37
 Goldschmid, A., 217, 221; 234
 Gooch, J.L. *See* Schopf, T.J. M., 145; 151
 Goosen, N. *See* Kromkamp, J., 80
 Gordon, A.D. *See* Hall, S.J., 148
 Goshima, S. *See* Fuji, A., 78
 Gosse, P., 129, 132, 133, 136, 137, 145; 148
 Gosselin, L.A., 160, 195; 234
 Gould, D.J. *See* Pike, E.B., 42
 Gould, D.M., 56, 74; 79
 Gouleau, D., 57; 79
 Graham, A. *See* Fretter, V., 175, 269; 234, 309
 Granéli, W. *See* Sundbäck, K., 71, 72; 85
 Grange, N. *See* De Villiers C.J., 308
 Grant, J., 57, 68, 69, 70; 79
 Grant, W.S., 162; 234
 Grassl, H., 29; 38
 See Schluessel, P., 43
 Gravenhorst, J.L.C., 131; 148
 Gravier, C.J., 136, 137; 148
 Gray, C.A., 269; 309
 Gray, D.R., 262, 267, 272, 273, 274, 275, 276, 277, 293; 309
 Greene, R.W., 105, 106, 113, 114; 124
 See Muscatine, L., 113; 126
 See Trench, R.K., 127
 Grenz, C. *See* Plante-Cuny, M.R., 83
 Griffiths, C.C. *See* Kruger, L.M., 129, 130; 149
 Griffiths, R.J., 130; 148
 Grimm, R.B. *See* Craig, A.K., 308
 Grøntved, J., 48, 53, 57; 79
 Gros, P. *See* Blanchard, G.F., 76
 See Guarini, J.-M., 79
 Grosberg, R.K. *See* McFadden, C.S., 150
 Groves, S., 224; 234
 Gruber, G. *See* Rittschof, D., 198; 241
 Guarini, J.-M., 67; 79
 See Blanchard, G.F., 76
 Gubbay, S., 157, 158, 162; 234
 Guckert, J.B. *See* Dobbs, F.C., 78
 Guerra, A., 205; 234
 Guerriero, A. *See* Lemée, R., 125
 Guisado, C., 179; 235
 Gul'bin, V.V., 192; 235
 Gust, G. *See* Huettel, M., 53; 80
 Gwilliam, G.F., 155, 225; 235
 Gyr, P. *See* Endean, R., 233
 Hackney, J.M., 49; 79
 Hadfield, M.G., 154, 204; 235
 Hadley, C.D., 224, 225; 235
 Hadry, H., 145; 148
 Hagiwara, S. *See* Ozawa, S., 239
 Haines, M.A., 24, 25; 38
 Haldorson, L., 217, 220; 235
 Hale, M.S., 33; 38
 Hall, S.J., 129; 132; 148
 Hammond, D.E. *See* Hartman, B., 14, 18, 19, 20; 38
 Hancock, D.A., 207, 209, 210; 235
 Hand, C., 130; 148
 See Bucklin, A., 147
 Handley, L.L. *See* Raven, J.A., 126
 Hanotte, O. *See* Bruford, M.W., 147
 Hanson, R.B., 65; 79
 Harbour, D.S. *See* Turner, S.M., 44
 Harding, S.P. *See* Hawkins, S.J., 309
 Hardy, J.T., 26, 33; 38
 Hare, P.E. *See* Macko, S.A., 125
 Hargrave, B.T., 57, 73; 79
 See Hunding, C., 54; 80

AUTHOR INDEX

- Hargraves, P.E. *See* Kennett, D.M., 49; 80
 Harms, J., 165; 235
 Harnisch, J., 16; 38
 Harrington, S.A. *See* Simpson, R.D., 291, 292; 313
 Harris, N. *See* Houghton, J.T., 38
 Harris, P.R., 224; 235
 Harrison, S.J. *See* Guarini, J.-M, 79
 Harrison, W.G. *See* Platt, T., 60; 83
 Harriss, R.C. *See* Matson, P.A. 15; 41
 Hart, M.W., 188; 235
 Hartman, B., 14, 18, 19, 20; 38
 Hartnoll, R.G., 163; 235
 See Hawkins, S.J., 118, 163, 246, 272, 278; 124, 235, 309
 Hartwig, E.O., 57, 65; 79
 Harvey, G.W., 26; 38
 Harvey, R.S. *See* Rodgers, J.H., 70; 84
 Hasse, L., 11; 38
 See Peterson, E.W., 20; 42
 See Smith, S.D., 43
 Haszprunar, G., 247; 309
 Haussecker, H., 12; 38
 Haven, N., 297; 309
 Hawkins, C.M., 57; 79
 Hawkins, S.J., 118, 163, 246, 272, 278; 124, 235
 See Davies, M.S., 267, 280; 308
 See Hartnoll, R.G., 163; 235
 Hay, M.E., 94, 121; 124
 Hayduk, W., 4; 38
 Hayes, F.R., 164; 235
 Haylor, G.S., 130, 133, 134, 135, 142, 144; 148
 Haymon, R. *See* Lupton, J.E., 40
 Haynes, D.L. *See* Smith, J.H., 43
 Healey, M.C., 213, 216; 235
 Healy, J. *See* Hodgson, A.N., 247; 309
 Healy, J.M., 247, 288; 309
 Hedgecock, D. *See* Bucklin, A., 142, 143; 147
 Hegeman, J. *See* Cadée, G.C., 55; 76
 Heimann, M. *See* Hesshaimer, V., 38
 See Schimel, D.S., 43
 Heinemann, D. *See* Kendrick, G.A., 80
 Heinemann, K. *See* Marra, J., 53; 81
 Heinz, G. *See* Jähne, B., 39
 Helder, W. *See* den Daas, J.H., 37
 Hellebust, J.A., 71; 79
 See Lewin, J.C., 71; 81
 Hempel, G. *See* Rosenthal, H., 214; 241
 Henderson, L. *See* Endean, R., 154; 233
 Henrichs, S.M. *See* Carlucci, A.F., 36
 See Williams, P.M., 45
 Hernandez, P.A., 16; 38
 Herndl, G., 130; 149
 Herndl, G.J., 57, 65, 68; 79
 Hertzman, O. *See* Smith, S.D., 43
 Hesany, V. *See* Jessup, A.T., 39
 Hesshaimer, V., 2, 21; 38
 Hesslein, R. *See* Broecker, W.S., 36
 Hesslein, R.H. *See* Torgersen, T., 44
 Heunert, H.H. *See* Koop, H.U., 125
 Heymer, A. *See* Zander, C.D., 217, 220, 221; 244
 Hiatt, R.W., 213, 216; 235
 Higbie, R., 7; 38
 Higgins, B.J. *See* Asher, W.E., 35
 Hill, A. *See* Black, R., 306
 Hill, A.S. *See* Hawkins, S.J., 309
 Hinde, R., 106, 107, 108, 112, 113, 114, 115, 116, 118, 121; 124
 Hindman, C.L. *See* Lee, P.H. Y., 40
 Hinga, K.R. *See* Sieburth, J.M., 43
 Hinzpeter, H. *See* Clauss, E., 37
 Hirano, Y., 261, 274, 275, 287, 293, 295, 298; 309
 Hitchcock, G. *See* Wanninkhof, R., 44
 Ho, D. *See* Nightingale, P., 41
 Ho, D.T., 6, 32; 38
 See Clark, J.F., 36
 See Wanninkhof, R., 44
 Hoagland, K.D. *See* Roemer, S.C., 84
 Hochlowski, J.E., 269; 309
 Hodgson, A.N., 245–314; 247, 271, 272, 286, 288, 289, 290; 309, 310
 See De Villiers C.J., 250, 251, 269; 308
 See Frescura, M., 247; 309
 See Gray, D.R., 262, 267, 272, 273, 274, 275, 276, 277, 293; 309
 See Ridgway, S.A., 313
 Hoffman, D.L., 158, 168; 235
 Hoffman, R.J., 135; 149
 See Zamer, W.E., 135; 152
 Holdway, D.A. *See* Nriagu, J.O., 41
 Holland, A.F., 70; 79
 Hollibaugh, J.T. *See* Chambers, R.M., 77
 Holligan, P.M. *See* Turner, S.M., 44
 Holmen, K., 8, 9; 38
 See Saltzman, E.S., 43
 Holmes, K.S. *See* Darley, W.M., 77
 Holmes, R.W., 79
 Holm-Hansen, O., 64, 66; 79, 80
 Hooper, I.R. *See* Rittschof, D., 241
 See Standing, J.D., 242
 See Keifer, P.A., 236
 Hoover, T.E., 27, 28, 31; 38
 Hopkins, T.L. *See* Rau, G.H., 126
 Hopkinson Jr, C.S., 57, 65; 80
 Høpner Petersen, G., 160; 235
 Hopper, C.M. *See* Grant, J., 79
 Hori, T. *See* Satoh, M., 126
 Horner, R., 57, 65; 80
 See Matheke, G.E.M., 57, 65, 68; 81
 Horrigan, S.G. *See* Williams, P.M., 45

AUTHOR INDEX

- Hoshiai, T., 165, 206, 207, 208; 235
Houghton, J.T., 2, 29; 38, 39
Houlihan, D.F., 252; 310
Howarth, R.W. *See* Marino, R., 12; 40
Huang, C.L., 188; 236
Huang, H.L. *See* McKeown, W., 41
Huang, R., 70; 80
Hubbard, D.M. *See* Page, H. M., 82
Hubendick, B., 246, 247, 248, 249, 250, 278, 285, 286, 302; 310
Huber, G. *See* Haszprunar, G., 247; 309
Huber, W. *See* Jähne, B., 39
Hubick, K.T. *See* Farquhar, G.D., 124
Huettel, M., 53; 80
Hughes, R.N., 139, 156, 191, 193, 194, 227; 149, 236
 See Burrows, M.T., 191, 193, 194; 230
 See Dunkin, S. de B., 193, 194; 232
Hughes, T.M.C. *See* Sarmiento, J.L., 43
Hui, E., 165, 171; 236
Hulings, N.C., 261, 274, 292, 295; 310
Humphrey, G.F. *See* Jeffrey, S.W., 64; 80
Hunding, C., 54; 80
Hunt, A., 130, 135; 149
Hunt, W.G. *See* Moriarty, D.J. W., 82
Hurd, L.E. *See* Dean, T.A., 165; 232
Hurley, A.C., 168, 208, 217; 236
Hustedt, F., 49; 81
Hutchinson, S. *See* Hawkins, S.J., 309
Hutchison, C.A., 143; 149
Hutton, F.W., 185; 310
Hyman, L.H., 246, 247, 250; 310
- Iannuzzi, T.J., 57, 65; 80
Ilmberger, J. *See* Jähne, B., 39
Imboden, D. *See* Jähne, B., 39
Inaba, A. *See* Hirano, Y., 261, 274, 293, 295; 309
Incze, L.S., 73; 80
Innes, A.J., 250, 251, 252; 310
Ireland, C.M. *See* Biskupiak, J.E., 306
Isaksen, I. *See* Schimel, D.S., 43
Iwasaki, K., 261, 262, 268, 269, 272, 273, 274, 275, 279, 280, 281, 282, 283, 284, 285, 287, 292, 295, 298; 310
- Jacobs, C.M. J., 15; 39
Jacobs, W.P., 104; 124
Jacoby, C.A. *See* Kendrick, G.A., 80
Jähne, B., 2, 4, 5, 7, 8, 10, 11, 12, 16, 18, 21, 24, 25; 39
 See Broecker, W.S., 36
 See Haussecker, H., 12; 38
Jahnke, R.A., 53, 57; 80
James, H. *See* Clark, J.F., 37
Jansson, B.-O. *See* Hopkinson Jr, C.S., 80
Jaquet, J.M. *See* Jähne, B., 39
- Jara, H.F., 269, 279, 280; 310
 See Moreno, C.A., 312
Jean-Baptiste, P., 16; 39
Jeffrey, S.W., 64; 80
Jenkin, G.J. *See* Houghton, J.T., 39
Jenkins, B.W., 246, 247, 278, 285, 292, 293; 310
Jenkins, W.J., 16; 39
Jenness, M. L., 65, 69; 80
Jennison, B.L., 131, 138; 149
Jensen, A.C. *See* Collins, K.J., 231
Jensen, A.S., 175; 236
Jensen, K.R., 87, 88, 89, 90, 91, 92, 93, 94, 95, 96, 97, 98, 99, 104, 107, 113, 114, 115; 124, 125
 See Clark, K.B., 123
 See Raven, J.A., 126
 See Theisen, B.F., 90, 118; 127
Jerlov, N.G., 69; 80
Jernakoff, P., 164, 175, 182, 184; 236
 See Underwood, A.J., 118, 269, 278, 279; 127, 314
Jessup, A.T., 25, 30; 39
Jewett, S.C., 171; 236
 See Paul, A.J., 240
Jillett, J.B. 217, 223; 236
Jillson, D.A., 195; 236
Johannessen, O.M. *See* Espedal, H.A., 37
Johnen, F.J. *See* Plass-Dülmer, C., 42
Johnson, A.S. *See* Frew, N.M., 37
Johnson, B.D. *See* Anderson, M.L., 23; 35
 See Farmer, D.M., 37
 See Haines, M.A., 24, 25; 38
 See Smith, S.D., 43
Johnson, C.R., 217, 218; 236
Johnson, J.E., 1; 39
Johnson, K.M. *See* Sieburth, J.M., 43
Johnson, K.S., 28; 39
Johnson, L.E., 154; 236
Johnson, M.S., 287, 304; 310
 See Black, R., 135, 137, 139, 283; 146, 306
Johnson, M.W. *See* Sverdrup, H.U., 85
Johnston, A.M. *See* Maberly, S.C., 125
Johnston, G., 133; 149
Johnstone, R.W., 57, 65; 80
Joint, I.R., 57, 69; 80
Jonas, P. *See* Schimel, D.S., 43
Jones, E.P. *See* Smith, S.D., 15; 43
Jones, H.D., 266; 310
Jönsson, B. *See* Sundbäck, K., 59, 66; 85
 See Wulff, A., 86
Joos, F. *See* Schimel, D.S., 43
Joose, J. *See* Geraerts, W.P. M., 290; 309
Jørgensen, B.B. *See* Revsbech, N.P., 53, 72; 83
 See Lassen, C., 81
Juniper, S.K., 73; 80

AUTHOR INDEX

- Kabaya, Y. *See* Wada, E., 127
 Kahma, K.K., 20; 39
 Kahn, H.R., 297; 311
 See Saleuddin, A.S. M., 313
 Kamykowski, D., 70; 80
 Kamykowski, D.L. *See* Miller, R.L., 66; 82
 Kaplan, I.R. *See* Rau, G.H., 126
 Karande, A.A., 157; 236
 Karl, D.M. *See* Martin, J.H., 81
 Karl, S.A., 145; 149
 Karle, L.M. *See* Asher, W.E., 35
 Karlton, D.P. *See* McFadden, C.S., 150
 Katsaros, K.B., 30; 39
 See Oost, W.A., 42
 Kattenberg, A. *See* Houghton, J.T., 38
 Katz, C.H., 199; 236
 Kawaguti, S., 106, 117; 125
 Kawamura, H. *See* Ebuchi, N., 37
 Kayanne, H. *See* Yamamuro, M., 128
 Kaye, J.G. *See* Solé-Cava, A.M., 152
 Keeling, C.D., 2; 39
 Keeling, R.F., 23, 24; 39
 Keeling, T.F. *See* Quicke, D.L.J., 151
 Keifer, P.A., 154; 236
 Kelley, B.J., 57; 80
 Kendrick, G.A., 65; 80
 Kennett, D.M., 49; 80
 Kenny, R. *See* Endean, R., 233
 Kent, E. *See* Taylor, P.K., 44
 Kentouri, M., 213; 237
 Keough, M.J., 270; 311
 See Povey, A., 225; 240
 Kerman, B.R., 9, 25; 39
 Keswick, B.H., 17; 39
 Khedim, A. *See* Plass-Dülmer, C., 42
 Kieber, D.J., 198; 237
 Kilburn, R., 249; 311
 Kim, K.H., 1; 39
 King, D.B., 3, 5; 39
 See Saltzman, E.S., 43
 King, R.J. *See* Clayton, M.N., 104; 123
 Kirby, G.C. *See* Ottaway, J.R., 135, 137, 139; 150
 Kirby, R. *See* Chambers, R.J., 307
 Kirk, G.J. D., 28, 29; 39
 Kishinevsky, M.K., 9; 39
 Kitaigorodskii, S.A., 7, 9; 40
 Klein, B., 49; 80
 Klein, B. *See* Riaux-Gobin, C., 83
 Klinkhammer, G.P. *See* Lupton, J.E., 40
 Knauer, G.A. *See* Fitzwater, S.E., 78
 See Martin, J.H., 81
 Knox, G.A., 291, 302; 311
 Knox, M. *See* Wanninkhof, R.H., 28; 45
 Knudsen, M.F. *See* Burger, J.F., 230
 Knulst, J. *See* Espedal, H.A., 37
 Koehl, M.A. R. *See* Rubenstein, D. L., 129; 151
 See Denny, M.W., 232
 Köhler, A., 246, 250, 285; 311
 Kohn, A.J., 175, 186; 237
 Kohsiek, W., 14, 15; 40
 See Jacobs, C.M. J., 39
 Koop, H.U., 105; 125
 Koop, K. *See* Johnstone, R.W., 80
 Koppmann, R. *See* Plass-Dülmer, C., 42
 Korzun, E.A. *See* Belanger, T.V., 32; 35
 Koss, R. *See* Chia, F.-S., 154, 204; 230
 Kotani, M. *See* Ohgushi, R., 312
 Kotrschal, K. *See* Goldschmid, A., 217, 221; 234
 Kremer, B.P., 115, 116; 125
 Kromer, B., 14, 19, 20; 40
 See Münnich, K.O., 41
 See Roether, W., 14; 42
 Kromkamp, J., 57; 80
 Kruger, L.M., 129, 130; 149
 Kulichov, V.A. *See* Serov, O.L., 151
 Kunigelis, S.C. *See* Saleuddin, A.S.M., 313
 Kuosa, H. *See* Plass-Dülmer, C., 42
 Kwak, T.J., 73; 81
 Kyriakides, M.P. *See* Hawkins, S.J., 309
 L.B.Cahoon. *See* Sigmon, D.E., 71, 72; 84
 Laane, R.W. P.M. *See* Admiraal, W., 75
 Lackey, G.J. *See* Rizzo, W.M., 84
 Lacy, R.C., 145; 149
 Lake, B.M. *See* Lee, P.H.Y., 40
 Lal, M. *See* Schimel, D.S., 43
 Lalli, C.M. *See* Parsons, T.R., 82
 Lamb, A.N. *See* Shick, J.M., 142; 152
 Lamontagne, R.A., 23; 40
 Landers, W.S., 168; 237
 Langdon, C. *See* Wanninkhof, R., 44
 Lantry, T.P. *See* Asher, W.E., 35
 Larew III, H.G. *See* Darley, W.M., 77
 Large, W.G., 21; 40
 Largen, M.J., 189, 193, 194; 237
 Larkin, A.W.D. *See* Johnstone, R.W., 80
 Larkman, A.U., 138, 139; 149
 LaRoche, J.L., 213, 214, 215; 237
 Lasiak, T.A., 282, 283; 311
 Lasker, H.R. *See* Coffroth, M.A., 148
 Lassen, C., 68; 81
 Laudie, H. *See* Hayduk, W., 4; 38
 Laughlin, T.F. *See* Turner, B.J., 152
 Lavie, B., 145; 149
 See Noy, R., 150
 Lavoie, D.M. *See* Sieburth, J.M., 43
 Law, C.S., 1, 16; 40
 See Owens, N.J.P., 42
 Laws, R.A., 49; 81
 See Cahoon, L.B., 49, 70; 77
 Leach, J.H., 57; 81
 Leavitt, E. *See* Miyake, M., 41

AUTHOR INDEX

- Leck, C. *See* Saltzman, E.S., 43
 Ledwell, J.R., 5, 7, 8, 9, 11, 16, 21, 28; 40
 See Broecker, W.S., 36
 See Wanninkhof, R., 45
 See Watson, A.J., 17; 45
 Lee, C. *See* Sun, M.-Y., 85
 Lee, C.C. *See* Bunt, J.S., 76
 Lee, E. *See* Bunt, J.S., 76
 Lee, P.H. Y., 20; 40
 Lee, W.Y. *See* Macko, S.A., 125
 Lee Chen, Y.-L. *See* Parsons, T.R., 100; 126
 Legler, D.M. *See* Bourassa, M.A., 36
 Legrand, C. *See* Malinsky-Rushansky, N.Z., 27; 40
 Lemée, R., 119; 125
 Lemmin, U. *See* Jähne, B., 39
 Lépez, M.I. *See* Moreno, C.A., 239
 Lepparanta, M. *See* Kahma, K.K., 20; 39
 Le Quere, C. *See* Sarmiento, J.L., 43
 Lester, L.J. *See* McCommas, S.A., 135, 142, 143; 150
 Leuning, R. *See* Webb, E.K., 45
 Levin, I. *See* Hesshaimer, V., 38
 Levings, S.C., 196, 259, 261, 273, 274, 280, 285, 286, 287, 292, 293, 295, 299, 301; 237, 311
 See Bertness, M.D., 306
 See Garrity, S.D., 196, 227, 268, 269, 273, 277, 284; 234, 309
 Levinton, J.S., 156; 237
 Lewin, J.C., 71; 81
 See Hellebust, J.A., 71; 79
 Lewin, R.A. *See* Lewin, J.C., 71; 81
 Lewis, J.B., 166; 237
 See Hawkins, C.M., 57; 79
 Lewis, J.R., 159, 163, 193, 206; 237
 See Sebens, K.P., 188, 189; 241
 Lewontin, R.C., 140; 149
 Ley-Lou, F. *See* Day, J.W., 77
 Li, Y.-H. *See* Bopp, R.F., 36
 See Peng, T.-H., 42
 Libby, R.C. *See* Riznyk, R.Z., 84
 Libby, W.F. *See* Berger, R., 28; 35
 Libner, P. *See* Jähne, B., 39
 Liddicoat, M.I. *See* Law, C.S., 40
 See Liss, P.S., 40
 Upstill-Goddard, R.C., 44
 Lindberg, D.R., 263; 311
 Lindley, D.S. *See* Hodgson, A.N., 309
 Lindquist, D. *See* Posey, M., 83
 Linnaeus, C., 133, 134; 149
 Linnenbom, V.J. *See* Lamontagne, R.A., 40
 Liss, P. *See* Holmen, K., 8, 9; 38
 Liss, P. S, 4, 6, 10, 11, 12, 14, 18, 19, 22, 25, 28, 29, 30, 31, 32; 40
 See Nightingale, P.D., 41
 See Turner, S.M., 44
 See Upstill-Goddard, R.C., 44
 See Watson, A.J., 45
 Little, C., 246, 272, 275; 311
 Littlejohn, M.J., 143; 149
 Littler, D. *See* Littler, M., 81
 Littler, M., 60; 81
 Littler, M.M. *See* Seapy, R.R., 158; 241
 Liu, J.H., 263, 269, 281, 299, 304; 311
 Liu, W.T. *See* Bourassa, M.A., 36
 Lively, C.M., 156, 176, 177, 182; 237
 Llewellyn, C.A. *See* Owens, N.J. P., 42
 See Riaux-Gobin, C., 83
 Lobert, J.M., 1; 40
 Loewen, M.R. *See* Jessup, A.T., 39
 Loftus-Hills, T.J. *See* Littlejohn, M.J., 149
 Lohani, B.N. *See* Banks, R.B., 35
 Lomstein, B.A. *See* Therkildsen, M.S., 72; 85
 Longhurst, A., 51, 52; 81
 Longhurst, A.R., 129; 149
 Loosanoff, V.L. *See* Galtsoff, P.S., 206; 234
 Lopez, E., 106; 125
 López Gappa, J.J. *See* Tablado, A., 314
 López Gappa, L., 261, 272, 274, 277, 295; 311
 Lorenzen, C.J., 64, 65, 66; 81
 See Holm-Hansen, O., 79
 Losey, G.S., 217, 218; 237
 Lovelock, J.E. *See* Charlson, R.J., 36
 Lubbock, R., 130; 149
 Lubchenco, J., 118, 278; 125, 311
 Luckens, P.A., 158, 164, 165, 167, 181, 182, 186, 196, 197, 206, 207, 225; 237
 Ludden, E., 72; 81
 Lukatelich, R.J., 65; 81
 See Gabrielson, J.O., 70; 78
 Lunecke, K.M. *See* Moreno, C.A., 239
 Lupton, J.E., 16; 40
 Lymbery, A. *See* Black, R., 306
 Lynch, S.M., 136; 149
 Maberly, S.C., 100; 125
 MacAlister, H. *See* Davenport, J., 257, 258, 264, 277; 308
 Macdonald, K.C. *See* Lupton, J.E., 40
 MacIntyre, H.L., 48, 54, 57, 67; 81
 See Miller, D.C., 82
 MacIntyre, S., 21; 40
 Mackay, T.F. C., 145; 150
 Macko, S.A., 100, 101; 125
 See Incze, L.S., 80
 Maclean, N. *See* Carvalho, G.R., 147
 Maconnachie, E. *See* Nixon, M., 204, 205; 239
 Madden, C.J. *See* Day, J.W., 77
 Madsen, K.N., 70; 81
 Maestrini, S.Y. *See* Antia, N.J., 75
 Magaldi, N. *See* López Gappa, L., 311
 Magaldi, N.H. *See* Tablado, A., 314
 Magre, E.J., 164; 237

AUTHOR INDEX

- Maita, Y. *See* Parsons, T.R., 82
 Malesroit, P. *See* Lemée, R., 125
 Malin, G. *See* Liss, P.S., 40
 See Nightingale, P., 41
 See Turner, S.M., 44
 See Upstill-Goddard, R. C., 44
 Malinsky-Rushansky, N.Z., 27; 40
 Malli, P. C., 258, 259; 311
 See Prasad, M.N., 312
 Malusa, J.R., 166, 176, 177; 237
 Mammen, T. *See* Schluessel, P., 43
 Manabe, S. *See* Sarmiento, J.L., 43
 Manhart, J.R. *See* Mujer, C.V., 126
 Mann, K.H. *See* Stephenson, R.L., 126
 Mansuri, A.P. *See* Malli, P.C., 311
 See Prasad, M.N., 312
 Mantoura, R.F.C. *See* Owens, N.J.P., 42
 Manuel, R.L., 130, 133, 144; 150
 Manziet, J.J., 26; 40
 Mapstone, G.M., 292, 294, 295, 300, 301; 311
 Marcus, E., 154, 204, 246, 248, 250, 260, 261,
 269, 285, 286, 287, 288, 292, 293; 237,
 311
 Mari, X. *See* Lemée, R., 125
 Marín, A., 96, 106, 108, 110, 112, 114, 116,
 118, 120, 121, 122; 125
 Marinelli, R.L., 71; 81
 See Jahnke, R.A., 80
 Marino, R., 12; 40
 Mariscal, R.N., 129; 150
 Marra, J., 53; 81
 Marsden, I.D. *See* Innes, A.J., 310
 Marsh, A.C. *See* Branch, G.M., 266, 267; 307
 Marsh, C.P., 225; 237
 Marshall, B.A., 247; 311
 Marshall, D.J., 251, 253, 254, 255, 256, 257,
 258, 259, 260, 265; 311
 Marshall, H.G. *See* Wendker, S., 59; 86
 Marshall, N., 57; 81
 See Newell, R.I.E., 82
 Martin, A.D. *See* Olla, B.L., 239
 Martin, J.H., 50, 51, 52; 81
 See Fitzwater, S.E., 78
 Martinelli, F.N., 9; 40
 See Liss, P.S., 40
 Maskell, K. *See* Houghton, J.T., 38
 Masselot, M. *See* Tillier, S., 314
 Masserini, R. *See* Wanninkhof, R., 44
 Matheke, G.E. M., 57, 65, 68; 81
 Mathieson, A.C. *See* Daly, M.A., 159; 231
 Mathieu, G. *See* Broecker, W.S., 36
 See Torgersen, T., 44
 Mathieu, G.G. *See* Peng, T.-H., 42
 Matson, P.A., 15; 41
 Matsumoto, G.K. *See* Hochlowski, J.E., 309
 Mauzey, K.P., 206, 207, 208, 209, 210, 211;
 237
 Maxwell, W.L., 290; 312
 Mayer, L.M. *See* Incze, L.S., 80
 Mayo, S.W. *See* Gerhart, D.J., 234
 Mayr, E., 140; 150
 McAlister, E.D., 29; 41
 See Ewing, G., 29, 30; 37
 McAlister, R.O., 258, 260, 264, 264, 273; 312
 McAlpine, D., 285; 312
 McBean, G.A., 15; 41
 See Miyake, M., 41
 McColm, D. *See* Endean, R., 233
 McComb, A.J. *See* Lukatelich, R.J., 65; 81
 McCommas, S.A., 135, 142, 143; 150
 McCook, L.J., 160; 237
 McDermott, J.J., 170; 238
 McDonald, A. *See* Cahoon, L.B., 76
 McDougall, K.D., 165, 166, 168, 212, 217; 238
 McFadden, C.S., 135, 142; 150
 McInroy, S.G. *See* Raven, J.A., 126
 McIntire, C.D., 48, 57; 81
 See Davis, W.M., 56; 77
 McKechnie, R.J., 217, 220; 238
 McKellar, H.N. *See* Kelley, B.J., 80
 McKeown, W., 30; 41
 McLean, J.H., 247, 249; 312
 McLean, N., 108; 125
 McLeish, W. *See* McAlister, E.D., 29; 41
 McMahan, R.F., 252; 312
 McNeil, C.L. *See* Farmer, D.M., 37
 McQuaid, C. *See* Gray, C.A., 309
 McQuaid, C.D., 186, 187; 238
 See Chambers, R. J., 247, 291, 294, 296, 301,
 302, 303; 307
 See Marshall, D.J., 251, 253, 254, 255, 256,
 257, 258, 259, 260, 265; 311
 McShane, P. *See* Black, R., 306
 Meadows, P.S., 49; 81
 Mearns, A.J. *See* Rau, G.H., 126
 Medlyn, R.A. *See* Durako, M.J., 78
 Meese, R.J., 225; 238
 Megard, R.O., 69; 81
 Meinesz, A., 118, 119, 120; 125
 See Lemée, R., 125
 Melnyk, J. *See* Meinesz, A., 125
 Memery, L., 23; 41
 See Broecker, W.S., 36
 See Jähne, B., 39
 See Merlivat, L., 6, 11, 23, 24; 41
 Menager, V. *See* Lemée, R., 125
 Menard, H.W., 50, 51, 52, 62; 81
 Menge, B.A., 158, 162, 165, 169, 193, 195,
 206, 207, 208, 209, 210, 211, 227, 228,
 246, 269, 270, 293; 238, 312
 See Menge, J.L., 208, 210, 211, 212; 238
 See Navarrete, S.A., 191, 208, 211; 239
 Menge, J.L., 176, 178, 180, 181, 208, 210, 211,
 212; 238

AUTHOR INDEX

- Menzel, D.W. *See* Yentsch, C.S., 66; 86
 Mercier, L., 172; 238
 Merlivat, L., 6, 11, 23, 24; 41
 See Broecker, W.S., 36
 See Jähne, B., 39
 See Liss, P.S., 4, 6, 10, 12, 14, 18, 19, 22,
 25, 29, 31; 40
 See Memery, L., 23; 47
 Mestayer, M.K., 292; 312
 Metzger, L., 9; 41
 Michaels, A.E. *See* Stoecker, D.K., 126, 127
 Michener, R.H., 100, 101; 126
 Mihalopoulos, N. *See* Jean-Baptiste, P., 39
 Miles, J. *See* Carter, M.A., 130, 137, 138, 139,
 140, 141, 144; 147
 Miller, D.C., 48, 49, 70; 82
 See MacIntyre, H.L., 81
 Miller, K.M., 173, 174, 175; 238
 Miller, M.C., 154, 201; 238
 Miller, R.L., 68; 82
 Miller, W.L., 33; 41
 Mills, A.L. *See* Powelson, D.K., 33; 42
 Mills, D.K., 67; 82
 Mills, E.L. *See* Grant, J., 79
 Milne-Edwards, H., 133; 150
 Minagawa, M., 101, 102; 126
 See Yamamuro, M., 128
 Mir, G.N. *See* Huang, C.L., 188; 236
 Mitchell, J.G. *See* Hale, M.S., 33; 38
 Mitlathaler, B. *See* Koop, H.U., 125
 Miura, T. *See* Ohgushi, R., 312
 Miyake, M., 14; 41
 Miyamura, S. *See* Satoh, M., 126
 Moat, B. *See* Taylor, P.K., 44
 Modin, J. *See* Gibson, R.N., 234
 Moffler, M.D. *See* Durako, M.J., 78
 Monahan, E.C., 21, 23, 24, 25; 41
 See Asher, W.E., 35
 Moncrieff, C.A., 57; 82
 See Sullivan, M.J., 59, 73; 85
 Montagna, P.A., 73; 82
 See Blanchard, G.F., 67; 76
 Montague, C.L. *See* Darley, W.M., 77
 Monteiro, F.A., 130, 131, 132, 134, 135, 139,
 142; 150
 Montzka, S.A. *See* Lobert, J.M., 40
 Moore, H.B., 189, 193, 194; 238
 Moore, L.B. *See* Cranwell, L.M., 166, 181;
 231
 Moore, R.M. *See* Smith, S.D., 43
 Moore, W.W. *See* McIntire, C.D., 48; 81
 Mopper, K. *See* Zhou, X.L., 33; 45
 Morales, C., 170; 238
 Moran, C., 143; 150
 Moran, M.J., 182, 185, 186, 196, 227; 238
 See Fairweather, P.G., 233
 See Underwood, A.J., 243
 Moran, P.J., 158; 238
 Morel, A., 63; 82
 Morel, F.M. M. *See* Price, N.M., 29; 42
 Moreno, C.A., 180, 226, 269, 284; 239, 312
 See Branch, G.M., 269, 284; 307
 See Godoy, C., 284; 309
 See Jara, H.F., 269, 279, 280; 310
 Moreno, L. *See* Bosch, M., 164; 230
 Morgan, P.R., 189, 194, 227; 239
 Moriarty, C.M. *See* Moriarty, D.J. W., 82
 Moriarty, D.J. W., 57; 82
 Mornet, F. *See* Blanchard, G.F., 76
 Morris, K.P. *See* Van Scoy, K.A., 44
 Morrison, J.P. E., 246, 249; 312
 Motion, J.E., 247; 312
 Moser, M. *See* Haldorson, L., 217, 220; 235
 Mosher, H.S. *See* Bender, J.A., 229
 Mueller-Glewe, J. *See* Clauss, E., 37
 Mujer, C.V., 106; 126
 Mulhearn, P.J. *See* Walsh, A.L., 24; 44
 Münnich, A.S., 7, 9; 41
 Münnich, K. *See* Jähne, B., 39
 Münnich, K.O., 18, 31; 41
 See Broecker, H.-C, 36
 See Jähne, B., 39
 Murdoch, W.W., 176, 179, 188, 191, 227, 228;
 239
 Murdock, G.R., 157, 158; 239
 Muscatine, L., 113; 126
 See Greene, R.W., 105, 113, 114; 124
 Myers, R.C. *See* Lobert, J.M., 40
 Myklestad, S.M., 27; 41
 Myksys, S.L. *See* Saleuddin, A.S. M., 313
 Nagabhushanam, R. *See* Thompson, M.-F., 242
 See Vitalina, Sr M., 243
 Nakai, S. *See* Hernandez, P.A., 38
 Navarrete, S.A., 170, 191, 208, 211, 269; 239,
 312
 See Wieters, E.A., 191; 243
 Naylor, E. *See* Della Santina, P., 276; 308
 Neame, P.A. *See* Hargrave, B.T., 79
 Nei, M., 132, 140; 150
 Nelson, B.V., 156; 239
 Nelson, J.R. *See* Jahnke, R.A., 80
 Nelson, R.K. *See* Frew, N.M., 26; 37
 Nemoto, T. *See* Wada, E., 127
 Nevison, C.N., 1; 41
 Nevo, E. *See* Lavie, B., 145; 149
 See Noy, R., 150
 Newbold, J.E. *See* Hutchison, C.A., 149
 Newell, R.I. E., 73; 82
 Newell, S.Y. *See* Currin, C.A., 77
 Newman, W.A., 154, 157, 217, 227; 239
 See Stanley, S.M., 156, 227; 242
 Nguyen, B.C. *See* Jean-Baptiste, P., 39
 Nichols, F.H. *See* Thompson, J.K., 73; 85

AUTHOR INDEX

- Nickell, L.A. *See* Gibson, R.N., 234
 Nicolaysen, K. *See* Ozawa, S., 239
 Nicotri, M. R, 99; 126
 Nielsen, L.P. *See* Rysgaard, S., 84
 Nightingale, P., 17, 18; 41
 Nightingale, P.D., 1, 16; 41
 See Liss, P.S., 40
 See Turner, S.M., 44
 See Upstill-Goddard, R. C, 44
 Nightingale, T.J. *See* Watts, P.D., 45
 Nigrelli, R.F. *See* Arvy, L., 154; 229
 Nilsson, C. *See* Wulff, A., 86
 Nilsson, P. *See* Madsen, K.N., 81
 Nixon, M., 204, 205; 239
 See Guerra, A., 205; 234
 Nixon, S.W. *See* Nowicki, B.L., 57; 82
 Niyogi, D.K. *See* Thom, R.M., 85
 Noda, T. *See* Fuji, A., 78
 NODC, 68; 52
 Nordsieck, N., 247, 248; 312
 Norkrans, B., 26; 47
 Normark, W.R. *See* Lupton, J.E., 40
 Norris, J.N. *See* Littler, M., 81
 Norton, T.A. *See* Hawkins, S.J., 309
 Notsu, K. *See* Hernandez, P.A., 38
 Nowicki, B.L., 57; 82
 Noy, R., 145; 150
 Nriagu, J.O., 1; 41
- O'Brien, J. *See* Bourassa, M.A., 36
 O'Brien, F.X., 208; 239
 Ogura, K. *See* Fuji, A., 78
 Ohgushi, R., 261, 262; 312
 Ohlman, C.T. *See* Darley, W.M., 77
 Ojeda, F.P. *See* Varas, E., 213; 243
 Oliver, J.S. *See* Dayton, P.K., 78
 Olivier, S.R., 260, 261, 282, 287, 292, 293,
 301, 304; 312
 Olla, B.L., 217, 218, 219; 239
 O'Muircheartaigh, I. *See* Monahan, E.C., 21,
 24; 41
 Oncley, S.P. *See* Businger, J.A., 15; 36
 Onuf, C.P. *See* Shaffer, G.P., 54, 58; 84
 Oost, W.A., 15, 21; 41, 42
 See Jacobs, C.M. J., 39
 Oremland, R.S. *See* Triska, F.J., 72; 85
 Ormond, R.F. G. *See* Gashout, S.E., 130, 137,
 138; 148
 Orr, J., 130, 135, 137, 141, 144; 148
 Ortega, S., 172, 175, 176, 178, 195, 228, 259,
 269, 282, 284; 239, 312
 See Sutherland, J.P., 172, 176, 177, 195, 284;
 242, 314
 Ortner, P.B. *See* Wanninkhof, R., 44
 Ostlund, G. *See* Broecker, W.S., 36
 Ottaway, J.R., 129, 130, 132, 135, 137, 138,
 139, 142, 144; 150
- Otto, N.C. *See* Quinn, J.A., 28, 31; 42
 Otway, N.M., 157; 239
 Oviatt, C.A. *See* Marshall, N., 81
 Owens, N.J. P., 1, 100, 101; 42, 126
 See Law, C.S., 1; 40
 See Rees, A.P., 42
 Ozawa, S., 155, 225; 239
- Pacala, S.W. *See* Sarmiento, J.L., 43
 Paerl, H.W. *See* Bebout, B.M., 76
 See Currin, C.A., 77
 See Pinckney, J., 82
 Page, H.M., 73; 82
 Page, J.S. *See* Wong, C.S., 45
 Paine, R.T., 165, 166, 169, 176, 177, 178, 181,
 186, 188, 205, 206, 207, 208, 209, 210,
 211, 217, 218, 225, 227, 228, 269; 239,
 240, 312
 Palmer, A.R., 155, 156, 157, 186, 187, 188,
 189, 190, 191, 207, 209, 250, 276; 240,
 312
 See Hart, M.W., 188; 235
 See Paine, R.T., 217, 218, 269; 240, 312
 Palmer, J.D., 276; 312
 Palmisano, A. *See* Dayton, P.K., 78
 Palmisano, A.C., 68; 82
 Pamatmat, M.M., 48, 57; 82
 See Hanson, R.B., 79
 Pankow, J.F. *See* Asher, W.E., 7; 35
 Parish G. *See* Endean, R., 233
 Parker, G.H., 130; 150
 Parker, P.L. *See* Macko, S.A., 125
 Parkes, R.J. *See* Underwood, G.J. C., 86
 Parkwell, T.L. *See* Thom, R.M., 85
 Parsons, T.R., 65, 100; 82, 126
 See Strickland, J.D. H., 64, 65, 66; 85
 Paterson, D.M., 69, 70; 82
 See Underwood, G.J. C., 70; 85, 86
 See Yallop, M.L., 86
 Paterson, H.E. H., 140, 141; 150
 Pattey, E., 16; 42
 Paul, A.J., 171; 240
 See Feder, H.M., 171; 234
 Paul, R. *See* Garabétian, F., 38
 Paul, V.J., 96, 99, 119, 122; 126
 Paulson, C. *See* Miyake, M., 41
 Pauly, D. *See* Longhurst, A.R., 129; 149
 Pavey, J. *See* Brace, R.C., 144; 147
 Pax, F., 131; 150
 Pearman, G.I. *See* Webb, E.K., 45
 Pearse, A.S., 168; 240
 Peduzzi, P. *See* Herndl, G.J., 79
 Peene, J. *See* Kromkamp, J., 80
 Peletier, H. *See* Delgado, M., 78
 Penas, E. *See* Varela, M., 59; 86
 Penchaszadeh, P.E. *See* Olivier, S.R., 260, 261,
 282, 287, 292, 293, 301, 304; 312

AUTHOR INDEX

- Peng, T.-H., 13, 14, 19, 20, 21; 42
See Broecker, W.S., 13, 14, 19, 20, 28; 36
- Pennock, J.R. *See* Schreiber, R.A., 58, 66; 84
- Pentcheff, N.D., 162; 240
- Perez, N.M. *See* Hernandez, P.A., 38
- Perkins, R.J., 176, 179, 188; 240
- Perrin, M. C. **129–152**; 133, 138, 139, 140, 141, 142, 143, 144, 145; 150
- Perry, D.M., 176, 178, 179; 240
- Perry, M.J., 63; 82
- Petermann, J. *See* Broecker, H.-C., 36
- Peters, V. *See* Carriker, M.R., 230
- Peterson, C.H., 99, 165, 199, 207, 228; 126, 240
- Peterson, E.W., 20; 42
- Petraitis, P.S., 164; 240
- Pettersson, K. *See* Sundbäck, K., 85
- Phillips, B.F., 196; 240
- Phillips, G.A. *See* Hargrave, B.T., 79
- Phillips, L.F., 17, 30; 42
- Pierce, S.K., 105, 106, 107; 126
See Mujer, C.V., 126
- Pietra, F. *See* Lemée, R., 125
- Pihl, L. *See* Gibson, R.N., 234
See Wennhage, H., 73; 86
- Pike, E.B., 17; 42
- Pinckney, J., 67, 72, 73; 82
- Pinckney, J.L., 58; 82
- Plante, R., 65; 83
See Plante-Cuny, M.R., 72; 83
- Plante-Cuny, M.R., 50, 51, 54, 58, 63, 64, 65, 66, 68, 72; 83
See Barranguet, C., 76
See Bodoy, A., 55, 64; 76
See Brotas, V., 49; 76
See Plante, R., 83
- Plass-Dülmer, C., 1; 42
- Plate, E.J. *See* Jähne, B., 39
- Platt, T., 60; 83
See Longhurst, A., 81
- Ploug, H. *See* Lassen, C., 81
- Plumley, F.G. *See* Darley, W.M., 77
- Pollard, P.C. *See* Moriarty, D.J. W., 82
- Polteva, D.G., 130; 151
- Pomeroy, L.R., 48, 58; 83
- Pomeroy, W.G., 58; 83
- Pond, S. *See* Large, W.G., 21; 40
- Ponder, W.F. *See* Tillier, S., 247; 314
- Porumb, I. L., 213, 217; 240
- Posey, M., 73; 83
- Potter, S.S. *See* Hutchison, C.A., 149
- Potts, D.C. *See* Smith, B.L., 135; 152
- Potts, G.W., 154, 162, 169, 172, 199, 201; 240
- Povey, A., 225; 240
- Powell, C. *See* Posey, M., 83
- Powell, H.T. *See* Barnes, H., 154, 162, 199, 200, 201, 202, 204, 207; 229
- Powelson, D.K., 33; 42
- Prasad, M.N., 265, 279; 312
See Malli, P.C., 311
- Prather, M. *See* Schimel, D.S., 43
- Pratt, D.M., 180, 197, 199, 227; 240
- Price, N.M., 29; 42
- Privitera, L.A. *See* Losey, G.S., 237
- Prouse, N.J. *See* Hargrave, B.T., 79
- Prufert, L.E. *See* Bebout, B.M., 76
- Psalidas, A.T. *See* Darley, W.M., 77
- Purcell, J.E., 167; 240
- Purchon, R.D., 246, 247; 312
- Putt, M. *See* Rivkin, R.B., 68; 84
- Qasim, S.Z., 217, 222, 223; 240, 241
- Quicke, D.L. J., 130, 135, 136, 142, 143, 144, 145; 151
See Brace, R.C., 130; 147
See Donoghue, A.M., 148
- Quinn, G.P., 263, 269, 279, 280, 285, 287, 292, 294, 295, 298, 299, 300, 304; 312, 313
See Keough, M.J., 270; 311
See Ward, S., 181; 243
- Quinn, J.A., 28, 31; 42
- Raimondi, P.T., 154; 241
See Lively, C.M., 182; 237
- Ramage, C.S., 20; 42
- Ramaswamy, V. *See* Schimel, D.S., 43
- Randall, B.M. *See* Randall, R.M., 224; 241
- Randall, R.M., 224; 241
- Rangeley, R.W., 169, 170, 171; 241
- Rankin, J.C., 264; 313
- Rao, K.S., 159; 241
- Rapsomanikis, S. *See* Bange, H.W., 35
- Rau, G.H., 100, 101, 102; 126
- Raven, J.A., 101, 102; 126
See Maberly, S.C., 125
- Raynaud, D. *See* Schimel, D.S., 43
- Read, J. *See* Ayre, D.J., 146
- Read, K.R. H., 250; 313
- Read, R. *See* Barnes, H., 229
- Reay, W.G., 71; 83
- Redman, R.S. *See* Cahoon, L.B., 77
- Reeburgh, W.S. *See* Glover, D.M., 14, 20; 38
- Reed, P.H., 171; 241
- Rees, A.P., 18; 42
- Rees, T.D., 130, 137, 138, 144; 151
- Reese, E.S. *See* Barnes, H., 171, 225; 229
- Reichardt, H., 7; 42
- Reid, D.G. *See* Ridgway, S.A., 313
- Reid, F.M. H. *See* Williams, P.M., 45
- Renaud, P.E. *See* Peterson, C.H., 99; 126
- Repak, A. *See* Burkholder, P.R., 76
- Resando, D. *See* Lemée, R., 125
- Revercomb, H.L. *See* McKeown, W., 41
- Revsbech, N.P., 53, 54, 72; 83

AUTHOR INDEX

- Reynolds, H.A. *See* Brace, R.C., 130; 147
 Reys, J.-P. *See* Plante, R., 83
 Rhodes Jr, E.W. *See* Landers, W.S., 168; 237
 Riaux, C., 49; 83
 Riaux-Gobin, C., 62, 66; 83
 See Admiraal, W., 75
 See Klein, B., 49; 80
 Rice, S.H., 269; 313
 Richard, P. *See* Blanchard, G.F., 76
 See Riera, P., 73; 83
 Richardson, C.A. *See* Crisp, D.J., 308
 Ridgway, S.A., 249; 313
 Riemann, B., 64, 66; 83
 See Holm-Hansen, O., 64; 80
 Riera, P., 73; 83
 Rifkin, J. *See* Endean, R., 154; 233
 Rinehart Jr, K.L. *See* Keifer, P.A., 236
 Rippey, E. *See* Kilburn, R., 249; 311
 Risgaard-Petersen, N. *See* Rysgaard, S., 84
 Risk, M.J., 100; 126
 Risso, A., 131; 151
 Rittschof, D., 154, 197, 198; 241
 See Brown, B., 197; 230
 See Gerhart, D.J., 234
 See Kieber, D.J., 198; 237
 See Vitalina, Sr M., 243
 See Williams, L.G., 243
 Rivera, D. *See* Dayton, P.K., 78
 Rivkin, R.B., 68, 73; 84
 Riznyk, R.Z., 58; 84
 Rizzo, W.M., 58, 66, 71, 72; 84
 Roberts, P.V., 6, 12; 42
 Roberts, T.E. *See* Bender, J.A., 229
 Robertson, J.E., 29; 42
 See Van Scoy, K.A., 44
 Robertson, K.J. *See* Williams, P.M., 45
 Robinson, G.A. *See* Colebrook, J.M., 138; 148
 Robinson, I.S., 29; 42
 Robinson, S.M. C. *See* Sloan, N.A., 206, 207, 209, 211; 242
 Rochette, P. *See* Pattey, E., 42
 Rodgers, J.H., 70; 84
 Rodhe, H. *See* Schimel, D.S., 43
 Roemer, S.C., 70; 84
 Roether, W., 14; 42
 See Fuchs, G., 37
 See Kromer, B., 14, 19, 20; 40
 See Münnich, K.O., 41
 Roller R.A., 117; 126
 Roman, M.R., 70; 84
 Romano, J.C., 27; 42
 See Garabétian, F., 38
 Ronen, D. *See* Shatkay, M., 25; 43
 Ropes, J.W., 169; 241
 Ros, J.D. *See* Marín, A., 96, 106, 108, 110, 112, 114, 116, 118, 120, 121, 122; 125
 Rosenberg, G. *See* Vermeij, G.J., 249; 314
 Rosenthal, H., 214; 241
 Rosowski, J.R. *See* Roemer, S.C., 84
 Ross, A. *See* Newman, W.A., 154; 239
 Ross, D.M., 130; 151
 Rostron, J. *See* Rostron, M. A, 137, 138; 151
 Rostron, M. A, 137, 138; 151
 See Chia, F.S., 130, 137, 138, 140; 147
 Roughgarden, J. *See* Gaines, S.D., 213, 215, 217; 234
 Round, F.E., 48, 49; 84
 Rubenstein, D. L, 129; 151
 Rudolph, J. *See* Plass-Dülmer, C., 42
 Ruitton, S. *See* Lemée, R., 125
 Rumpho, M.E. *See* Mujer, C.V., 126
 See Pierce, S.K., 126
 Rungaldier, H. *See* Lee, P.H. Y., 40
 Runham, N.W., 198; 241
 Rushton, R. *See* Bender, J.A., 229
 Russ, G.R., 164; 241
 Russell-Hunter, W.D. *See* McMahon, R.F., 252; 312
 Russo, C.A. M., 130, 131, 135, 139, 143; 151
 See Monteiro, F.A., 150
 See Solé-Cava, A.M., 152
 Ryan, N.R. *See* Quinn, G.P., 285; 313
 Ryland, J.S. *See* Shaw, P.W., 151
 Rysgaard, S., 72; 84

 Sabbe, K., 49; 84
 Sadasivan, S. *See* Schimel, D.S., 43
 Sage, W.W. *See* Darley, W.M., 77
 Salazar, J.M. *See* Hernandez, P.A., 38
 Salen-Picard, C. *See* Plante-Cuny, M.R., 83
 Saleuddin, A.S. M., 297; 313
 See Kahn, H.R., 311
 Saltzman, E.S., 4; 43
 See King, D.B., 3, 5; 39
 Salvini-Plawen, L.V., 247, 248; 313
 Sambrotto, R. *See* Wanninkhof, R., 44
 Sammarco P.W. *See* Risk, M.J., 126
 Sandee, A. *See* Kromkamp, J., 80
 Sandulli, R. *See* Pinckney, J., 73; 82
 Sanford, E. *See* Bertness, M.D., 229
 Sanhueza, E. *See* Schimel, D.S., 43
 Santelices, B., 279, 280; 313
 Santos, P.J. P., 73; 84
 Santschi, P.H. *See* Bopp, R.F., 36
 Sarmiento, J.L., 2; 43
 See Siegenthaler, U., 2; 43
 Sarojini, P. *See* Thompson, M.-F., 242
 Sarojini, R. *See* Vitalina, Sr M., 243
 Sasekumar, A. *See* Newell, R.I. E., 82
 Sathyendrenath, S. *See* Longhurst, A., 81
 Satoh, M., 117; 126
 Savidge, T.W. *See* Cahoon, L.B., 77
 Schaadt, J.G. *See* Carriker, M.R., 230
 Schaefer, W., 130, 138, 139; 151

AUTHOR INDEX

- Schell, D.M. *See* Michener, R.H., 100, 101;
126
- Scheltema, R.S., 249; 313
- Schierwater, B. *See* Hadrys, H., 148
- Schimmel, D.S., 2; 43
- Schindler, D.W. *See* Emerson, S., 37
- Schlosser, P. *See* Clark, J.F., 36, 37
See Fuchs, G., 37
See Nightingale, P., 41
See Wanninkhof, R., 44
- Schluessel, P., 29; 43
- Schmidt, G.H., 163; 241
- Schmidt, H., 130, 131, 132, 133, 134; 151
- Schmitt, K.F., 15; 43
- Schmitz, K. *See* Kremer, B.P., 115, 116; 125
- Schollen, L.M. *See* Saleuddin, A.S. M., 313
- Schopf, T.J. M., 145; 151
- Schrader, G.C. *See* Horner, R., 57, 65; 80
- Schreiber, R.A., 58, 66; 84
- Schubauer, J.P. *See* Hopkinson Jr, C.S., 80
- Schuster, W.S. F. *See* Clark, J.F., 36
- Schwartz, H.P. *See* Risk, M.J., 126
- Schwartz, S.E., 1; 43
- Scott, J.C., 27; 43
- Scrimgeour, C.M. *See* Raven, J.A., 126
- Scullard, C. *See* Bayne, B.L., 193; 229
- Scully-Power, P., 27; 43
- Seapy, R.R., 158; 241
- Sebens, K.P., 129, 188, 189, 207; 151, 241
- Secord, D. *See* McFadden, C.S., 150
- Seiler, W. *See* Conrad, R., 12, 33; 37
- Sellner, K.G. *See* Iannuzzi, T.J., 80
- Serebryansky, V.T. *See* Kishinevsky, M.K., 9;
39
- Serov, O.L., 143; 151
- Shadrin, N.V. *See* Gul'bin, V.V., 192; 235
- Shaffer, G.P., 54, 58, 70; 84
- Shanks, A.L., 162; 241
- Sharp, G.D., 50, 51; 84
- Sharp, J.H., 27; 43
- Sharpe, J.S. *See* Elmhirst, R., 145; 148
- Shatkay, M., 25; 43
See Gat, J.R., 25; 38
- Shaw, D.D. *See* Moran, C., 150
- Shaw, P.W., 130, 135, 138, 142, 143, 144; 151
- Shelford, V.E., 162; 241
- Shelton, J.C. *See* Lee, P.H. Y., 40
- Shepherd, R. *See* Rittschof, D., 241
- Sherr, E.B. *See* Incze, L.S., 80
- Sherwood, C.R. *See* Asher, W.E., 35
- Shiaris, M.P. *See* Epstein, S.S., 78
- Shick, J.M., 130, 142; 151, 152
- Shine, K.P. *See* Schimmel, D.S., 43
- Shmid, R. *See* Koop, H.U., 125
- Shreffler, D.K. *See* Thom, R.M., 85
- Shumway, S.E., 217, 219, 252; 247, 313
- Sibert, J. *See* Burkholder, P.R., 76
- Sieburth, J.M., 26; 43
See Conover J.T., 164; 231
- Siefridt, L. *See* Boutin, J., 36
- Siegenthaler, U., 2; 43
See Jähne, B., 39
See Münnich, K.O., 41
- Siems, W., 9; 43
See Broecker, H.-C, 14; 36
- Sigmon, D.E., 71, 72; 84
- Sigoillot, J.C. *See* Garabétian, F., 38
- Sih, A., 156; 241
- Silva, P.C., 105; 126
- Silver, M.W. *See* Stoecker, D.K., 127
- Simmons Jr, G.M. *See* Reay, W.G., 83
- Simpson, H.J. *See* Clark, J.F., 36
- Simpson, J.W., 264; 313
- Simpson, R.D., 257, 258, 259, 260, 261, 263,
265, 279, 285, 286, 287, 291, 292, 301;
313
- Simsiridou, M. *See* Chintiroglou, C.C., 130,
132; 148
- Singh, R.-D. *See* Kirk, G.J. D., 28, 29; 39
- Sjoberg, T. *See* Nightingale, P., 41
- Skauen, D.M. *See* Marshall, N., 81
- Skerman, T.M., 167, 168; 241
- Skibinski, D.O. F., 143; 152
See Ward R.D., 143; 152
- Slade, N.A. *See* Tieszen, L.L., 127
- Slater, P.G. *See* Liss, P.S., 4, 29; 40
- Sleder, J., 176, 178; 241
- Sloan, N.A., 73, 205, 206, 207, 209, 211; 84, 242
- Sloth, N.P. *See* Rysgaard, S., 84
- Smethie, W.M., 14, 18, 19; 43
- Smith, B.L., 135; 152
- Smith, D.C. *See* Gallop, A., 124
See Hinde, R., 106, 107, 112, 114, 115, 116;
124
See Trench, R.K., 127
- Smith, G.A. *See* Palmisano, A.C., 82
- Smith, J.H., 9; 43
- Smith, P.M. *See* Asher, W.E., 35
- Smith, S.D., 14, 15, 16, 32; 43
See Oost, W.A., 42
- Smith, S.M. *See* Menard, H.W., 50, 51, 52, 62;
81
- Smith, S.V., 18, 19; 43
- Smith, W.D. *See* Lamontagne, R.A., 40
- Smith, W.L. *See* McKeown, W., 41
- Sobieski, P. *See* Bliven, L.F., 36
- Solé-Cava, A.M., 130, 131, 133, 134, 135, 138,
140, 141, 142, 143, 144, 145; 152
See Monteiro, F.A., 150
See Perrin, M.C., 129–152
See Russo, C.A. M., 130; 151
- Šoljan, T., 217, 220, 221; 242
- Solomon, D.J. *See* Child, A.R., 143; 147
- Solomon, S. *See* Schimmel, D.S., 43

AUTHOR INDEX

- Somero, G.N., 145; 152
 SooHoo, J.B. *See* Palmisano, A. C., 82
 Sorokin, Yu. I., 58, 59; 84, 85
 Soule, M. *See* Somero, G.N., 145; 152
 Sourmia, A., 49, 59, 66; 85
 See Charpy-Roubaud, C., 51, 60; 77
 Sousa, W.P., 162; 242
 Southward, A.J., 154; 242
 Southward, E.C. *See* Southward, A.J., 154; 242
 Souza-Santos, L.P. *See* Santos, P.J. P., 84
 Spight, T.M., 188, 190, 191; 242
 Spillane, M.C. *See* Monahan, E.C., 23, 25; 41
 Srinivasan, J. *See* Schimel, D.S., 43
 Stal, L.J. *See* Yallop, M.L., 86
 Standing, J.D., 154; 242
 Stanley, S.M., 156, 227; 242
 See Newman, W.A., 227; 239
 Stanton, G.R. *See* Palmisano, A.C., 82
 Stauffer, R.E., 6; 43
 Stebbins, G.L., 143; 152
 Steckley, M. *See* Asher, W.E., 35
 Steele, J.H., 48, 59, 66; 85
 Steinberg, P.D. *See* Hay, M.E., 94, 121; 124
 Steiner, G. *See* Salvini-Plawen, L.V., 247; 313
 Stephens, G.C., 102; 126
 Stephenson, R.L., 101; 126
 Stephenson, T.A., 130, 132, 133, 136, 137; 152
 Stephenson, W. *See* Endean, R., 233
 Stepien Jr, W.P., 213; 242
 Stewart, W.C. *See* van Raalte, C., 86
 Stickle, W.B., 188, 189; 242
 Stickney, R.R. *See* Shumway, S.E., 217, 219;
 241
 Stimson, J., 174; 242
 Stirling, P. *See* Little, C., 275; 311
 Stirts, H.M., 106, 114; 126
 See Clark, K.B., 123
 Stockner, J.G. *See* Pomeroy, W.G., 58; 83
 Stoecker, D.K., 106; 126, 127
 Stofan, P.E. *See* Manziet, J.J., 40
 Stouffer, R.J. *See* Sarmiento, J.L., 43
 Strasburg, D.W. *See* Hiatt, R.W., 213, 216; 235
 Strathmann, M.F., 287, 291, 295; 313
 Strathmann, R.R. *See* Johnson, L.E., 154; 236
 Stribling, J.M., 73; 85
 Strickland, J.D. H., 64, 65, 66; 85
 See Holm-Hansen, O., 79
 Stubbings, H.G., 153; 242
 Stuver, M. *See* Braziuinas, T.F., 36
 See Broecker, W.S., 36
 Suijlen, J.M., 18; 44
 See den Daas, J.H., 37
 Sullivan, C.W. *See* Palmisano, A.C., 82
 Sullivan, M.J., 59, 73; 85
 See Moncrieff, C.A., 82
 See Shaffer, G.P., 70; 84
 Sumikawa, S., 288; 313
 Summers, R.W. *See* Feare, C.J., 223; 233
 Sun, M.-Y., 63, 66; 85
 Sundaram, K.S. *See* Rao, K.S., 159; 241
 Sundbäck, K., 59, 66, 71, 72; 85
 See Madsen, K.N., 81
 See Wulff, A., 86
 Sundquist, E.T. *See* Sarmiento, J.L., 2; 43
 Sutherland, J.P., 172, 176, 177, 195, 284; 242,
 314
 See Menge, B.A., 165, 193, 208, 210, 227,
 228; 238
 See Moreno, C.A., 312
 Sutter III, F. *See* Edwards, D.C., 232
 Sverdrup, H.U., 50; 85
 Sweeney, R.E. *See* Rau, G.H., 126
 Swennen, C., 154, 201, 202; 242
 Swinnerton, J.W. *See* Lamontagne, R.A., 40
 Szymanska, J. *See* Palmer, A.R., 240
 Tablado, A., 270, 280, 299; 314
 See López Gappa, L., 311
 Takahashi, T., 18; 44
 See Broecker, W.S., 36
 See Smethie, W.M., 43
 See Tans, P.P., 44
 Talbot, G.A. *See* Talbot, J.W., 17; 44
 Talbot, J.W., 17; 44
 Talbot, M.C. *See* Perry, M.J., 82
 Tan, F.C. *See* Stephenson, R.L., 126
 Tans, P.P., 2, 18, 29; 44
 Taylor, D. L., 106, 116; 127
 Taylor, J.D., 180, 181; 242
 See Ridgway, S.A., 313
 Taylor, P.K., 20; 44
 Teal, J.M. *See* Connor, M.S., 77
 See van Raalte, C., 86
 Templeton, A.R., 141, 142; 152
 Templeton, R., 133; 152
 Tenore, K.R. *See* Hanson, R.B., 79
 See Roman, M.R., 70; 84
 Terazaki, M. *See* Wada, E., 127
 Tesdahl, K.G. *See* Tieszen, L.L., 127
 Theisen, B.F., 90, 118; 127
 Therkildsen, M.S., 72; 85
 Thiele, J., 247; 314
 Thom, R.M., 59; 85
 Thomas, C.J., 73; 85
 See Cahoon, L.B., 76, 77
 Thomas, I.M. *See* Ottaway, J.R., 130; 150
 Thomas, L. *See* Palmer, A.R., 240
 Thomas, M.L. H. *See* Rangeley, R.W., 169,
 170, 171; 241
 Thomas, R.F., 262, 274, 278; 314
 Thompson, J.K., 66, 73; 85
 Thompson, M.-F., 154; 242
 Thompson, T.E., 154, 199, 200, 201, 204; 242
 See Yonge, C.M., 88; 128

AUTHOR INDEX

- Thorp, C.H. *See* Carter, M.A., 130, 135, 137, 138, 141, 144; 147
- Thorpe, J.P., 132; 152
See Allcock, A.L., 146
See Carter, M.A., 130, 132, 133, 134, 135, 139, 142, 143; 147
See Haylor, G.S., 148
See Monteiro, F.A., 150
See Orr, J., 150
See Perrin, M.C., 129–152
See Russo, C.A.M., 151
See Solé-Cava, A.M., 130, 133, 134, 135, 138, 140, 141, 142, 143, 144, 145; 152
- Thorpe, S.A., 24; 44
See Woolf, D.K., 23; 45
- Thorson, G., 291, 292, 302; 314
- Thurston, J.P. *See* Carvalho, G.R., 147
- Tieszen, L.L., 100, 101; 127
- Tietjen, J. *See* Hanson, R.B., 79
- Tillier, A. *See* Tillier, S., 314
- Tillier, S., 247; 314
- Toba, Y. *See* Ebuchi, N., 37
- Todd, C.D., 154, 202, 203, 204; 242
See Hall, S.J., 148
See Solé-Cava, A.M., 152
- Toews, D.P. *See* Gibson, G.D., 124
- Top, Z. *See* Münnich, K.O., 41
- Topinka, J.A. *See* Barnes, H., 229
- Torgersen, T., 8, 9; 44
See Broecker, W.S., 36
- Torres, J.J. *See* Rau, G.H., 126
- Torti, M.R. *See* Bastida, R., 306
- Tréguer, P. *See* Riaux-Gobin, C., 83
- Trench, R.K., 87, 105, 106, 107, 108, 114, 116, 117, 121; 127
- Triska, F.J., 72; 85
- Tronzo, C.R. *See* Cahoon, L.B., 77
- Trowbridge, C.D., 88, 96, 97, 99, 104, 105, 114, 118, 119, 120, 121, 122; 127
- Trueman, E.R. *See* Jones, H.D., 266; 310
- Tuesdale, G.A. *See* Downing, A.L., 9; 37
- Tugwell, G., 132, 133; 152
- Turner, B.J., 145; 152
- Turner, S.M., 1; 44
See Liss, P.S., 40
- Turnpenny, A.W. H. *See* Collins, K.J., 231
- Udhayakumar, M. *See* Karande, A.A., 157; 236
- Uher, G., 1; 44
- Underwood, A.J. 118, 158, 163, 172, 173, 182, 183, 186, 193, 196, 227, 228, 269, 278, 279; 127, 242, 243, 314
See Creese, R.G., 262, 277, 278, 283, 284; 308
See Denley, E.J., 164, 169, 173, 174, 182, 183; 232
See Fairweather, P.G., 182, 183, 184, 186, 198, 227; 233
See Moran, M.J., 238
- Underwood, G.J. C., 69, 70; 85, 86
- Upstill-Goddard, R.C., 16, 17, 18, 19, 20, 22, 34; 44
See Frost, T., 1–45
See Liss, P.S., 40
See Nightingale, P., 16; 41
See Rees, A.P., 42
See Watson, A.J., 45
- Vagle, S., 24; 44
- Valiela, I. *See* Connor, M.S., 77
See van Raalte, C., 86
- Van Alstyne, K.L. *See* Paul, V.J., 96, 99, 119; 126
- Van Beusekom, J.E. E. *See* de Jonge, V.N., 70; 78
- Van Buurt, G. *See* Colijn, F., 65; 77
- Vance, R.R., 208, 212; 243
See Nelson, B.V., 156; 239
- Van Engel, W.A. *See* Burrell Jr, V.G., 167; 230
- Van Es, F.B., 56; 86
- Van Raalte, C., 58; 86
- Van Rijswijk, P. *See* Kromkamp, J., 80
- Van Scoy, K.A., 29; 44
- Van Valen, L., 144; 152
- Vanvleet, E.S. *See* Williams, P.M., 45
- Varas, E., 213; 243
- Varela, M., 53, 59, 62; 86
- Vargo, G. *See* Wanninkhof, R., 44
- Vasserot, J., 170; 243
- Verderber, G.W., 261, 263, 273, 274; 314
- Vermeij, G.J., 249, 250, 259, 260; 314
- Vevers, H.G., 207, 209; 243
- Vilbaste, S., 66; 86
- Villalobos, C.R., 175, 176, 179, 188, 191, 195, 208, 210; 243
- Vink, S.M. *See* Chambers, R.M., 77
- Vitalina, Sr M., 154; 243
- Viviani, C.A., 206, 208, 209; 243
- Vojvodic, V., 27; 44
- Vollenweider, R.A., 66; 86
- von Bodungen, B. *See* Sloan, N.A., 73; 84
- Voss, N.A., 249, 280, 284, 287, 292, 294, 299; 314
- Vyverman, W. *See* Sabbe, K., 49; 84
- Wada, E., 101; 127
See Minagawa, M., 101, 102; 126
- Wagh, A.B., 165, 227; 243
- Wailles, G.H., 213, 214; 243
- Wainwright, S.A. *See* Newman, W.A., 239
- Wais, T. *See* Jähne, B., 39
- Wakita, H. *See* Hernandez, P.A., 38

AUTHOR INDEX

- Walker, D.I. *See* Raven, J.A., 126
See Williams S.I., 87–128
- Walker, G. *See* Young, G.A., 152
See Yule, A.B., 160, 162; 244
- Wallace, D.W.R., 11, 23; 44
- Walsh, A.L., 24; 44
- Walsh, J.J., 50, 51, 71; 86
- Wanders, J.B. W., 59; 86
- Wang, D.S. *See* Keswick, B.H., 17; 39
- Wang, Q. *See* Asher, W.E., 35
- Wanninkhof, R., 5, 6, 14, 16, 17, 18, 19, 20, 21, 22, 24, 28; 44, 45
See Asher, W.E., 17, 23, 24, 25; 35
See Clark, J.F., 36, 37
See Crucius, J., 22; 37
See Ho, D.T., 38
- Wanninkhof, R.H., 7, 8, 9, 11, 20, 27, 28; 45
See Asher, W.E., 17; 35
See Bliven, L.F., 36
- Ward, R.D., 143; 152
See Skibinski, D.O. F., 143; 152
- Ward, S., 181; 243
- Warner, G.F. *See* Schmidt, G.H., 163; 241
- Warren, S.G. *See* Charlson, R.J., 36
- Warwick, R.M. *See* Joint, I.R., 80
- Wassenberg, T.J. *See* Moriarty, D.J. W., 82
- Watanabe, H. *See* Fuji, A., 78
- Watson, A.J., 8, 9, 11, 16, 17, 18, 20, 24; 45
See Law, C.S., 40
See Liss, P.S., 40
See Robertson, J.E., 29; 42
See Van Scoy, K.A., 44
See Wanninkhof, R., 45
See Upstill-Goddard, R.C., 44
- Watson, D. *See* Dayton, P.K., 78
- Watson, D.C. *See* Hawkins, S.J., 309
- Watson, G.F. *See* Littlejohn, M.J., 149
- Watts, P.C. *See* Allcock, A.L., 146
- Watts, P.D., 20; 45
- Waugh, G.R., 106, 110, 112; 127
- Weaver, S., 100, 106, 118; 128
- Webb, E.K., 15; 45
- Weinstein, M.P. *See* Iannuzzi, T.J., 80
- Weiss, R.F. *See* Lupton, J.E., 40
See Nevison, C.N., 41
- Weiss, R. *See* Broecker, W.S., 36
- Weiss, W. *See* Jähne, B., 39
See Münnich, K.O., 41
- Wells, F.E., 88, 89, 90; 128
See Jensen, K.R., 90; 125
- Wells, N.C. *See* Robinson, I.S., 42
- Wells, R.M. G., 250, 251, 253; 314
- Welsh, B.L. *See* Baillie, P.W., 70; 76
- Wendker, S., 59; 86
- Wennhage, H., 73; 86
See Gibson, R.N., 234
- Weppernig, R. *See* Wanninkhof, R., 44
- Wesely, M.L., 15; 45
- West, L., 188, 191; 243
- Wetzel, R.L. *See* Rizzo, W.M., 58, 66; 84
- Wharton, G.W. *See* Pearse, A.S., 168; 240
- White, D.C. *See* Palmisano, A.C., 82
- White, D.R. A. *See* Lasiak, T.A., 282, 283; 311
- Whitman, W.G., 2, 3, 6, 7, 9; 45
- Whitney, D.E., 62, 64, 65, 67; 86
- Wickramanayake, B. *See* Banks, R.B., 35
- Wieghehl, J.G. *See* Crisp, D.J., 308
- Wienke, S.M. *See* Thompson, J.K., 85
- Wieters, E.A., 191; 243
- Wigley, T. *See* Schimel, D.S., 43
- Wigley, T.M. L., 1; 45
- Wilce R.T. *See* Ellis, D.V., 159, 160; 232
- Wilke, C.R., 5; 45
- Wilkinson, M. *See* Mills, D.K., 67; 82
- Wilkinson, P. *See* Moran, C., 150
- Wilkinson, V., 49, 59; 86
- Willey, A., 169; 243
- Williams, A.B. *See* Lee, P.H. Y., 40
- Williams, G.A., 263; 314
See Davies, M.S., 267, 268; 308
See Evans, M.R., 275; 309
- Williams, G.C., 144; 152
- Williams, J.P. F., 264; 314
- Williams, L.G., 198; 243
See Carriker, M.R., 175, 198; 230
See Rittschof, D., 241
- Williams, M.L., 87, 106; 128
- Williams, P.M., 26; 45
- Williams S. L., 87–128
- Willis, P.-J. *See* Sieburth, J.M., 43
- Wills, J.A. B. *See* Oost, W.A., 42
- Wimpee, B.B. *See* Darley, W.M., 77
- Wirick, C.D. *See* Wallace, D.W. R., 11, 23; 44
- Wise, D.L. *See* De Villiers C.J., 308
- Wiseman, W.J. *See* Wanninkhof, R., 44
- Wishart, J. *See* Ayre, D.J., 146
- Witting, J., 8; 45
- Wolcott, T.G., 265; 314
- Wollast, R., 50, 51; 86
- Womersley, H.B. S., 104, 115; 128
- Wong, C.S., 15, 29; 45
- Wong, P.P. S. *See* Wells, R.M. G., 250, 251, 253; 314
See Innes, A.J., 310
- Wong, R.L. J. *See* Thompson, J.K., 85
- Wood, J. Upstill-Goddard, R.C., 44
- Wood, L., 180, 191, 193, 197, 198, 199; 243
- Woodward, I. *See* Cao, M., 2; 36
- Wolf, D., 24; 45
- Wolf, D.K., 23, 27; 45
- Wootton, J.T., 225; 243, 244
- Wratten, S.D. *See* Carvalho, G.R., 147
- Wright, W.G. *See* Shanks, A.L., 162; 241

AUTHOR INDEX

- Wuebbles, D. *See* Schimel, D.S., 43
 Wulff, A., 69; 86
 Wyngaard, J.C., 15; 45
 Wynne, M.J. *See* Bold, H.C., 49, 69, 70; 76
- Yallop, M.L., 70; 86
 Yamamuro, M., 100; 128
 Yamasu, T. *See* Kawaguti, S., 106, 117; 125
 Yee, R. *See* Lee, P.H. Y., 40
 Yelland, M.J. *See* Taylor, P.K., 44
 Yentsch, C.S., 66; 86
 Yonge, C.M., 88, 246, 250; 128, 314
 Yoshiyama, R.M., 217, 220; 244
 Young, C.M. *See* Cowden, C., 231
 Young, D.R. *See* Rau, G.H., 126
 Young, G.A., 130; 152
 Yuen, H.C. *See* Lee, P.H. Y., 40
 Yule, A.B., 160, 162; 244
 See Young, G.A., 152
- Zakijan, S.M. *See* Serov, O.L., 151
 Zamer, W.E., 129, 135; 152
 Zamorano, J.H. *See* Moreno, C.A., 269; 312
 Zander, C.D., 213, 216, 217, 220 221; 244
 Zappa, C.J. *See* Jessup, A.T., 39
 Zedler, J.B., 49, 59; 86
 See Fong, P., 78
 See Kwak, T.J., 73; 81
 Zepp, R.G. *See* Miller, W.L., 33; 41
 Zhang, J. Z. *See* Wanninkhof, R., 44
 Zhou, X. *See* Schimel, D.S., 43
 Zhou, X.L., 33; 45
 Zingmark, R.G., 66; 86
 See Holland, A.F., 79
 See Kelley, B.J., 80
 See Pinckney, J., 67; 82
 See Pinckney, J.L., 58; 82
 Zischke, J.A., 286, 287, 292, 295, 304; 314
 Zullo, V.A. *See* Newman, W.A., 239

SYSTEMATIC INDEX

References to sections of articles are given in *italics*; references to pages are given in normal type.

- Abudefduf*, 217
Acanthina, 175–79, 176, 177, 178, 179, 180
 angelica, 156, 176, 177
 brevidentata, 176, 177, 178, 195, 284, 285
 punctulata, 176, 178
 spirata, 176, 178, 179
Acanthoclinus quadridactylus, 217, 223
Acanthocyclus gayi, 170
 hassleri, 170
Acetabularia, 105, 111
 acetabulum, 96, 110, 118, 120, 121, 122
Acipenser transmontanus, 217, 220
Acmaea digitalis, 173
 paradigitalis, 173
 pelta, 173
 scutum, 173
Acrosiphonia, 99
Actinia, 129, 130, 131, 132, 133, 135, 136,
 137, 138, 139, 140, 141, 142, 143, 144,
 145, 146
 bermudensis, 131, 135, 139
 cari, 131
 equina, 129, 131, 132, 133, 134, 135, 136,
 137, 138, 139, 141, 142, 143, 144, 145,
 146
 equina atlantica, 134
 equina equina, 134
 equina mediterranea, 132, 134
 equina var. *fragacea*, 132, 133
 equina var. *mesembryanthemum*, 133
 fragacea, 131, 132, 133, 134, 139
 prasina, 131, 133, 134, 138
 sali, 131, 134, 135
 schmidti, 131, 132, 134, 135, 139
 striata, 132
 tenebrosa, 132, 137, 139, 144
Actiniaria, 129
Actiniidae, 143
Actophila, 248
Aglaja diomedea, 98
Alderia modesta, 88, 97, 115, 118
Amphibola crenata, 252, 253
Amphibolidae, 247, 248
Amphiboloidea, 247
Amphiboloidei, 248
Amphora, 49
Anachis, 175
 boivini, 175
 rugosa, 175, 195
Annelida, 169
Anthozoa, 129, 167
Aphelasterias japonica, 206, 207
Aphriza virgata, 225
Aplysiopsis, 119
 enteromorphae, 97, 114, 119, 120
 smithi, 97, 114, 119
 zebra, 97, 115
Arbacia punctulata, 212
Archaeogastropoda, 172
Archidoris montereyensis, 98
Archosargus probatocephalus, 217
 rhomboidalis, 213
Arenaria interpres, 223
Artemia, 214
Arthropoda, 169–72
Arthropyrenia balanophila, 166
Asciidiella aspera, 165
Ascobulla, 88, 89
 fischeri, 89, 90, 95
 ulla, 95, 113
Ascoglossa, 88
Asterias, 209, 210
 amurensis, 206, 207
 forbesi, 206, 207, 209, 210
 rubens, 205, 206, 207, 209, 210
 vulgaris, 206, 207, 210
Asteroidea, 205–12
Austrocochlea constricta, 285
Avrainvillea, 103, 105, 111, 114, 115
 nigricans, 96, 97
Bacillus, 18
 globigii, 17, 18
Balanidae, 156, 220, 221
Balanoidea, 158
Balanus, 154, 168, 171, 174, 178, 190,
 192, 207, 208, 209, 211, 214, 217,
 220, 223
 albicostatus albicostatus, 165, 197
 algicola, 172

SYSTEMATIC INDEX

- amphitrite*, 176, 177, 181, 197, 227, 285
amphitrite cirratus, 167
amphitrite communis, 159
balanus, 157, 158, 201, 202
crenatus, 157, 158, 165, 171, 173, 174, 200, 201, 202, 203, 204, 206, 207, 211
eburneus, 154, 155, 168, 197, 198, 199, 207, 226
glandula, 155, 156, 160, 162, 163, 164, 171, 172, 173, 174, 176, 178, 179, 187, 188, 189, 190, 191, 204, 207, 208, 209, 211, 212, 215, 225, 226
improvisus, 157, 165, 168, 170
laevis, 165, 170, 180, 218, 219
nubilus, 160, 187, 188, 197, 207, 208, 210, 211
pacificus, 168, 208
perforatus, 157, 158, 170
porcatus, 201, 202
rostratus, 197
subalbidus, 197
trigonus, 164, 165, 167, 182, 197
 Basommatophora, 247, 248
 Batophora, 97
Bedera paivae, 181
Benhamina, 248, 249, 291, 303
obliquata, 251, 252, 262, 272, 274, 277, 287, 292, 293, 294, 295, 299, 301, 303
Berthelinia, 89
australis, 95
babai, 95
caribbea, 95, 113
chloris, 113
ganapati, 95
limax, 95
rotnesti, 91, 95
typica, 95
Biddulphia, 95
Blennius galerita, 217, 220, 221
incognitus, 217, 221
nigriceps, 221
pavo, 217, 221
pholis, 217, 221, 222
sanguinolentus, 217, 221
sphynx, 217, 221
zvonimiri, 217, 221
Bosellia mimetica, 97, 114
 Bosellidae, 107, 113
Botryllus schlosseri, 165
Brachidontes semilaevis, 182
 Bryopsidaceae, 110
Bryopsis, 97, 99, 103, 104, 111
corticulans, 96, 97
plumosa, 95, 96, 97, 98
 Buccinidae, 180
Buccinum undatum, 206
Bunodactis verrucosa, 139
Calidris maritima, 223
Caliphylla, 106
mediterranea, 97, 114
Calliopaea oophaga, 97
 Cancer, 170
borealis, 169
irroratus, 169
magister, 170, 171
pagurus, 170
Carcinus maenas, 169, 170, 171
Cassidula aurisfelis, 252
Catomerus polymerus, 182
Caulerpa, 87, 88, 91, 92, 94, 95, 97, 102, 103, 104, 105, 110, 111, 112, 113, 114, 115, 117, 119, 122
ambigua, 95
ashmeadii, 96
brownii, 95
cupressoides, 95, 96
fastigiata, 97
filiformis, 113
geminata, 95
mexicana, 96
okamurai, 95
paspaloides, 95, 96
prolifera, 95
racemosa, 95, 96, 104, 113, 117
scalpelliformis, 95
sertularioides, 95, 96, 108, 113, 117
simpliciuscula, 95
taxifolia, 119, 120
verticillata, 95, 97, 98, 113, 114
 Caulerpaeae, 110
 Caulerpales, 104, 110, 111, 112, 114, 115, 118, 121, 122
Cellana, 277, 283, 284
capensis, 283
grata, 267
toreuma, 279, 281, 282, 285
tramoserica, 163, 173, 174
Centronotus gunnellus, 217, 223
Centrostephanus coronatus, 212
 Cephalopoda, 204–5
Ceramium, 120
codicola, 120
Chaetomorpha, 95, 97, 98, 103, 104, 111, 114, 115, 119
aerea, 98
linum, 96, 98, 118, 119
moniligera, 98
Chamaesipho, 184, 185
brunnea, 164, 181, 182, 186, 206
columna, 164, 165, 181, 182, 184, 185, 186, 206
tasmanica, 185
Chelonia mydas, 218
Chelonibia, 192

SYSTEMATIC INDEX

- Chelonibia patula*, 192
 Chilinoidei, 248
 Chilopoda, 171
Chionoecetes bairdi, 171
Chirona amaryllus, 165
Chlorodesmis, 96, 111, 114
 comosa, 97
 Chlorophyta, 99, 102, 119, 122
 Chondria, 165
Chondrus crispus, 195
 Chrysophyta, 111, 122
Chthamalus, 156, 158, 162, 163, 165, 166, 167,
 173, 176, 177, 178, 179, 181, 182, 187, 191,
 193, 194, 196, 197, 202, 207, 209, 218
 anisopoma, 156, 163, 166, 172, 176, 177, 182
 antennatus, 181, 182, 184, 185, 225
 belyaevi, 186
 challengeri, 165, 167, 197, 206, 207, 281, 285
 cirratus, 180, 218, 219
 dalli, 163, 164, 172, 173, 174, 176, 178, 187,
 188, 189, 190, 191, 192, 204, 207, 208,
 209, 211, 225, 226
 dentatus, 162, 163, 186, 187
 depressus, 164
 fissus, 162, 172, 174, 176, 177, 178, 179,
 188, 191, 196, 284
 fragilis, 162
 malayensis, 227
 montagui, 157, 165, 166, 193, 194
 panamensis, 175
 scabrosus, 165, 180, 218, 219, 226
 stellatus, 157, 162, 164, 166, 193, 194, 220
 stellatus stellatus, 159
Ciona intestinalis, 165
 Cirripedia, 221
Cladophora, 95, 97, 98, 103, 104, 111, 114
 columbiana, 119
 fuliginosa, 97, 115
 rupestris, 96, 98
 Cladophorales, 113, 114, 115
Cladophoropsis, 98, 103, 104
Clinocottus, 217
 analis, 217, 220
Clupea harengus, 213, 214
 pallasii, 213, 214
 sprattus, 213, 214
 Cnidaria, 129
Cocconeis, 49
 Codiaceae, 110
 Codiales, 113, 114, 115
Codium, 95, 96, 97, 99, 102, 103, 105, 111,
 113, 116, 117, 119, 120, 121, 122
 convolutum, 96
 fragile, 95, 96, 105, 106, 107, 117, 120, 121
 fragile ssp. *tomentosoides*, 96
 setchellii, 96, 119, 121
 stephensiae, 97
 Coelenterata, 167
Collisella, 163, 283
 digitalis, 172
 onychitis, 283
 strongiana, 163, 172
Colpomenia sinuosa, 164
Concholepas, 180
 concholepas, 179–80
Corallina pilulifera, 281
Coryphoblennius galerita, 217, 220, 221, 222, 223
Costasiella, 89
 liliana, 97, 108, 109, 115
 ocillata, 97
 Cottidae, 214
Crassostrea gigas, 165
 nippona, 165
 virginica, 198
Crenilabrus melops, 217, 221
Crossaster papposus, 206, 207
 Ctenophora, 167
Cyerce, 89
 antillensis, 97, 114
 nigra, 97
Cympolia, 103, 105
 barbata, 97, 114

Damalichthys vacca, 217, 220
Dasya, 97
 Dasycladales, 114
Dendronotus iris, 98
 Derbesiaceae, 110
 Derbesiales, 114, 115
Dexiospira foraminosus, 165
Dicathais aegrota, 196
 orbita, 196
Dicentrarchus labrax, 213, 214, 216
Dictyosphaeria cavernosa, 98
Dictyota, 165
Diplodus cervinus, 213, 214
 sargus, 213, 214
Diploneis, 49
Diplosoma mitsuhurii, 165
 Diptera, 172
Doris bilamellata, 154
Drosophila, 143
Drupa, 180, 181
 clathrata clathrata, 180
 ricinus, 180
 rubusidaeus, 18
Drupella cariosa, 180

 Echinodermata, 205–12
 Echinoidea, 212
Edwardsia danica, 154
 longicornis, 154
 Eleotridae, 216
 Ellobiidae, 247

SYSTEMATIC INDEX

- Elminius*, 162, 165, 181, 182
adelaide, 181
modestus, 157, 158, 162, 163, 164, 165, 167,
170, 181, 182, 186, 193, 194, 201, 202,
205, 207, 209, 223
plicatus, 158, 164, 225
- Elysia*, 88, 91, 94, 106, 116
atroviridis, 95, 106, 117
australis, 95, 106, 107, 113
canguzua, 95
catulus, 95, 113
cauze, 96, 113
cauzescops, 108
chlorotica, 95, 106, 107, 113
evelinae, 95, 113
expansa, 92, 96
filicauda, 96
furvacauda, 99, 106, 112, 113, 117
fusca, 96
halimeda, 96
hedgpathi, 96, 99, 113
maoria, 96, 106
ornata, 96
papillosa, 96
punctata, 96
serca, 96, 114
subornata, 96, 119, 120
timida, 96, 106, 110, 112, 114, 116, 118, 120
tuca, 96, 114, 121
viridis, 96, 99, 106, 107, 108, 112, 114, 116,
117, 118
- Elysiella pusilla*, 96
- Elysiidae, 89, 91, 95, 96, 97, 107, 113, 114
- Elysoidea, 91
- Embiotoca lateralis*, 217, 220
- Emplectonema*, 169
gracile, 169
- Engina*, 180
- Enteromorpha*, 95, 104, 164, 280, 281, 282
intestinalis, 113
- Epiactis prolifera*, 137
- Epopella*, 165, 182
plicata, 165, 181, 182, 186
- Ercolania boodlea*, 98
coerulea, 98, 115
funerea, 98
fuscata, 98, 115
gopalai, 98
nigra, 98, 118
vanellus, 98
viridis, 98
- Eulalia viridis*, 169
- Eupleura caudata etterae*, 198
- Eupulmonata, 247, 248
- Eustylochus meridionalis*, 168
- Evasterias*, 211
troscheli, 207, 211
- Fasciolaria*, 181
hunteria, 181
- Fasciolariidae, 180, 181
- Favorinus branchialis*, 98
- Fiona*, 204
marina, 204
pinnata, 204
- Fissurella*, 284
picta, 284
virescens, 284
- Fissurellidae, 283
- Foraminifera, 106
- Forcipulatida, 206, 207
- Fucus distichus*, 155, 163
serratus, 163
vesiculosus, 163
- Galeolaria*, 169
caespitosa, 169
- Gastropoda, 88, 172–5, 245
- Gastropterion pacificum*, 98
- Gelidium*, 184
pusillum, 164
- Gibbula magus*, 205
- Girella laevifrons*, 213
- Gobiesox maeandricus*, 217, 218
- Gobius cephalarges*, 213, 216, 217
melanostomus, 213, 217
microps, 213, 216
minutus, 213, 216
paganellus, 221
- Graus nigra*, 213
- Griffithsia*, 97, 115
floculosa, 97
- Halimeda*, 97, 103, 105, 111, 114, 121
cuneata, 96
discoidea, 96, 110
incrassata, 96, 110, 121
macroloba, 96
tuna, 96, 97
- Haliplanella luciae*, 142
- Halodule wrightii*, 96
- Halophila engelmanni*, 96
- Haminoea virescens*, 98
- Heliaster*, 228
helianthus, 206, 207
kubiniji, 207, 227, 228
- Helisoma*, 297
- Hermaea*, 92
bifida, 97, 115
cruciata, 97, 115
evelinemarcusae, n. sp. 93
smithi, 97
vancouverensis, 97
- Hermaeidae, 93, 97, 107, 114, 115
- Hermaeina smithi*, 114

SYSTEMATIC INDEX

- Hermisenda crassicornis*, 98
Hexacorallia, 129
Hipponoë gaudichauda, 169
Homalaspis plana, 170
Hygrophila, 248
Hypsoblennius, 217
- Iridaea boryana*, 280, 284
conucopiae, 263, 280
Isthmia nervosa, 97
- Jehlius*, 165
cirratus, 165, 170, 171, 180, 226
Julia, 88
japonica, 95
Juliidae, 91, 94, 95, 107, 113
- Kerguelenella*, 248, 249, 291, 302, 303
lateralis, 257, 258, 259, 260, 261, 263, 265,
266, 267, 269, 272, 277, 287, 291, 301,
302, 303
stewartiana, 291, 302, 303
- Lacuna marmorata*, 119
Lagodon rhomboides, 217
Lamellidoris bilamellata, 154
Laminaria, 223
Laomedea, 165
Larus glaucescens, 225
occidentalis, 225
Lepadidae, 204
Lepas, 204
anatifera, 155, 223, 226
anserifera, 169
Lepsiella, 181–2
scobina, 181, 182
vinosa, 181
Leptasterias, 211, 212
hexactis, 155, 207, 208, 210, 211, 212
littoralis, 208
Leucozonia, 180
Limapontia capitata, 98, 115, 118
cocksii, 98
depressa, 98, 115, 118
Limapontiidae, 92, 93, 97, 98, 103, 107, 110,
115
Limapontioidea, 92, 94, 105
Limnophora aestuum, 172
Liriola, 248
Lithognathus mormyrus, 213
Lithotrya valentiana, 180
Littorina, 164, 178, 180
africana knysnaensis, 187
littorea, 164, 169
obtusata, 169
scutulata, 119
- Liza aurata*, 213, 214, 216
ramada, 213, 214, 216
saliens, 213, 214, 216
Lobiger, 89
serradifalci, 95
souverbiei, 95, 113
Lophogobius cyprinoides, 223
Lottia, 174, 284
digitalis, 172, 173, 174, 175
gigantea, 174
stipulata, 284
strigatella, 172
Lymnaeoini, 248
- Malacostraca*, 169–71
Maritrema arenaria, 224, 225
Marthasterias glacialis, 204, 208
Mediaster, 206
aequalis, 206, 207
Megabalanus algicola, 162
californianus, 216
decorus, 186
psittacus, 170, 218, 219, 226
rosa, 165
stultus, 166
tintinnabulum, 165, 186, 208, 211, 227
tintinnabulum rosa, 197
tintinnabulum var. *concinus*, 166
volcano, 165
Melampus bidentatus, 252
Melobesioidea, 165
Metridium, 167
senile, 167
Meyenaster gelatinosus, 206, 208
Microdictyon, 113
Millepora, 166
complanata, 166
Mnemiopsis leidyi, 167
Mollusca, 87, 172–205
Monocanthus hispidus, 217
Morula, 180, 182, 183, 184, 185, 186, 196
anaxeres, 180
ferruginosa, 182
granulata, 180
marginalba, 163, 164, 182–6, 196
marginatra, 180
Mourgona, 89
germaineae, 97
Muricanthus, 186
nigritus, 186, 228
Muricidae, 180
Myoxocephalus aenaeus, 213, 215
octodecemspinosus, 213, 215
scorpius, 213, 215
Mytilus californianus, 166, 211, 225
edulis, 154, 158, 165, 168, 171, 179, 193, 199
trossulus, 191, 192, 211

SYSTEMATIC INDEX

- Nacella concinna*, 257
Navicula, 49
Neopanope texana sayi, 170
Neothais, 186
 nesiotes, 186
 scalaris, 186
Nerita, 180
 scabricosta, 196
Nitzschia, 49
Notoacmea petterdi, 299, 300
Notobalanus flosculus, 165, 218, 219
Notoplana australis, 169
 inquieta, 168
Nucella, 154, 173, 180, 187, 188, 189, 190,
 191, 192, 193, 194, 195, 196, 210
 aculeata, 180
 bronni, 186
 canaliculata, 187–92
 clavigera, 186
 dubia, 186–7
 emarginata, 155, 178, 187–92, 227
 freycineti, 186
 fusconigra, 180
 haemastoma, 188, 196
 haemastoma floridana, 192
 heyseana, 192
 lamellosa, 155, 187–92
 lapillus, 158, 162, 169, 192, 193–5, 198
 lima, 187–92
 melones, 195
 orbita, 164, 190, 196
 pansa, 196
 rudolphi, 180
 savignyi, 180
Nudibranchia, 199–204

Ocenebra, 196–7
Octomeris angulosus, 186, 187
Octopus vulgaris, 204, 205
Oedoparena glauca, 171, 172
Olea hansineensis, 98
Onchidioidei, 248
Onchidoris, 201, 202
 bilamellata, 154, 199, 200, 201, 202, 203,
 204
 fusca, 154, 200
Oncorhynchus gorbusha, 213, 214
Opisthobranchia, 87, 88
Orthasterias, 211
 kochleri, 208, 211
Orthurethra, 248
Otinoidei, 248
Oxynoacea, 90, 94, 104
Oxynoe, 89, 107
 antillarum, 95, 113
 azuropunctata, 95, 113, 119, 120
 n. sp., 95
 panamensis, 95, 113
 viridis, 95, 106, 113
Oxynoidae, 91, 92, 94, 95, 107, 113

Padina, 97, 111
Pagurus bernhardus, 170
Panopeus herbsti, 170
Paralithodes camtschatica, 171
Patella, 205, 266
 cochlear, 172, 267
 flexuosa, 282, 284
 granatina, 267
 granularis, 187, 256, 257, 267
 longicosta, 267
 vulgata, 172, 205, 260, 267
Patelliformia, 247
Patelloida alticostata, 299, 300
 latistrigata, 163, 164, 175, 183
Patellopsis, 303
Penicillus, 97, 103, 105, 114
 capitatus, 96, 97
 dumetosis, 97
Peristernia, 180
Perumytilus purpuratus, 226
Petalonia, 280
 fascia, 164
Phaeophyta, 122
Philine denticulata, 97
Pisaster, 212, 228
 brevispinus, 208, 210, 211
 giganteus, 208, 210
 ochraceus, 166, 208, 209, 210, 211, 212, 227
Placida, 121
 capensis, 97
 dendritica, 97, 99, 106, 108, 115, 118, 119,
 120, 121
 kingstoni, 97, 115
 viridis, 97
Plakobranchea, 91, 94, 98
Plakobrancheidae, 91, 92, 95, 96, 97, 103, 105,
 107, 110, 113, 114
Plakobranchoidea, 91, 94
Plakobranchus ianthobapsus, 114
 ocellatus, 96, 114
Platyhelminthes, 167–9
Platylepas hexastylus, 218
Pollicipes, 191, 211, 225, 226
 elegans, 226
 pollicipes, 171
 polymerus, 154, 155, 158, 163, 166, 169,
 171, 173, 176, 179, 188, 191, 204, 207,
 208, 209, 210, 211, 225, 226
Polybranchia, 88
 viride, 97
Polybranchiidae, 97, 103, 107, 114
Polybranchioidea, 92
Polychaeta, 169

SYSTEMATIC INDEX

- Polyphysa peniculus*, 95, 96
Polysiphonia pacifica, 97
Pomatoschistus microps, 213, 216
 minutus, 213, 216
Porphyra, 280
Pterygota, 171–2
Pulmonata, 245, 247, 248
Purpura, 154
 lapillus, 193
Pycnopia helianthoides, 155, 209, 211
- Ralfsia*, 163, 280, 281
 verrucosa, 164
Retusa truncatula, 97
Rhizoclonium, 95, 97, 111
 riparium, 98
Rhodophyta, 122
Roburnella wilsoni, 92
- Sacoglossa, 88, 89, 100, 107, 110, 112, 116, 122
Sagartia ornata, 143
 troglydites, 143
 troglydites var. *decorata*, 143
Salinator, 247
Sargassum, 99, 113
Scartichthys viridis, 213
Schizoporella, 165
 unicornis, 165
Schizothrix, 280
 calicola, 280
Scolioplanes maritimus, 171
Scytosiphon, 280
Sebastes, 215
 mystinus, 213, 216
Semibalanus, 166, 190, 194, 214
 balanoides, 153, 154, 157, 158, 159, 160, 162, 163, 164, 165, 166, 169, 170, 171, 172, 186, 193, 194, 195, 197, 198, 199, 200, 201, 202, 203, 205, 207, 210, 214, 219, 224, 226
 cariosus, 155, 156, 160, 162, 163, 173, 174, 187, 188, 189, 190, 191, 207, 208, 209, 211, 212
 Semicossyphus maculatus, 217, 219
 Sicyases sanguineus, 217, 218, 219
Sigmurethra, 248
Siphonales, 110
Siphonaria, 245, 246, 247, 248, 249, 253, 255, 257, 259, 263, 264, 265, 267, 269, 271, 278, 280, 281, 282, 283, 284, 286, 287, 290, 291, 294, 295, 296, 297, 298, 301, 302, 303, 304
 alternata, 260, 261, 263, 274, 275, 276, 278, 286, 287, 292, 295, 303, 304
 anneae, 291, 296, 303
 aspera, 264, 282
 atra, 261, 267, 268, 269, 274, 275, 278, 286, 287, 291, 293, 294, 295, 303
 australis, 292
 baconi, 292, 295, 303
 bifurcata, 294
 capensis, 249, 251, 252, 253, 255, 256, 257, 258, 260, 262, 265, 266, 267, 268, 269, 271, 272, 273, 274, 275, 276, 278, 279, 286, 288, 289, 291, 293, 296, 301, 303
 compressa, 249, 291, 303
 concinna, 251, 252, 253, 255, 258, 262, 263, 266, 269, 271, 272, 274, 275, 276, 277, 283, 287, 291, 293, 296, 299, 301, 303
 cookiana, 286, 293, 294
 dayi, 291, 303
 denticulata, 262, 263, 269, 279, 281, 283, 286, 287, 292, 293, 295, 297, 298, 299, 301, 303, 304
 diemenensis, 263, 269, 270, 280, 285, 287, 292, 295, 298, 299, 300, 303, 304
 exigua, 286
 gigas, 259, 260, 261, 268, 269, 274, 280, 284, 285, 286, 287, 292, 293, 294, 295, 299, 301, 303
 guamensis, 259
 hispidata, 260, 261, 269, 286, 287, 288, 292, 303, 304
 japonica, 259, 260, 261, 267, 268, 269, 274, 275, 276, 278, 281, 287, 292, 293, 294, 295, 298, 301, 303, 304
 jeanae, 287, 304
 kurracheensis, 259, 260, 261, 279, 283, 291, 294, 303
 laciniosa, 259, 261, 274, 292, 295, 303
 laeviuscula, 286, 293
 lepida, 292
 lessoni, 249, 260, 261, 266, 269, 270, 274, 277, 280, 281, 284, 285, 286, 287, 292, 293, 295, 301, 303, 304
 maura, 259, 260, 261, 269
 nigerrima, 291, 303
 normalis, 259, 261, 269, 270, 274, 275, 276, 278, 293
 obliquata, 294
 oculus, 251, 253, 254, 258, 266, 291, 303
 palmata, 261
 pectinata, 249, 258, 260, 262, 264, 265, 274, 278, 279, 280, 284, 286, 287, 292, 294, 295, 297, 298, 299, 303, 304
 serrata, 249, 257, 258, 262, 263, 264, 266, 269, 272, 282, 287, 288, 291, 293, 299, 301, 302, 303
 sipho, 261, 278, 292, 293, 295, 303
 siphonaria, 258, 259
 sirius, 262, 267, 268, 269, 272, 274, 275, 279, 280, 281, 282, 283, 284, 285, 287, 292, 293, 295, 298, 303

SYSTEMATIC INDEX

- tasmanica*, 287, 292, 294, 295, 302, 303
tenuicostulata, 291, 303
thersites, 258, 259, 260, 262, 263, 266, 267,
 269, 272, 273, 274, 276, 280, 287, 291,
 295, 302, 303
tristensis, 294
virgulata, 262, 277, 281, 283, 286, 292, 294,
 299, 302, 303, 304
zelandica, 250, 251, 252, 264, 270, 292
 Siphonariidae, 245, 246, 247, 248, 257, 303,
 305
 Siphonarioidea, 247
 Siphonarioidei, 248
 Siphonocladales, 115
Solaster, 209
 dawsoni, 206, 207
 papposus, 206, 207, 209
 Soleolifera, 248
Sparus auratus, 213, 214, 216
 Spinulosida, 206, 207
Spongites yendoi, 280, 281
Spongomorpha, 99
 Stenoglossa, 175
Stichaster australis, 206, 209
 striatus, 206, 209
Stiliger, 88
 aureomarginatus n. sp., 93
 fuscovittatus, 97
 vesiculosus, 98
 Stiligeridae, 89, 92, 97, 98, 107, 115
 Stiligerioidea, 92
Striatobalanus amaryllus, 165
Styela gibbsii, 154
Stylochus, 167, 168
 ellipticus, 168, 169
 tripartitus, 168
 zanzibaricus, 167, 168
 Stylommatophora, 247, 248
Syringodium filiforme, 96
 Systellommatophora, 248

Tautoga onitis, 217, 219
Tautogolabrus adpersus, 217, 219
Tegulo pulligo, 155
 Tentaculata, 167
Tesseropora, 184, 185, 186
 rosea, 157, 163, 164, 169, 173, 174, 175,
 182, 183, 184, 185, 196
Tetrachthamalus obliteratus, 180
Tetraclita, 158, 166, 175, 177, 179, 182, 187,
 208, 210
 panamensis, 177
 rosea, 183
 rubescens, 176, 179, 188, 191, 210
 serrata, 162, 163, 186, 187
 squamosa, 176, 177, 186, 208
 squamosa rubescens, 158, 208, 211
 squamosa rufotincta, 180
 stalactifera, 175, 176, 177, 195
 stalactifera confinis, 166
 stalactifera panamensis, 196
Tetraclitella purpurascens, 164, 169, 173, 182,
 183, 185, 206
 Tetraclitidae, 156
 Thaididae, 176
Thais, 154
 armigera, 269, 270
 clavigera, 268
 lapillus, 193
Thalassia testudinum, 96
Thalassoma duperry, 217, 218
 Thalassophila, 247, 248
Thunnus alalunga, 217, 223
Tridachia, 106
 crispata, 97, 106, 114, 116, 117
Tridachiella diomedea, 97, 114
Triglops murrayi, 213, 215
 Trimusculidae, 247, 248, 269
 Trimusculiformes, 247, 248
Trimusculus, 247
Tripterygion melanurus, 221
 xanthosoma, 221
Trypetesa lampas, 197
 Turbellaria, 167

Udotea, 96, 103, 105, 111, 114
 flabellum, 97
Ulva, 104, 164, 280, 282
 lactuca, 96, 164
Urosalpinx, 180, 195, 197–9
 cinerea, 197, 198, 199
 cinerea cinerea, 197
 cinerea follyensis, 197, 198
Urospora, 97

Valenciennea strigata, 213, 216
 violifera, 213, 216
Valonia, 98, 103
 Valvatida, 206, 207
Vaucheria, 94, 95, 97, 98, 111, 113, 115, 118
Verruca, 203
 stroemia, 157, 203
Volvatella, 89
 pyrifomis, 95
 Volvatellidae, 90, 94, 95, 107, 113

Williamia, 248, 249
 vernalis, 286

Xentrobus pulex, 164

Zostera marina, 95

SUBJECT INDEX

References to complete articles are given in **bold type**; references to sections of articles in *italics*; references to pages are given in normal type.

- Accessory boring organism (ABO), 156, 181, 198, 199
- Actinia equina* species group, population structure, gene dispersal and reproduction, **129–52**
- A. equina* as a model species, *144–5*
- population genetics in the British Isles, *135–40*
- column and foot colour, *135–6*
- dispersal and gene flow, *140*
- origins of brooded offspring, *136–40*
- possible mechanisms of speciation, *142–3*
- problems in species definition, *140–2*
- systematics, 129, *130–5*
- Adriatic Sea, 65, 68
- Africa, 58, 65
- Air-sea gas exchange into the millennium: progress and uncertainties, **1–45**
- basic concepts, 2–6
- friction velocity and drag coefficient, 6
- Schmidt number, 5
- comparisons of field and laboratory data, *18–34*
- biogeochemical role of the sea surface layer, *32–4*
- breaking waves and bubbles, *22–5*
- chemical enhancements of gas exchange, *27–9*
- cool skin of the oceans, *29–30*
- fetch dependence of k_w , *21–2*
- humidity, *31–2*
- irreversible thermodynamics, *30*
- rain, 32
- surfactant films, *25–7*
- thermal stability, *30–1*
- wind speed and the non-linear dependence of gas exchange, *20–1*
- direct estimates of n , *8–10*
- mechanistic models of gas exchange, 6–8
- film models, 6–7
- rubber cloth model, 8
- surface renewal models, 7–8
- techniques to measure gas exchange in the field, *11–18*
- controlled flux, 12
- dissolved gas balance, *11–12*
- floating box, 12
- micrometeorological, *14–16*
- natural and bomb-produced $^{14}\text{CO}_2$, 13
- purposefully-released tracers, *16–18*
- radon deficit, *13–14*
- wind-tunnel and wave-tank data, *10–11*
- Alaska, asteroids preying on cirripedes, 211
- cirripedes, 171
- Nucella*, 187
- Aldabra atoll, cirripedes, 180
- Algae-sacoglossan associations, calcified coenocytic alga, 105
- Caulerpa*, 104
- Codium*, 105
- filamentous green algae, *104–5*
- Algal population dynamics and distribution, effects of sacoglossans on, *118–22*
- grazing parts of the algal thallus, *121–2*
- quantity of algae consumed, *118–21*
- quantity of algae grazed and kleptoplasty, *121*
- Algal tannins, effect on cirripedes, 164
- Algeria, siphonariid limpets, 287, 292
- Allorecognition, *Actinia*, 130
- Allozyme electrophoresis, 132, 283
- Antarctic, siphonariid limpets, 249
- Antifouling, by cirripedes, 154
- Arctic Ocean, 62
- Arctic shores, cirripedes, 160
- Argentina, siphonariid limpets, 261, 287, 292
- Asteroids, diet of barnacles, 206, 207, 208, 209, 210, 211, 212
- method of feeding on cirripedes, 210
- predators of cirripedes, 206, 207, 208, 209
- toxic secretions, 206
- tube feet and chemoreception, 205
- Atlantic, *Actinia*, 131
- Atlantic, siphonariid limpets, 249, 278
- Atlantic Ocean, 2, 11, 25, 26, 29, 62
- Atlantic surface water, 2
- Australia, 57, 65
- Actinia*, 132, 137, 139
- cirripedes, 163, 164, 173, 181, 182, 185, 186
- sacoglossans, 106, 112

SUBJECT INDEX

- siphonariid limpets, 270, 283, 287, 292, 297, 298
- Australian shores, effect of trampling by man, 225
predation, 228
- Baffin Island, cirripedes, 159, 160
- Baja California, 26
cirripedes, 178
- Baltic Sea, 62
fishes feeding on cyprids, 216
- Bamfield, Vancouver Island, cirripedes, 173
- Barbados, 57
- Barbados, cirripedes, 166
- Barnstable Harbor, USA, 49
- Basommatophoran pulmonate limpets, 245
- Bay of Marseilles, France, 26
- Beaufort Sea, 65
- Beaufort, NC, USA, 49
- Benthic microalgae, their role in neritic ecosystems, **47–86**
a new paradigm, 73–5
benthic microalgal biomass, 62–7
benthic microalgal production, 53–62
grazing interactions, 72–3
light limitation, 67–9
microalgae and the sediment/water interface, 69–72
effects on other biogeochemical processes, 72
nutrient fluxes, 70–2
sediment stabilisation, 69–70
previous reviews, 48–53
of microalgal taxonomic composition, 49–50
of neritic ecosystems, 50–3
- Bering Sea, 62
- Bermuda, siphonariid limpets, 261, 276
- Biogeochemical role of the sea surface layer, 32–4
- Biological Species Concept, 140, 141
- Birds preying on cirripedes, 223–5
- Black Sea, 60, 62
gobies, 216, 217
- Blue crabs, 192
- Boring of cirripede shells, 182
- Boundary layer model, 7
- Brazil, 59
Actinia, 131, 139
siphonariid limpets, 261, 287, 292
- Britain, *Actinia*, 129, 131, 132, 133, 134, 135, 136, 137, 138, 144, 145, 146
- British Isles, cirri in fish stomachs, 222, 223
- Bulldozing of barnacles, 166, 173, 174, 196
- California lakes, 18, 19
- Canada, 58, 68
asteroids preying on cirripedes, 210
- Canadian Arctic Archipelago, cirripedes, 160
- Canary Islands, *Actinia*, 134
- Cape Verde Island, *Actinia*, 131, 135
- Capillary ripple decay, 25
- Capillary waves, 11
- Caribbean, *Actinia*, 131
sacoglossans, 103
siphonariid limpets, 249
- Centipedes, in cirripedes, 171
- Chemical enhancements of gas exchange, 27–9
- Chemoreception, 175, 197, 198, 205
- Chile, cirripedes, 165, 170, 180
siphonariid limpets, 280, 284
- Chilean shores, asteroids preying on barnacles, 206
effect of trampling by man, 226
- China Sea, 60
- Chlorophyllides, 62
- Chlorophytes, 47, 49
- Chukchi Sea, 65
- Cirripedes, mortality of, **153–244**
biological interactions other than predation, 163–7
bulldozing and grazing, 166–7
prevention of settlement and/or removal by algae, 163–4
smothering and overgrowing, 164–6
- diseases, 154
- effects of waves, 160–2
- ice scour, 159–60
- physical factors, 158–9
- predation, 167–227
Anthozoa, 167
Archaeogastropoda, 172–5
Asteroidea, 205–12
birds, 223–5
Cephalopoda, 204–5
Chilopoda, 171
Echinoidea, 212
fishes, 212–13
Malacostraca, 169–71
man, 225–7
Nudibranchia, 199–204
Polychaeta, 169
Pterygota, 171–2
Stenoglossa, 175–99
Tentaculata, 167
Turbellaria, 167–9
- protective characteristics, 155–8
avoidance of predation, 155–6
strength of shells, 156–8
- Citric acid cycle, 101
- ¹⁴CO₂, natural and bomb-produced, 13
- Controlled flux, 12
- Cool skin of the oceans, 29–30
- Costa Rica, siphonariid limpets, 269, 284
cirripedes, 175, 177, 195

SUBJECT INDEX

- Curacao, 59
Cyanobacteria, 47, 49, 69, 72
- Denmark, 56, 57
 sacoglossans, 118
- Diatoms, centric, 47
 pennate, 47, 49, 69
- Dissolved gas balance, 11–12
- Downwelling, 2
- Dredging on Indian coasts, effect on cirripedes, 227
- Drilling of shells, 156, 176, 177, 178, 195, 197
- Dugongs, 218
- Dungeness crab, 170
- East African Seas, 62
- Eddy Correlation (EC) method, 15
- Electrophoretic comparison of enzymes,
 Actinia, 131, 135, 137
- England, 18, 57
 cirripedes, 172
- Eniwetok Atoll, siphonariid limpets, 269
- Estonia, 66
- Euglenoids, 49
- Europe, 51
 Actinia, 129, 133, 134
 cirripedes, 153, 163, 170, 172
 Nucella, 193
- European shores, asteroids, 206, 209
- Extracellular polymeric substances (EPS), 69, 70, 74
- Falklands, siphonariid limpets, 302
- Fetch dependence of k_w , 21–2
- Fick's law of diffusion, 3
- Fiji, sacoglossans, 119
- Fishes, feeding on cirripedes, 212, 213, 214, 215, 216, 217, 220, 221,
- Floating box method, 12
- Florida, USA, *Actinia*, 131
 sacoglossans, 100
 siphonariid limpets, 261, 262, 287
- Flux capping, 33
- Foraging, birds, factors affecting, 223
 crabs and environmental factors, 169
 siphonariid limpets, 261, 262
 techniques of predators, 156
- France, 49, 55, 57, 58, 64, 65, 66, 68
 Actinia, 133, 134
 fishes, preying on cirripedes, 212–23
- Fucoid whiplash, 162
- Gas exchange coefficient, 4
- George's Bank ecosystem, 73
- Georgia Strait, 11
- GEOSECS, 19, 21
- Glycolysis in sacoglossans, 101
- Great Barrier Reef, 57, 65
- Greenland, frozen shore, 159, 160
- Greenland Sea, 2
- Gulf of Aqaba, siphonariid limpets, 261, 292
- Gulf of California, cirripedes, 156, 163, 166, 176, 177, 182, 183, 186, 62
 Nucella, 187
- Gulf of Maine, USA, 26
- Gulf of St Lawrence, cirripedes, 160, 165
- Gulf Stream Current, 29
- Halifax, Nova Scotia, cirripedes, 160
- Halos, created by predation, 183, 227
- Hawaii, cleaning of turtles by wrasse, 218
 siphonariid limpets, 261
- Heidelberg circular wind tunnel, 9
- Helgoland, cirripedes, 165
- Henry Law Constant, 4
- Hong Kong, siphonariid limpets, 263
- Hudson Bay, 50
- Humidity, 31–2
- Hypobranchial gland extract of *Acanthina*, 178
- Ice foot, 159
- Ice scour, and cirripede mortality, 159–60
- India, cirripedes, 157, 159
- Indian Ocean, siphonariid limpets, 62, 249
- Indo-Pacific, coral reefs, 180
 siphonariid limpets, 245, 248, 249
- Infrared camera, 12
 radiometer, 12
 radiometry, 30
- Ingestive conditioning, 199
 in flatworms, 168
 of predators, 191
- Irreversible thermodynamics, 30
- Isotopes, as signature of diet, 102
- Italy, 57
- Japan, cirripedes, 165, 167, 170, 186, 192
 Ocenebra, 196
 siphonariid limpets, 292
- Kleptoplasty in sacoglossans, 87, 99, 102, 121, 122
 history of research, 105–7
 how kleptoplasty occurs, 107–10
 methods of identifying, 116–17
 seasonal trends, 112–16
 taxonomic trends, 110–12
- Kuroshio current, 29
- Lagrangian studies, 18
- Langebaan Lagoon, siphonariid limpets, 249
- Limpets, behavioural adaptations—homing and foraging activity, 272–8

SUBJECT INDEX

- biology of siphonariid, **245–314**
 embryonic and larval development, 300–4
 fecundity and energetics of reproduction, 299–300
 interactions with other intertidal organisms, 278–85
 physiological and morphological adaptations to intertidal habitats, 249–72
 reproduction and life histories, 285–99
 Long Island Sound, USA, 49, 55, 65, 66
- Madagascar, 58, 66, 68
 Manatees, 218
 Mangroves, 181
 Marine Boundary Layer Project, 12
 Marshall Islands, 58
 McMurdo Sound, Antarctica, 65, 68
 Mediterranean, sacoglossans, 112, 118, 119, 120
Actinia, 131, 132, 133, 134, 135
 drill holes of octopus, 205
 siphonariid limpets, 249
 Mediterranean Sea, 26, 60, 62
 Mesoherbivore-macroalgal interactions:
 feeding ecology of sacoglossan sea slugs, **87–128**
 algae-sacoglossan associations, 102–5
 calcified coenocytic alga, 105
Caulerpa, 104
Codium, 105
 filamentous green algae, 104–5
 diet of sacoglossans, 94–102
 background to stable isotopes, 100–2
 food choice experiments, 98–100
 nitrogen uptake by sacoglossans, 102
 stable isotope ratios as ‘natural tracers’ of diet, 100
 using stable isotopes to determine sacoglossan diets, 102
 effects of sacoglossans on algal population dynamics and distribution, 118–22
 grazing parts of the algal thallus, 121–2
 quantity of algae consumed, 118–21
 quantity of algae grazed and kleptoplasty, 121
 identity of sacoglossans, 88–94
 kleptoplasty, 105–17
 history of research, 105–7
 how kleptoplasty occurs, 107–10
 methods of identifying, 116–17
 seasonal trends, 112–16
 taxonomic trends, 110–12
- Mexico, 56
 Microbial tracer technology, 17
 Microphytobenthos, 47, 48
 Molecular diffusion coefficient, 4
 Mortality, of cirripedes, **153–244**
 of *Patella*, 256, 257
 of *Siphonaria*, 256, 257
- Netherlands, 49, 56, 57
 New Caledonia, 64
 New England, asteroids preying on cirripedes, 206, 210
 cirripedes, 162
 New York Harbour, cirripede parasites, 154
 New Zealand, 49, 59
Actinia, 132
 asteroids preying on barnacles, 206
 cirripedes, 164, 165, 181, 186
 cirripedes in fish stomachs, 223
Ocenebra, 196
 shores, effects of trampling by man, 225
 siphonariid limpets, 249, 262, 272, 287, 292
- North Africa, *Actinia*, 133
 North America, 51
 asteroids preying on cirripedes, 210
 siphonariid limpets, 272
 North Sea, 9, 21, 65
 Norwegian Sea, 2
 Nova Scotia, 57
 foraging of sandpipers, 223
 Nuclear bomb testing, 13
 Nudibranchs, 199, 200, 201, 202, 203
- Octopus, drilling of shells, 204
 Oil spill, effect on cirripedes, 154
 Oligotrophic ocean waters, 69
 Olympic Peninsula, USA, cirripedes, 163, 166, 173
 Opisthobranch, meaning of, 88
 Optimal foraging theory, 227
 Oregon, crab fishery, 171
 sacoglossans, 118, 119
 Orkney Islands, 62
 Oviparity, *Actinia*, 134
 Oxygen consumption, aerial:aquatic in pulmonates, 252
 Oystercatchers, 224
- Pacific coast, Mexico, 26
 siphonariid limpets, 249, 260
 USA, 26
 USA, cirripedes, 163
 Pacific Islands, 59
 Pacific Ocean, 29, 29, 62
 Palau, siphonariid limpets, 291
 Palau, siphonariid limpets, 261, 287
 Panama, *Nucella*, 196
 siphonariid limpets,
 Panamanian land bridge, 249
 Panamanian rocky shores, siphonariid limpets, 259, 260
 Paralyzing toxin, 187
Acanthina, 177, 178, 179
Octopus, 205
 used on cirripedes, 179

SUBJECT INDEX

- Persian Gulf, 60
 siphonariid limpets, 291, 292
- Peru, cirripedes, 180
- Phagocytosis, 108
- Polynesia, 59, 65, 66
- Population genetics of *Actinia* in the British Isles, 135–40
 column and foot colour, 135–6
 dispersal and gene flow, 140
 origins of brooded offspring, 136–40
- Port Erin, Isle of Man, centipedes on cirripedes, 171
- Portugal, *Actinia*, 134
 siphonariid limpets, 278
- Prandtl number, 5
- Predation on cirripedes, 167–227
- Predator switching, 179, 182, 194, 228
- Profile method of measuring air-sea gas exchange, 14
- Propionate metabolites, 269
- Purple sandpiper, 223
- Q_{10} for siphonariids, 255
- Quebec, ice cover, 195
- Radon deficit, 13–14
- Radula, function, 198
 in *Siphonaria*, 279
- Rain, 32
 effect on cirripedes, 158
- Red Sea circulation, 13
- Reef production, 51
- Relaxed Eddy Accumulation (REA), 15
- Rhodamine-B, 16
- Rhodamines WT and Sulpho-G, 17, 18
- Ruddy turnstone, 223
- Russia, *Actinia*, 133
- Sacoglossans, food choice experiments, 98–100
 nitrogen uptake by sacoglossans, 102
 stable isotope ratios as ‘natural tracers’ of diet, 100
 taxonomy, 90, 91, 92, 93, 110
 using stable isotopes to determine sacoglossan diets, 102
 feeding ecology, **87–128**
- San Francisco Bay, 49
- Schmidt number exponent, 5, 9
- Scotland, 57, 66
 cirripedes, 166, 172
- Scott reefs, Indian Ocean, 58
- Sea butterflies, 88
- Sea hares, 88
- Sea turtles, 218
- Siphonariid limpets, biology of, **245–314**
 behavioural adaptations—homing and foraging activity, 272–8
 activity patterns, 272–7
 homing, 277–8
 embryonic and larval development, 300–4
 fecundity and energetics of reproduction, 299–300
 geographic distribution, 248–9
 interactions with other intertidal organisms, 278–85
 intra- and interspecific interactions, 282–5
 limpet-algal interactions, 278–82
 physiological and morphological adaptations to intertidal habitats, 249–72
 anthropogenic effects, 270
 parasitism, 271–2
 predation and predator avoidance, 268–70
 respiration, 250–7
 salinity tolerances and osmoregulation, 264–6
 temperature and desiccation tolerances, 257–64
 wave action, tenacity and pedal mucus, 266–8
 reproduction and life histories, 285–99
 copulatory behaviour, 293–4
 gametogenesis, 286–8
 oogenesis, 290–2
 spawning, 294–9
 spermatozoon morphology and spermatogenesis, 288–90
 systematics and evolutionary relationships, 247–8
- Snow crab, 171
- South Africa, 56
Actinia, 132, 133
 cirripedes, 162, 172, 186
 siphonariid limpets, 249, 259, 262, 266, 271, 272, 282, 283, 287, 290, 291, 303, 304
- South America, siphonariid limpets, 302
- South China Sea, 50
- South Orkney Islands, 56
- Spain, 59, 65
Actinia, 134
 shell middens, 205
- Sperm, of *Siphonaria*, 288, 289
- Spermatophores, of *Siphonaria*, 294
- St Croix, Virgin Islands, 55, 64, 68
- Stable isotopes, background to, 100–2
- Stagnant boundary layer, 33
- Stone crab, 170
- Strait of Magellan, siphonariid limpets, 249
- Strawberry anemone, 132, 133, 144
- Sub-Antarctica, 291
 siphonariid limpets, 257, 260, 261, 272, 287, 288, 302
- Surfactant films, 25–7
- Surfperch, 220

SUBJECT INDEX

- Sweden, 26, 59, 66
 Synthetic Aperture Radar (SAR), 27
- Tautog, 219
 Telemetry, for waves, 160
 Tenacity of limpets, 267
 Tethys Sea, siphonariid limpets, 248
 Thermal stability, 30–1
 Tierra del Fuego, siphonariid limpets, 302
 Total gas transfer velocity, 4
 Toxic secretions, *Nucella*, 188
 starfish, 206
 Tracers, purposefully-released, 16–18
 Trampling, effects of, 225, 226
 Tuna, Atlantic, 223
 Tychopelagic forms, 49, 70, 74
- University of Sydney, 227
 Uruguay, siphonariid limpets, 249
 USA, sacoglossans, 112
 USA, east coast, 55, 56, 57, 58, 59, 65, 68, 73
 foraging by turnstones, 224
 predators, 228
 siphonariid limpets, 262, 287, 291, 292,
 USA, west coast, 57, 58, 59, 65
 associations, 227, 228
 asteroids preying on cirripedes, 210, 211
 cirripedes, 171, 172, 2173, 175, 178, 189,
 190, 191,
 effects of trampling by man, 225, 226
 effects of wave-borne debris on cirripedes,
 162
 gulls feeding on barnacles, 225
 predators, 228
- Vancouver Island, cirripedes, 191
 Vietnam, 59
 Viviparity, in *Actinia*, 132, 134
- Wadden Sea, Netherlands, 55
 Waves, breaking, and bubbles, 11, 12, 22–5, 27
 effects on cirripede mortality, 160–2
 West Africa, siphonariid limpets, 249
 Western Australia, 102
 siphonariid limpets, 261, 262
 White sturgeon, 220
 Whitecap simulation tank, 24
 Whitecapping, 25
 Wind and wave exchange tanks, 8, 9, 10, 11,
 14, 21
 Wind lag, 14
 Wind speed and the non-linear dependence of
 gas exchange, 20–1