Quantitative description of mainland New Zealand's shallow subtidal reef communities

SCIENCE FOR CONSERVATION 280

Department of Conservation
Te Papa Atawhai

Quantitative description of mainland New Zealand's shallow subtidal reef communities

Nick T. Shears and Russell C. Babcock

SCIENCE FOR CONSERVATION 280

Published by
Science & Technical Publishing
Department of Conservation
PO Box 10420, The Terrace
Wellington 6143, New Zealand

Cover: New Zealand's common sea urchin *Evechinus chloroticus* feeding on blades of the dominant kelp *Ecklonia radiata* at Leigh, northeastern New Zealand.
Photo: N.T. Shears.

Science for Conservation is a scientific monograph series presenting research funded by New Zealand Department of Conservation (DOC). Manuscripts are internally and externally peer-reviewed; resulting publications are considered part of the formal international scientific literature.
Individual copies are printed, and are also available from the departmental website in pdf form. Titles are listed in our catalogue on the website, refer www.doc.govt.nz under *Publications*, then *Science & technical*.

ISSN 1173-2946 (hardcopy)
ISSN 1177-9241 (web PDF)
ISBN 978-0-478-14352-2 (hardcopy)
ISBN 978-0-478-14353-9 (web PDF)

This report was prepared for publication by Science & Technical Publishing; editing and layout by Sue Hallas. Publication was approved by the Chief Scientist (Research, Development & Improvement Division), Department of Conservation, Wellington, New Zealand.

In the interest of forest conservation, we support paperless electronic publishing. When printing, recycled paper is used wherever possible.

CONTENTS

Appendix 1

Appendix 2

Appendix 3

Appendix 4

Appendix 5

Appendix 6

Quantitative description of mainland New Zealand's shallow subtidal reef communities

Nick T. Shears[1,2] and Russell C. Babcock[1,3]

[1] Leigh Marine Laboratory, University of Auckland, PO Box 349, Warkworth, New Zealand

[2] Current address: Marine Science Institute, University of California Santa Barbara, Santa Barbara, California 93106, USA. Email: shears@msi.ucsb.edu

[3] Current address: CSIRO Marine Research Floreat, Private Bag No. 5, Wembley, 6913 WA, Australia

ABSTRACT

Conservation and management of the marine environment requires a general understanding of how biological communities differ from place to place and the major factors that control them. Current knowledge of the ecology of New Zealand's subtidal reefs is limited, being based on studies from a small number of locations. In this study, surveys of shallow subtidal reef communities were carried out at 43 locations (247 sites) throughout mainland New Zealand. National and regional patterns in community structure are described, and their relationships with environmental variables are investigated. The shallow reefs (< 12 m depth) surveyed were generally typical of temperate systems, being dominated by large leathery seaweeds. However, other algal groups, sponges, mussels, ascidians and bryozoans were also abundant at some places where large seaweeds were rare, e.g. locations subjected to extreme wave action and poor water clarity (Raglan, Karamea, Cape Foulwind, Jackson Head), or where sea urchins (*Evechinus chloroticus*) were abundant (Gannet Rock, Abel Tasman, Nelson, Paterson Inlet). Strong associations were found between the biological patterns and environmental conditions such as water clarity and wave exposure, but these associations differed among regions. This unprecedented New Zealand-wide survey of subtidal reefs provides a framework for marine conservation planning and further ecological study, and a valuable baseline for assessing change associated with environmental variation, human-related impacts and management actions (e.g. marine reserves).

Keywords: bioregions, community structure, kelp forests, macroalgae, macroinvertebrates, marine reserves, sea urchins, temperate reefs

This paper may be cited as:
Shears, N.T.; Babcock, R.C. 2007: Quantitative description of mainland New Zealand's shallow subtidal reef communities. *Science for Conservation 280*. Department of Conservation, Wellington. 126 p.

1. Introduction

The systematic collection of biological data and description of patterns across large spatial scales is necessary for understanding important structuring processes and trophic relationships in communities (Underwood et al. 2000). Furthermore, large-scale studies aid in interpreting variability seen across smaller spatial scales (e.g. Broitman et al. 2001). From a conservation management perspective, the collection of quantitative data on species composition and community structure over a variety of spatial scales is valuable not only for developing a large-scale biogeographic framework for systematic planning (Lourie & Vincent 2004), but also for understanding local- and regional-scale variation in biodiversity. This is essential to ensure that conservation efforts achieve their goals of establishing networks of marine protected areas that are representative and comprehensive (Day et al. 2002). Systematically collected biological data also provide a valuable baseline for assessing changes associated with management actions (e.g. establishment of marine reserves), anthropogenic disturbance, introduced species and environmental change.

Shallow subtidal reef communities represent one of the most productive habitats in temperate marine ecosystems (Schiel & Foster 1986) and are of enormous commercial, recreational and cultural value to society. These habitats are typically dominated by large brown algae of the orders Laminariales and Fucales (Schiel & Foster 1986), although in many systems throughout the world grazing by sea urchins may remove large areas of kelp forest and form an 'urchin barrens' habitat (Lawrence 1975; Harrold & Pearse 1987). In addition to grazing by sea urchins and to a lesser extent fishes (Jones & Andrew 1990), the organisation of an algal community is strongly influenced by the life history characteristics of its key species (Reed 1990), as well as a variety of physical factors such as storms (Cowen et al. 1982), temperature (Leliaert et al. 2000), climatic variations (Dayton 1985), eutrophication (Eriksson et al. 2002), salinity (Schils et al. 2001), turbidity (Lumb 1989) and sedimentation (Airoldi & Virgillio 1998). Algal assemblage structure and species composition vary across environmental gradients (e.g. Harrold et al. 1988; Gorostiaga et al. 1998; Leliaert et al. 2000), and the physical factors responsible for those gradients are often strongly interrelated and covary, making it difficult to separate the effects of differing factors (Irving & Connell 2002; Schiel et al. 2006). In order to understand fundamental ecological processes, there is a need for biotic patterns to be described (Fowler-Walker & Connell 2002), and for environmental gradients to be quantified.

For mainland New Zealand, much of our understanding of subtidal reef community structure is based on descriptive studies carried out along the northeastern coast (Choat & Schiel 1982; Grace 1983; Cole 1993; Walker 1999; Shears & Babcock 2004b) and a few locations further south, e.g. Abel Tasman (Davidson & Chadderton 1994), Wellington, Kaikoura, Banks Peninsula and Fiordland (Schiel 1990; Schiel & Hickford 2001). From these studies, subtidal reef communities in New Zealand appear to be typical of most temperate areas in that they are dominated by large brown algae (Schiel 1990), and sea urchins are a conspicuous component of many reefs. The common sea urchin *Evechinus chloroticus* has been shown to have an important top-down influence on algal assemblages (Andrew

& Choat 1982; Shears & Babcock 2002) and it forms urchin barrens habitat in northern New Zealand. However, in central and southern parts of the country, urchin-dominated areas are thought to be rare (Schiel 1990; Schiel & Hickford 2001), with the exception of Abel Tasman (Davidson & Chadderton 1994) and Fiordland (Villouta et al. 2001). Descriptive studies of the northeastern part of New Zealand have shown that algal community structure and the abundance of sea urchins changes in a predictable manner over a wave-exposure gradient (Grace 1983; Cole 1993; Walker 1999; Shears & Babcock 2004b) with sea urchins being rare on sheltered reefs but becoming more prevalent, and overgrazing to greater depths, with increasing exposure. However, at the most exposed of these northeastern sites, sea urchins are rare and mixed stands of large brown algae predominate (Choat & Schiel 1982; Shears & Babcock 2004b). These findings suggest that the association between macroalgae and sea urchins varies across environmental gradients, but the applicability of findings from these studies to other regions of New Zealand is not known. In general much of the New Zealand coastline remains undescribed and our understanding of the important factors structuring algal assemblages both within and across regions in New Zealand is poor (Schiel 1990; Hurd et al. 2004).

A nationwide study of mainland New Zealand's subtidal benthic reef communities was carried out between 1999 and 2005. One component of this study has resulted in the division of the mainland New Zealand coast, based on macroalgae species composition, into two biogeographic provinces ('Northern' and 'Southern') and 11 biogeographic regions (hereafter 'bioregions') (Fig. 1; Shears et al. in press). This provides a hierarchical spatial framework for conservation planning but also for investigating ecological processes responsible for maintaining the observed patterns and their association with environmental variables. This report aims to provide a resource for ecologists and conservation workers by providing a national overview of New Zealand's subtidal reef communities, as well as descriptions of reef assemblages within bioregions and how these vary across environmental gradients.

2. Methods

2.1 STUDY LOCATIONS

Shallow subtidal reef communities were quantified at 247 sites within 43 locations throughout New Zealand (Fig. 1; see Appendices 1 and 2 for site positions). Locations were selected to provide a representative coverage of mainland New Zealand's subtidal reefs, but were somewhat determined by ease of access, availability of sufficient subtidal reef systems and sea conditions. Where conditions allowed, sites were stratified within locations across wave-exposure gradients (e.g. Fiordland and Stewart Island locations). An attempt was made to space sites every 0.5–1 km within locations; however, at exposed locations the position and number of sites were restricted by sea conditions during the sampling period. In most cases, sites with moderately sloping reefs were selected so that reefs could be sampled to a depth of 12 m. However, at some coastal locations the depth of available reef was insufficient to sample all

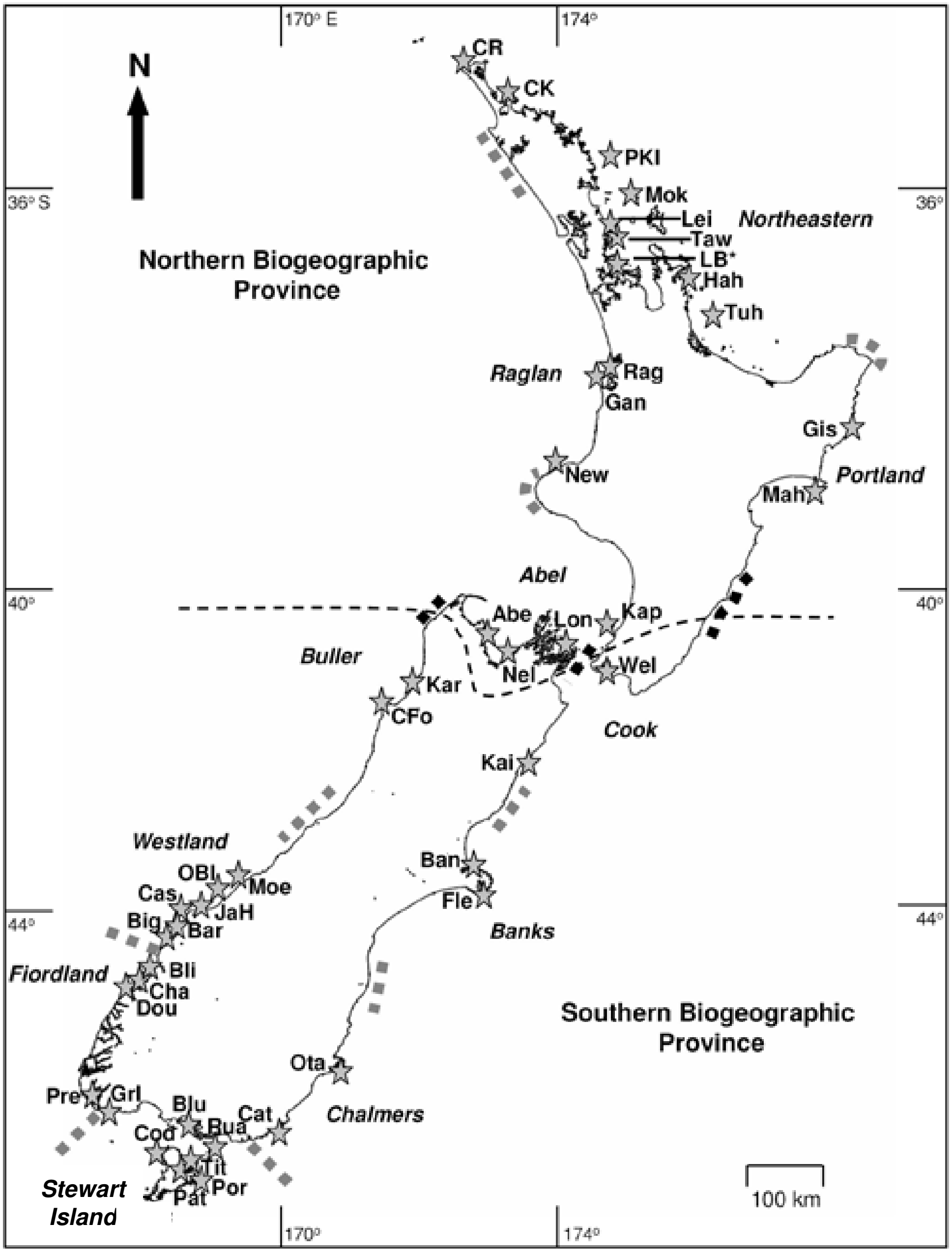


Figure 1. Sampling locations around New Zealand and the two biogeographic provinces and 11 bioregions (*italicised*) for mainland New Zealand based on macroalgal species composition (Shears et al. in press). Dashed line indicates the proposed biogeographic division between the Northern and Southern Provinces, and dashed grey bars indicate proposed transition zones between bioregions. See Appendices 1 and 2 for site positions within each location. Locations: Cape Reinga (CR), Cape Karikari (CK), Poor Knights Islands (PKI), Mokohinau Islands (Mok), Leigh (Lei), Tawharanui (Taw), Long Bay (LB) (not included in the biogeographic analyses of Shears et al. in press), Hahei (Hah), Tuhua (Tuh), Gisborne (Gis), Mahia (Mah), Raglan (Rag), Gannet Rock (Gan), New Plymouth (New), Kapiti Island (Kap), Wellington (Wel), Long Island (Lon), Nelson (Nel), Abel Tasman (Abe), Karamea (Kar), Cape Foulwind (CFo), Kaikoura (Kai), Banks Peninsula North (Ban), Flea Bay (Fle), Moeraki (Moe), Open Bay Islands (OBI), Jackson Head (JaH), Cascades (Cas), Barn (Bar), Big Bay (Big), Bligh Sound (Bli), Charles Sound (Cha), Doubtful Sound (Dou), Preservation Inlet (Pre), Green Islets (GrI), Bluff (Blu), Codfish-Ruggedy (Cod), Ruapuke Island (Rua), Titi Islands (Tit), Paterson Inlet (Pat), Port Adventure (Por), Otago Peninsula (Ota) and Catlins (Cat).

depth ranges (e.g. Raglan). For this reason, sites from Long Bay (located in the inner Hauraki Gulf) were not included in the biogeographic analyses of Shears et al. (in press) as only one or two depth strata could be sampled due to the limited extent of subtidal reef. The majority of the sampling was carried out over the summer of 1999/2000 and 2000/2001, although additional sampling was carried out at Gisborne and Mahia in January 2002, Moeraki, Big Bay and Barn in December 2003, and Preservation Inlet, Green Islets, Bluff, Ruapuke Island, Codfish-Ruggedy and Port Adventure in February 2005. To assess any effects of temporal variation on comparisons between sites sampled in 2000 and 2005 in the Stewart Island region two sites in Paterson Inlet (Ulva East and Tamihou Island; originally sampled 1 February 2000) were re-sampled on 19 March 2005. No differences were found in macroalgal community structure or macroinvertebrate assemblages between these two sampling dates suggesting the communities remained stable over this period.

2.2 SAMPLING PROCEDURE

At each site a lead-weighted transect line was run perpendicular to the reef from the mean low water mark out to a maximum depth of 12 m or the reef edge (whichever came first sand). Mean low water was approximated by the lower limit of intertidal species and upper limit of the subtidal macroalgal assemblage. Five 1-m^2 quadrats, placed as randomly as possible in each of four depth ranges (< 2 m, 4–6 m, 7–9 m and 10–12 m), were sampled to provide information on the abundance and size structure of macroalgae and macroinvertebrates. Depths were corrected to the mean low water mark to ensure accurate positioning of quadrats within the desired depth range. When the maximum depth of the reef was less than 10 m, the deepest strata were omitted. Within each quadrat all large brown macroalgae and conspicuous mobile macroinvertebrates (> 1 cm maximum length) were counted and measured, using a 1-m-long measuring tape marked at 5-cm intervals for macroalgae and a 200-mm ruler marked at 5-mm intervals for macroinvertebrates. Individual thalli were counted for macroalgae, as it is often difficult to determine individual plants for many species. The total lengths of macroalgae were measured, with an additional measure of stipe length made for *Ecklonia radiata* and *Durvillaea* spp. The stipe diameter for *Durvillaea* spp. was also recorded. For *Lessonia variegata* the stipe length and total length of the whole plant was measured and the number of thalli counted. For *Carpophyllum* spp. it was not always possible to measure all thalli, so those greater than 25 cm total length were grouped into 25-cm length categories (25–50 cm, 50–75 cm, etc.) and counted. The primary (substratum) percentage cover of foliose algae (c. 5–25 cm height), turfing algae (< 5 cm height), encrusting algal species, encrusting invertebrates, bare rock and sediment were visually assessed for each quadrat and recorded. Quadrats were divided into quarters to assist in estimating percentage cover of dominant forms, whereas the cover of minor forms was estimated on the basis that a 10 × 10-cm area equates to 1% cover. This technique was considered to be the most suitable as it is efficient and ensures that percentage covers are recorded for all forms, unlike point-intercept methods (Benedetti-Cecchi et al. 1996). Furthermore, the same two experienced divers carried out 73% of the quadrat sampling, reducing the potential influence of inter-observer variability. Macroalgal species were identified using Adams

(1994) and with the assistance of Dr Wendy Nelson (Museum of New Zealand Te Papa Tongarewa). The test diameter (TD) of all sea urchins greater than 5 mm was measured, and their behaviour recorded (cryptic or exposed). The largest shell dimension (width or length) was measured for gastropods, the actual measurement depending on species shell morphology (i.e. shell height for *Cantharidus purpureus*; shell width for *Turbo smaragdus*, *Trochus viridis* and *Cookia sulcata*). All macroalgae thalli were carefully searched for gastropods. The total length of *Haliotis* spp., limpets (*Cellana stellifera*) and chitons was also measured.

2.3 BIOLOGICAL DATASETS

2.3.1 Macroalgal community structure

Patterns in macroalgal community structure were investigated among sites and locations using a structural group-type approach to reduce the influence of species composition and emphasise structural patterns among algal communities. Genera of large habitat-forming brown algae (orders Laminariales, Durvillaeales and Fucales) formed their own groups, whereas less conspicuous brown, red and green algal species were grouped (Table 1). In total, all macroalgae species were divided into 23 species groups. Algal measurements were converted to biomass in order to allow comparisons between all algal groups irrespective of sampling units (e.g. percentage cover as compared to counts), and also to adjust counts for different sizes of algae. The dry weight of large algal species was calculated using length–weight relationships whereas percentage cover–weight relationships were used for turfing and encrusting algal species groups. Biomass equations were calculated for all of the dominant species and where possible at several locations (Appendix 3). To establish length–weight relationships, plants covering a range of sizes were collected, length was measured to the nearest centimetre, and they were dried at 80°C for a minimum of 3 days and weighed to the nearest 0.1 g. The weights of the stipe and lamina were calculated for *Ecklonia radiata* using two separate equations (Shears & Babcock 2003). To convert percentage cover estimates of foliose, turfing and encrusting algae to dry weight, several 10 × 10-cm samples were collected (equivalent to 1% of a 1-m^2 quadrat), dried and weighed. It was not possible to calculate biomass equations for all species, so for some of the rarer species, which were typically only small contributors to total biomass, an equation from a species with similar morphology was used. Dry-weight estimates were converted to ash-free dry weight (AFWD) for all macroalgae, excluding corallines, by multiplying the dry weight by 0.91. This constant was based on the assumption that the proportion of $CaCO_3$ and other inorganic material is relatively constant among a variety of New Zealand seaweeds (9% of the dry weight; R.B. Taylor, unpubl. data). For coralline algae, however, $CaCO_3$ made up c. 45% of the dry weight (N.T. Shears, unpubl. data).

2.3.2 Mobile macroinvertebrate assemblages

This dataset included count data, averaged for each site across all quadrats, for 47 of the mobile macroinvertebrate species recorded.

TABLE 1. MACROALGAL SPECIES GROUPS USED IN ANALYSES OF MACROALGAL COMMUNITY STRUCTURE. CODE INDICATES THE ABBREVIATION USED FOR EACH SPECIES GROUP IN FIG. 2.

GROUP/SPECIES	CODE	NO. OF TAXA	DESCRIPTION/SPECIES
Phaeophyta			
Ecklonia radiata	Eckl	1	
*Carpophyllum flexuosum**	Flex	1	
Other *Carpophyllum*	Carp	3	*Carpophyllum angustifolium*, *C. maschalocarpum*, *C. plumosum*
Lessonia variegata	Less	1	
Landsburgia quercifolia	Land	1	
Sargassum spp.	Sarg	2	*Sargassum sinclairii*, *S. verruculosum*
Xiphophora spp.	Xiph	2	*Xiphophora chondrophylla*, *X. gladiata*
Macrocystis pyrifera	Macr	1	
Marginariella spp.	Marg	2	*Marginariella urvilliana*, *M. boryana*
Durvillaea willana	Durv	1	
Cystophora spp.	Cysto	4	e.g. *Cystophora retroflexa*, *C. platylobium*
Small browns	SmBr	9	Small terete brown algal species; e.g. *Carpomitra costata*, *Halopteris* spp., *Zonaria* spp.
Ephemeral browns	EpBr	8	Small foliose brown algal species; e.g. *Dictyota* spp., *Desmarestia ligulata*, *Glossophora kunthii*, *Spatoglossum chapmanii*
Brown encrusting	BrEn	2	Encrusting fleshy brown algae, e.g.*Ralfisa* sp.
Rhodophyta			
Red foliose	ReFo	89	5–30 cm in height; e.g. *Osmundaria colensoi*, *Euptilota formosissima*
Red encrusting	ReEn	2	Encrusting fleshy red algae, e.g. *Hildenbrandia* spp.
Red turf	ReTu	8	Fleshy red algae less than 5 cm in height
Coralline turf	CoTu	1	Geniculate coralline algae
Crustose corallines	CCA	1	Non-geniculate coralline algae
Chlorophyta			
Caulerpa spp.	Caul	5	e.g. *Caulerpa flexilis*, *C. brownii*
Codium spp. (encrusting)	Codi	2	*Codium convolutum*, *C. cranwelliae*
Ulva spp.	Ulva	1	
Other greens	Gree	9	e.g. *Codium fragile*, *Chaetomorpha* spp., *Cladophora* spp.

* *Carpophyllum flexuosum* was treated as a separate group because of its differing morphology and habitat (generally deeper water) compared with other *Carpophyllum* species.

2.3.3 Benthic community structure

All sessile organisms were divided into 29 structural groups (Table 2), using a functional group-type approach (cf. Steneck & Dethier 1994). Macroalgae were divided into functional groups based on Steneck & Dethier (1994), whereas sessile invertebrates were divided subjectively into broad structural classes for each phylum (Table 2). This approach was used to allow comparisons of the relative contributions of phylogenetically distinct taxonomic groups, e.g. macroalgae v. sessile invertebrates, in the same analysis of overall benthic community structure. The biomass (AFDW) of macroalgal groups was calculated using the same procedure as above, whereas for sessile invertebrate groups biomass was calculated using percentage cover–biomass relationships (Appendix 4). To convert percentage cover estimates to AFDW, conversion values were calculated for several species within each structural group. Three 10 × 10-cm samples were collected for each species, shell-free dry weight was measured by drying samples to a constant weight at 80°C, and AFDW was then determined by incineration at 500°C in a muffle furnace. Most invertebrate structural group samples were collected from Leigh and the Mokohinau Islands. It was therefore assumed that

TABLE 2. BENTHIC STRUCTURAL GROUPS USED IN ANALYSES OF BENTHIC COMMUNITY STRUCTURE. NR = NOT RECORDED TO THE SPECIES LEVEL. CODE INDICATES THE ABBREVIATION USED FOR EACH GROUP IN FIG. 9.

PHYLA	GROUP	CODE	NO. OF TAXA	EXAMPLE
Algae*	Crustose	Al_crust	3	*Ralfsia* spp., crustose corallines
	Articulated	Al_artic	1	*Corallina officinalis*
	Filamentous	Al-fil	16	*Cladophora feredayi*, *Chaetomorpha coliformis*
	Foliose	Al_fol	1	*Ulva* sp.
	Corticated foliose	Al_CFA	61	*Dictyota* spp., *Kallymenia* spp.
	Corticated terete	Al_CTA	53	*Pterocladia lucida*, *Caulerpa* spp., *Halopteris* spp.
	Leathery macrophytes	Al_leath	21	*Carpophyllum* spp., *Marginariella* spp.
Annellida	Serpulid tubeworms	Tube	NR	*Galeolaria* sp.
Chordata	Compound ascidian	As_comp	NR	*Didemnum* spp.
	Sea tulip	As_tulip	1	*Pyura pachydermatina*
	Solitary ascidian	As_sol	NR	*Asterocarpa* spp.
	Stalked ascidian	As_stalk	NR	*Pseudodistoma* spp.
Crustacea	Barnacles	Barn	NR	*Balanus* spp.
Mollusca	Oyster	Oyster	NR	*Anomia walteri*
	Large mussels	Mus_lge	NR	*Perna canaliculus*, *Mytilus* spp.
	Small mussels	Mus_sm	NR	*Xenostrobus pulex*
Brachiopoda	Brachiopod	Brachi	NR	
Bryozoa	Branched bryozoan	Br_br	NR	*Bugula dentata*
	Encrusting bryozoan	Br_enc	NR	*Membranipora* sp.
Cnidaria	Colonial anemone	An_col	NR	*Anthothoe albocincta*, *Corynactis australis*
	Large solitary anemone	An_sol	NR	*Oulactis* sp., *Phlyctenactis* sp.
	Black coral	Co_black	1	*Antipathes fiordensis*
	Cup coral	Co_cup	2	*Culicia rubeola*, *Monomyces rubrum*
	Soft coral	Co_soft	NR	*Alcyonium* sp.
Hydrozoa	Hydroid turf	Hy_turf	NR	*Amphisbetia bispinosa*
	Hydroid tree	Hy_tree	NR	*Solanderia ericopsis*
Porifera	Encrusting sponge	Sp_enc	NR	*Cliona celata*
	Finger sponge	Sp_fing	NR	*Raspailia topsenti*
	Massive sponge	Sp_mas	NR	*Ancorina alata*

* Algal groups include Chlorophyta, Phaeophyta and Rhodophyta and are based on the definitions of Steneck & Dethier (1994).

the biomass of structural groups would be broadly consistent among regions. Because percentage cover estimates did not take into account differences in the vertical height or size of encrusting forms (e.g. sponges, mussels), an attempt was made to collect specimens covering a range of sizes for biomass estimates. These potential artefacts were considered to have little effect on interpretation of overall patterns as analyses were based on fourth-root transformed data.

2.4 ENVIRONMENTAL VARIABLES

The environmental variables that were assessed for each site included wind fetch (as an estimate of wave exposure), turbidity, sedimentation, reef slope and maximum depth. Wind fetch (km) was calculated for each site by summing the potential fetch for each 10-degree sector of the compass rose. For open sectors of water the radial distance was arbitrarily set to be 300 km. Turbidity was measured using a standard 25-cm-diameter black and white Secchi disc (Larson & Buktenica 1998). The reading taken was the average depth (m) of descending disappearance and ascending reappearance. The percentage cover of sediment on the reef (measured during quadrat sampling) was used as an estimator of sedimentation. Reef slope at each site was expressed as a percentage calculated by dividing the maximum depth sampled by the length of the transect line run from the low water mark to a depth of 12 m or the edge of the reef. The density of exposed *Evechinus chloroticus* (averaged across all depths at each site) was also used as an explanatory variable in multivariate analyses given its strong controlling influence on macroalgal community structure (Andrew 1988). The management status of each site (i.e. Reserve or Non-reserve) was also treated as an explanatory variable as increased predator abundance in marine reserves can have indirect effects on urchins and macroalgal assemblages (Shears & Babcock 2002, 2004a).

2.5 STATISTICAL ANALYSES

All analyses were carried out at the level of individual sites, based on biological data averaged for all quadrats across all depths. However, given that the vertical structure of reef communities is highly variable and likely to be related to environmental conditions, it was necessary to assess the extent to which depth-averaged biomass was representative of a species' biomass at individual depth strata. Calculation of Spearman's rank correlations between biomass at each depth stratum and the depth-averaged biomass, for a subset of species, revealed that there was generally high correspondence across individual depths (65–72%). This can be interpreted as the depth-averaged biomass being able to explain approximately 70% of the variation at any individual depth stratum. Variation in benthic communities with depth is described separately for each bioregion in section 3.4.

2.5.1 Principal coordinates analysis

To visualise the variation in community patterns among locations and sites, and how the patterns relate to explanatory variables, principal coordinates analysis was carried out based on Bray-Curtis similarities using the PCOORD program (Anderson 2000). All datasets were fourth-root transformed. The environmental and species group variables were correlated with principal coordinates (PC) axes 1 and 2 and the correlation coefficients plotted as bi-plots, in which the position of the symbol indicates the correlation between the explanatory variable and the PC axes.

2.5.2 Multiple regression

The relationships between the multivariate datasets and explanatory variables were investigated using non-parametric multivariate multiple regression (McArdle & Anderson 2001). This technique investigates the relationships between community data and sets of explanatory variables (e.g. Anderson et al. 2004), using the computer program DISTLM (Anderson 2002). The spatial variables Northing and Easting (New Zealand Map Grid) for each site were included as a set of explanatory variables, along with the set of environmental variables measured at each site. For each set of explanatory variables, individual variables were analysed for their relationship with the biological dataset, then subjected to a forward selection procedure whereby each variable was added to the model in the order of greatest contribution to total variation. All analyses were based on Bray-Curtis similarities, calculated on fourth-root transformed site-level data for each biological dataset. Marginal tests (examining a single variable or set of variables) were carried out with 4999 permutations of the raw data, whereas conditional tests (used for the forward selection procedure) were based on 4999 permutations of residuals under the reduced model. Analyses were carried out on each biological dataset at all spatial scales. However, bioregional analysis was carried out only for Northeastern, Abel, and Stewart Island sites, as the number of sites sampled in other bioregions was too low for analysis.

To investigate potential associations between the abundance of *Evechinus chloroticus* and both the environmental and spatial variables a forward-backward stepwise multiple regression was run in the statistical program S+. Analyses were carried out at two spatial scales (national and bioregional) to generate hypotheses about the important environmental factors controlling urchin abundance at different spatial scales.

2.5.3 Bioregional patterns in reef communities

To investigate variation in algal community structure among sites within each bioregion, principal coordinates analysis was carried out on site-level data (based on the macroalgal community structure dataset that had been fourth-root transformed), using the same procedure as for the national level analysis (see above). There were too many sites within each location to present data for each site and pooling data across all sites potentially masks important variation among sites within each location. Therefore, sites within each bioregion were grouped using hierarchical cluster analysis (PRIMER, Clarke & Warwick 1994), based on the macroalgal group data that had been fourth-root transformed. Depth-related patterns in algal communities, urchin abundance, mobile invertebrates and dominant substratum cover were then described for the groupings of sites identified for each location. In each case, data for the ten most abundant taxa or species groups for a particular bioregion are presented.

3. Results

Sections 3.1–3.3 describe national and bioregional patterns in macroalgal community structure (3.1), mobile macroinvertebrate species assemblages (3.2) and benthic community structure (3.3) among locations, and their association with key environmental variables.

Section 3.4 describes variation in reef communities among sites within each bioregion and the association between biological patterns and environmental gradients. Depth-related patterns in abundance, biomass or cover are also described for dominant species or groups.

3.1 MACROALGAL ASSEMBLAGES

3.1.1 National variation in macroalgal community structure

Over 150 macroalgal taxa were recorded at the shallow reef sites sampled in this study (Appendix 5). Large brown algal species made up 79% of the total biomass, with *Ecklonia radiata* and *Carpophyllum maschalocarpum*, the two most common large brown macroalgal species, accounting for 48% of the total macroalgal biomass (25% and 23%, respectively, Table 3). There was large variation in macroalgal community structure, based on the biomass of the 23 macroalgal species groups, among sites both within and among locations (Fig. 2A). Locations with the greatest variation among sites were where sites were sampled across a large environmental gradient, e.g. Paterson Inlet, Flea Bay and Long Island, or where only a small number of sites were sampled, e.g. Gannet Rock and Charles Sound. The spread of locations along the axis of greatest variation PC1 reflected a weak latitudinal gradient from north to south (Fig. 2B), with sites of the Northern Province generally being located on the left of the ordination and Southern sites on the right, and PC1 strongly correlated with the spatial variables (Northing and Easting) (Fig. 2B). Notable exceptions were the Banks locations, which were grouped with Northern locations. There was some division between east and west coast locations along PC2 with the majority of west coast locations grouped on the lower poriton of the ordination. All of the environmental variables were significantly related to macroalgal community structure and explained 31% of the variation (Table 4). Individually, these variables explained only a low proportion of the variation at the national scale and were not strongly correlated with PC1 or PC2. Several species groups were strongly correlated with PC1: *Carpophyllum* spp. were negatively correlated, whereas coralline turf, red turfing and foliose algae, and some large brown algal species (*Lessonia variegata*, *Landsburgia quercifolia*, *Xiphophora* spp. and *Marginariella* spp.) were positively correlated (Fig. 2C). *Ecklonia radiata* and *Carpophyllum flexuosum* were strongly correlated with PC2 and were absent at most locations clustered in the lower portion of the ordination, e.g. Raglan, Karamea, Cape Foulwind, Jackson Head and Cascades on the west coast, and Otago Peninsula and Catlins on the east coast (Appendix 5).

At the provincial level the importance of the variables varied between the two provinces (Table 4). For the Northern Province, Secchi explained the greatest

TABLE 3. DOMINANT MACROALGAL SPECIES OR SPECIES COMPLEXES ACCORDING TO THEIR CONTRIBUTION TO TOTAL BIOMASS (AFDW) AND THE PERCENTAGE OF ALL SITES AT WHICH EACH SPECIES OCCURRED (% OCC.).

NO.	SPECIES	GROUP	% OCC.	MEAN AFWD (g/m^2)	% AFWD	GENERAL DISTRIBUTION
1	*Ecklonia radiata*	Phaeophyta	63.2	102.14	25.47	New Zealand
2	*Carpophyllum maschalocarpum*	Phaeophyta	60.3	92.30	23.01	Northern
3	*Lessonia variegata*	Phaeophyta	29.6	30.61	7.63	New Zealand
4	*C. flexuosum*	Phaeophyta	56.7	19.56	4.88	New Zealand
5	Crustose corallines*	Rhodophyta	100.0	15.46	3.86	New Zealand
6	*C. angustifolium*	Phaeophyta	16.6	14.39	3.59	Northeastern
7	Articulated coralline turf*	Rhodophyta	90.7	13.29	3.31	New Zealand
8	*Landsburgia quercifolia*	Phaeophyta	37.2	11.69	2.92	New Zealand
9	*Durvillaea willana*	Phaeophyta	9.7	10.93	2.73	Southern
10	*Xiphophora gladiata*	Phaeophyta	21.9	8.11	2.02	Southern
11	Red turfing algae*	Rhodophyta	79.8	7.79	1.94	New Zealand
12	*Marginariella boryana*	Phaeophyta	12.6	7.20	1.80	Southern
13	*M. urvilliana*	Phaeophyta	12.6	5.84	1.46	Southern
14	*Macrocystis pyrifera*	Phaeophyta	12.1	5.43	1.36	Southern
15	*Caulerpa brownii*	Chlorophyta	21.1	4.93	1.23	Southern
16	*Cystophora platylobium*	Phaeophyta	9.3	3.84	0.96	Southern
17	*Halopteris* spp.	Phaeophyta	55.5	3.82	0.95	New Zealand
18	*Pterocladia lucida*	Rhodophyta	42.9	3.59	0.90	Northern
19	*Osmundaria colensoi*	Rhodophyta	21.9	2.96	0.74	Northern
20	*Plocamium* spp.*	Rhodophyta	57.1	2.72	0.68	New Zealand
21	*Asparagopsis armata*	Rhodophyta	29.1	2.66	0.66	New Zealand
22	*Ballia callitrichia*	Rhodophyta	20.6	2.15	0.54	Southern
23	*Codium convolutum*	Chlorophyta	50.6	1.89	0.47	New Zealand
24	*C. plumosum*	Phaeophyta	21.1	1.89	0.47	Northeastern
25	*Zonaria* spp.	Phaeophyta	56.7	1.72	0.43	New Zealand
26	*Hymenena durvillaei*	Rhodophyta	17.8	1.59	0.40	Southern
27	*Hymenena palmata*	Rhodophyta	20.6	1.58	0.39	Southern
28	*Lophurella hookeriana*	Rhodophyta	24.3	1.19	0.30	Southern
29	*Cystophora retroflexa*	Phaeophyta	18.2	1.17	0.29	New Zealand
30	*Sargassum sinclairii*	Phaeophyta	55.1	1.13	0.28	New Zealand
31	*Ulva* spp.*	Chlorophyta	37.2	1.01	0.25	New Zealand
32	*Euptilota formosissima*	Rhodophyta	36.0	1.00	0.25	New Zealand
33	*Rhodymenia* spp.*	Rhodophyta	10.5	0.93	0.23	New Zealand
34	*Xiphophora chondrophylla*	Phaeophyta	21.1	0.91	0.23	Northern
35	*Microzonia velutina*	Phaeophyta	29.6	0.91	0.23	Southern
36	*Anotrichium crinitum*	Rhodophyta	29.1	0.90	0.22	Southern
37	*Craspedocarpus erosus*	Rhodophyta	18.6	0.70	0.17	Southern
38	*Rhodophyllis gunnii*	Rhodophyta	28.7	0.69	0.17	Southern
39	*Caulerpa flexilis*	Chlorophyta	7.7	0.67	0.17	Northern
40	*Glossophora kunthii*	Phaeophyta	54.7	0.58	0.14	New Zealand

* Groups of species that were not identified to the species level. The distribution patterns in biomass of some of these species groups are given in Fig. 4.

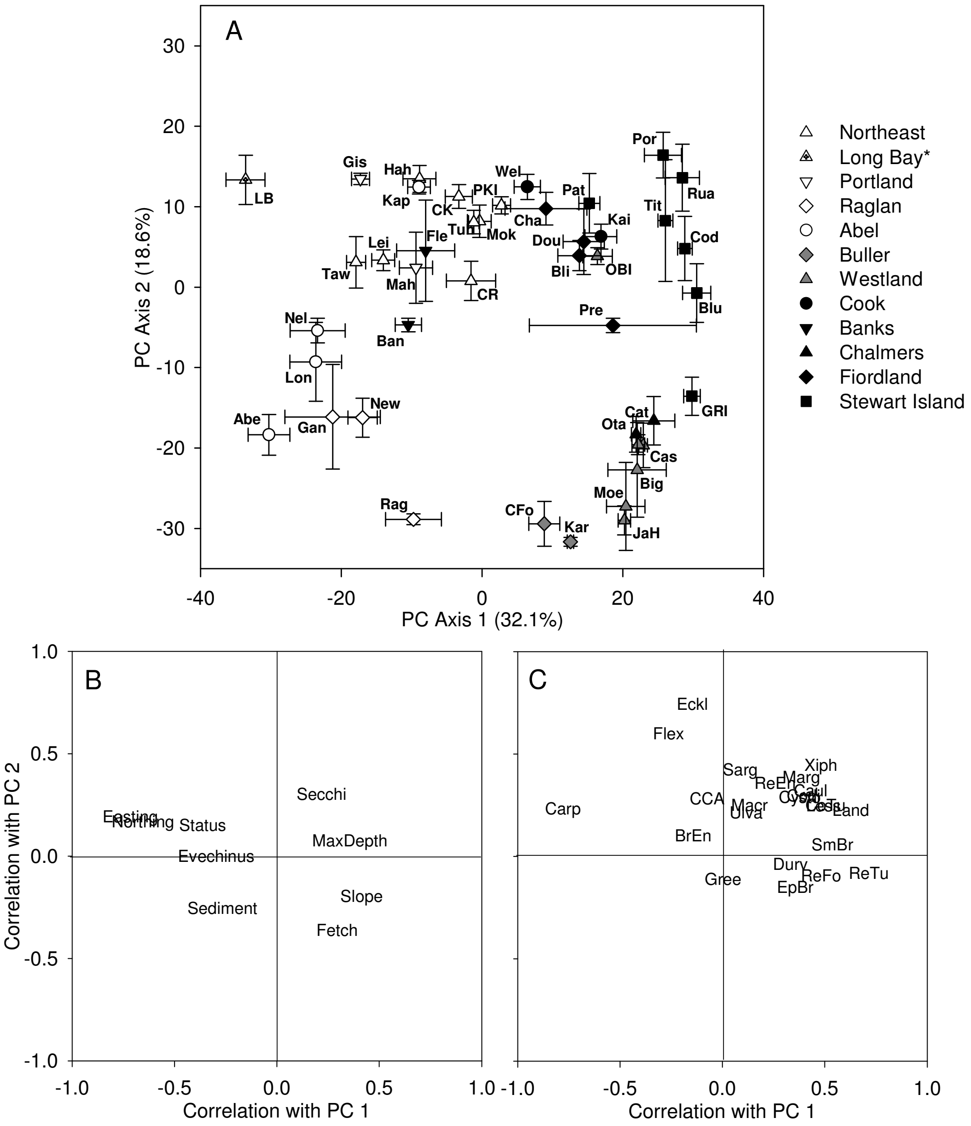


Figure 2. Macroalgal community structure (fourth-root transformed biomass of 23 groups) from principal coordinates analysis on all 247 sites (A) (see Fig. 1 for location codes and Table 1 for species group codes). Centroids are plotted for each location; standard error bars indicate the variation among sites at each location. Shaded symbols indicate bioregions in the Southern Province and open symbols indicate bioregions in the Northern Province. Bi-plots give correlations between principal coordinates axes and environmental variables (B) and original macroalgal species groups (C). * Long Bay is distinguished from other Northeastern locations as it was not included in biogeographic analyses (Shears et al. in press).

variation (13%), whereas for the Southern Province, Fetch explained 14% of the variation. Evechinus accounted for only a small proportion of the variation in algal community structure at the national (4%) and provincial scale (< 5%), but between 9% (Northeastern) and 17% (Stewart Island) at the bioregional level. Overall, the amount of variation explained by site-level environmental variables tended to increase with decreasing spatial scale: national < biogeographic province < bioregion. These patterns in algal community structure and their relationship with environmental variables are described in detail for each bioregion in section 3.4.

3.1.2 National patterns in dominant macroalgal species

Clear differences were apparent in total algal biomass among bioregions, despite considerable variability among sites and locations within each (Fig. 3). Macroalgal biomass was lowest at west coast bioregions, particularly in the Southern Province. *Ecklonia radiata* and *Carpophyllum* spp., predominantly *C. maschalocarpum*, dominated in Northern bioregions, whereas the Southern bioregions were dominated by a mixture of large brown algae including *E. radiata*, *Lessonia variegata*, *Landsburgia quercifolia*, *Durvillaea willana*, *Macrocystis pyrifera*,

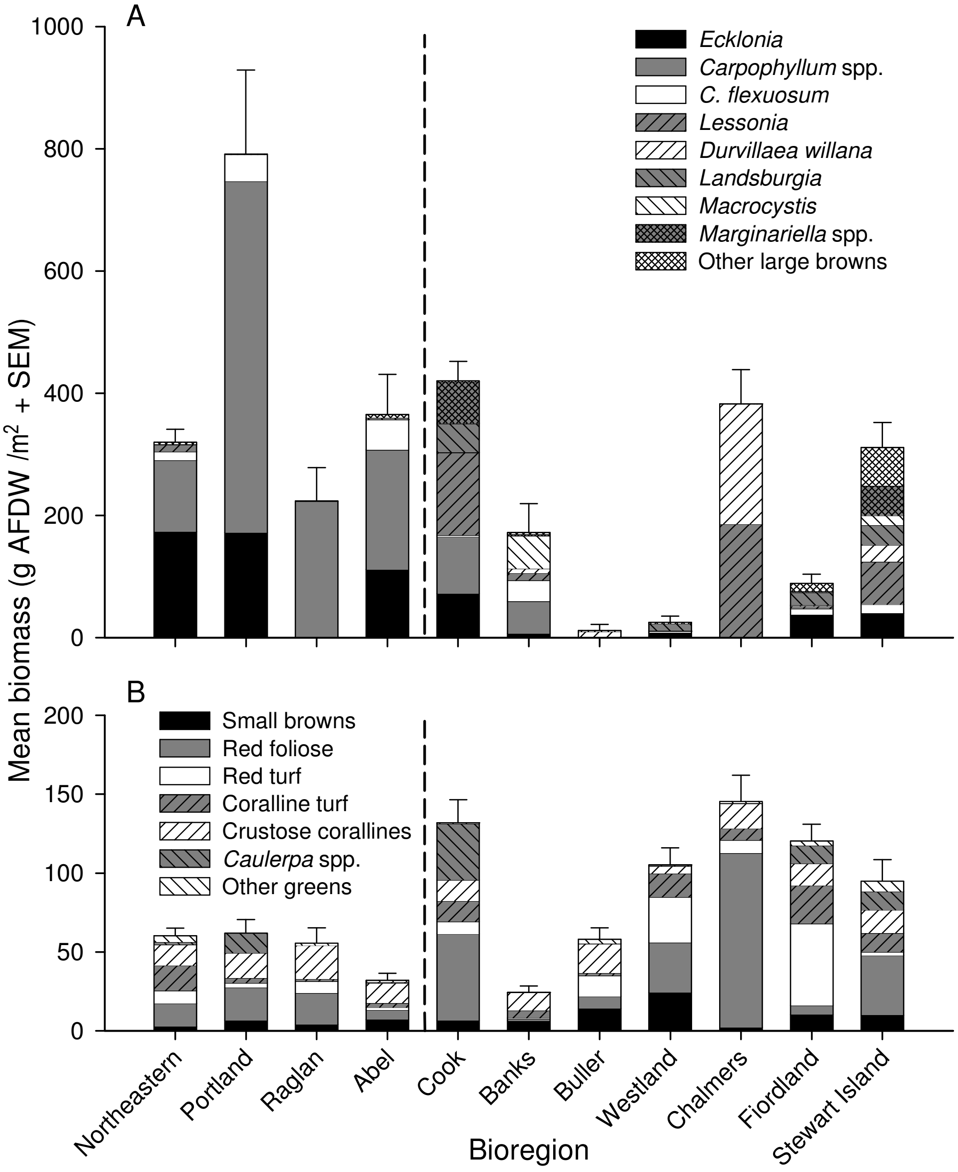
TABLE 4. RESULTS OF NON-PARAMETRIC MULTIVARIATE REGRESSION OF MACROALGAL COMMUNITY STRUCTURE DATA (FOURTH-ROOT TRANSFORMED BIOMASS OF 23 ALGAL GROUPS), AND ENVIRONMENTAL AND SPATIAL VARIABLES AT DIFFERING BIOGEOGRAPHIC SCALES. THE PERCENTAGE VARIANCE EXPLAINED BY EACH VARIABLE IS GIVEN (ns = NOT SIGNIFICANT), ALONG WITH THE CUMULATIVE FREQUENCY EXPLAINED FOLLOWING FORWARD SELECTION OF FACTORS (THE SIGNIFICANT FACTORS FROM THIS PROCEDURE ARE LISTED IN DESCENDING AMOUNT OF VARIATION EXPLAINED).

		BIOGEOGRAPHIC PROVINCES		BIOREGIONS		
	NZ	NORTHERN	SOUTHERN	NORTHEASTERN	ABEL	STEWARTI
n	247	135	112	81	37	42
Local variables						
Fetch	7.3	3.9	13.6	8.3	6.5	19.9
Status	5.1	ns	4.0	ns	ns	ns
Slope	6.7	4.2	ns	15.4	ns	ns
MaxDepth	5.1	8.1	3.6	25.2	ns	ns
Secchi	5.5	13.1	7.4	23.5	21.0	18.1
Evechinus	4.1	2.1	4.7	8.7	11.2	16.7
Sediment	4.5	8.0	5.4	6.0	18.8	19.9
Cumulative %	**30.9**	**29.5**	**36.6**	**37.5**	**41.1**	**32.3**
Significant factors	All	All, excl. Status	All	MaxDepth, Secchi, Fetch	Secchi, Sediment, Evechinus, Fetch	Fetch. Evechinus, Sediment
Spatial—Northing and Easting	22.4	24.3	26.4	30.7	23.1	22.5

Marginariella spp. and several other large brown algal species such as *Xiphophora gladiata* (Fig. 3A). *Ecklonia radiata* occurred throughout the country (Fig. 4A), although it was not recorded in some bioregions (Buller, Westland (excluding Open Bay Islands) and Chalmers) and some locations (Nelson, Abel Tasman, Raglan, Preservation Inlet, Bluff and Green Islets), and was rare at others, e.g. Banks Peninsula North, Flea Bay and New Plymouth (Appendix 5). *Ecklonia radiata* was typically most abundant at Northeastern locations, although dense forests were also present at Gisborne, Mahia and Kapiti Island.

The four *Carpophyllum* species made up 32% of the total macroalgal biomass recorded (Table 3). *Carpophyllum maschalocarpum* was the most abundant and had a northern distribution, but was also abundant in the Cook and Banks bioregions (Fig. 4A). Both *C. angustifolium* and *C. plumosum* were recorded only at locations in the Northeastern bioregion (Appendix 5). *Carpophyllum flexuosum* was an important contributor to total algal biomass at bioregions throughout the country (Figs 3A and 4A), but was not recorded at several bioregions including Raglan, Buller, Westland (excluding Open Bay Islands) and Chalmers, as well as some specific locations (Cape Reinga, Kaikoura and Green Islets; Appendix 5). *Lessonia variegata* was the third largest contributor to total algal biomass (8%) and was most abundant in Southern bioregions (e.g. Cook, Chalmers and Stewart Island) but also occurred at exposed locations in the Northeastern bioregion (Fig. 4A). *Lessonia variegata* was not recorded at Portland, Raglan, Abel, Buller

Figure 3. Mean biomass of dominant large brown algae (A) and other macroalgal groups (B) for all bioregions. Dashed line indicates division between the Northern and Southern Provinces.



or Westland (excluding Open Bay Islands). *Landsburgia quercifolia* exhibited a similar southern distribution but was also abundant in the Westland and Fiordland bioregions. Several other large brown algal species were regionally abundant, but made up only a small proportion of total algal biomass. For example, *Durvillaea willana* was the dominant large brown algae at Chalmers locations, and some Stewart Island sites, but rare in other regions (Figs 3A and 4B). *Macrocystis pyrifera* also had a southern distribution and was most abundant at Stewart Island and Banks Peninsula (Fig. 3A), but also occurred at some Wellington, Long Island and Fiordland sites. A number of other species were typically most abundant at locations in the Stewart Island bioregion, e.g. *Xiphophora gladiata*, *Marginariella* species and *Cystophora platylobium* (Fig. 4B).

The crustose coralline and articulated coralline turf species complexes were dominant contributors to total algal biomass on a national scale (3.9% and 3.3%, respectively), and were recorded at most sites (Table 3) and all bioregions (Fig. 3B). The red turf species complex made up c. 2% of the total algal biomass and on average was most abundant in Buller, Westland and Fiordland (Fig. 3B).

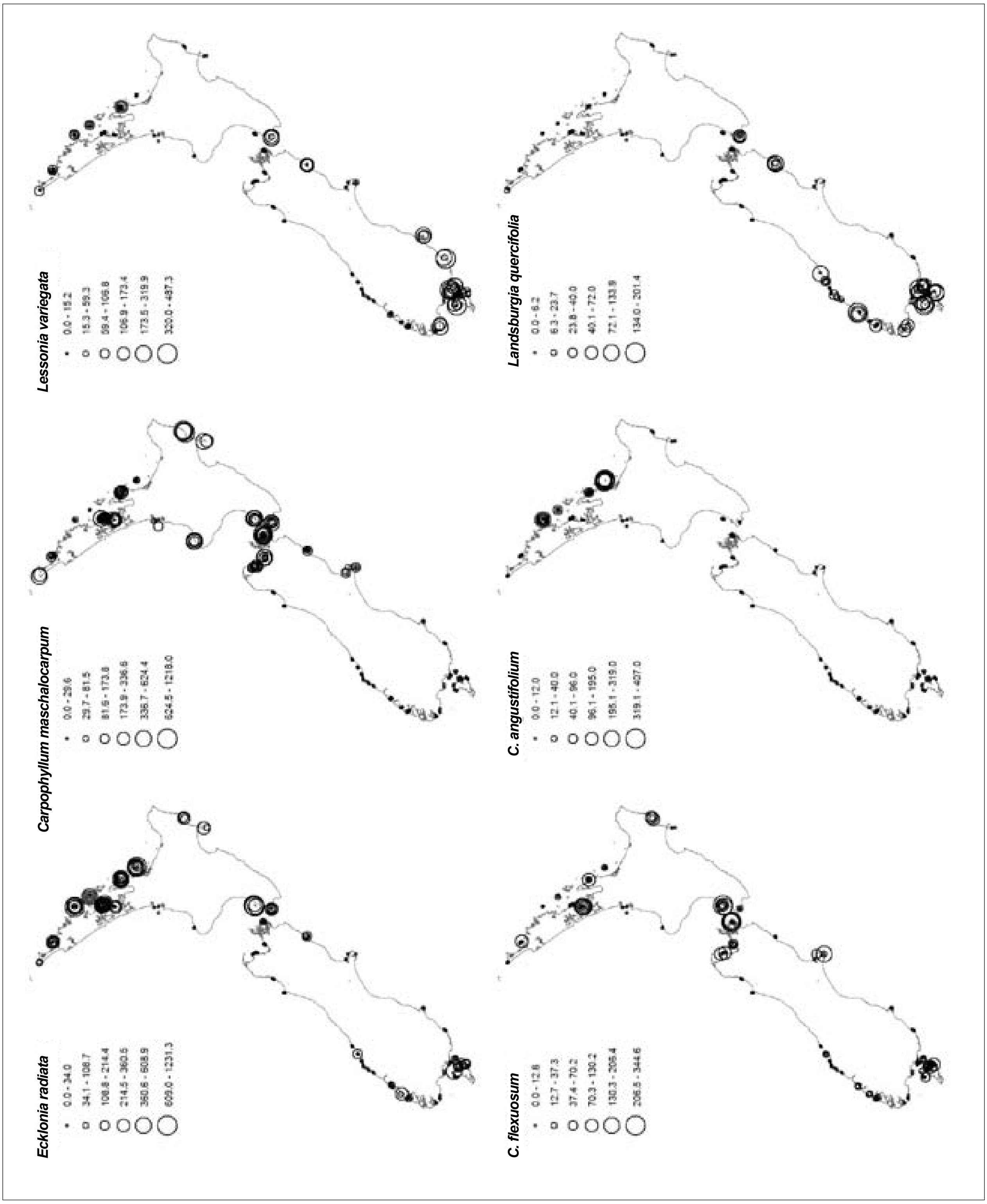


Figure 4A. Mean biomass (g AFDW/m^2) of dominant large brown macroalgal species at all sites, averaged across all depths sampled.

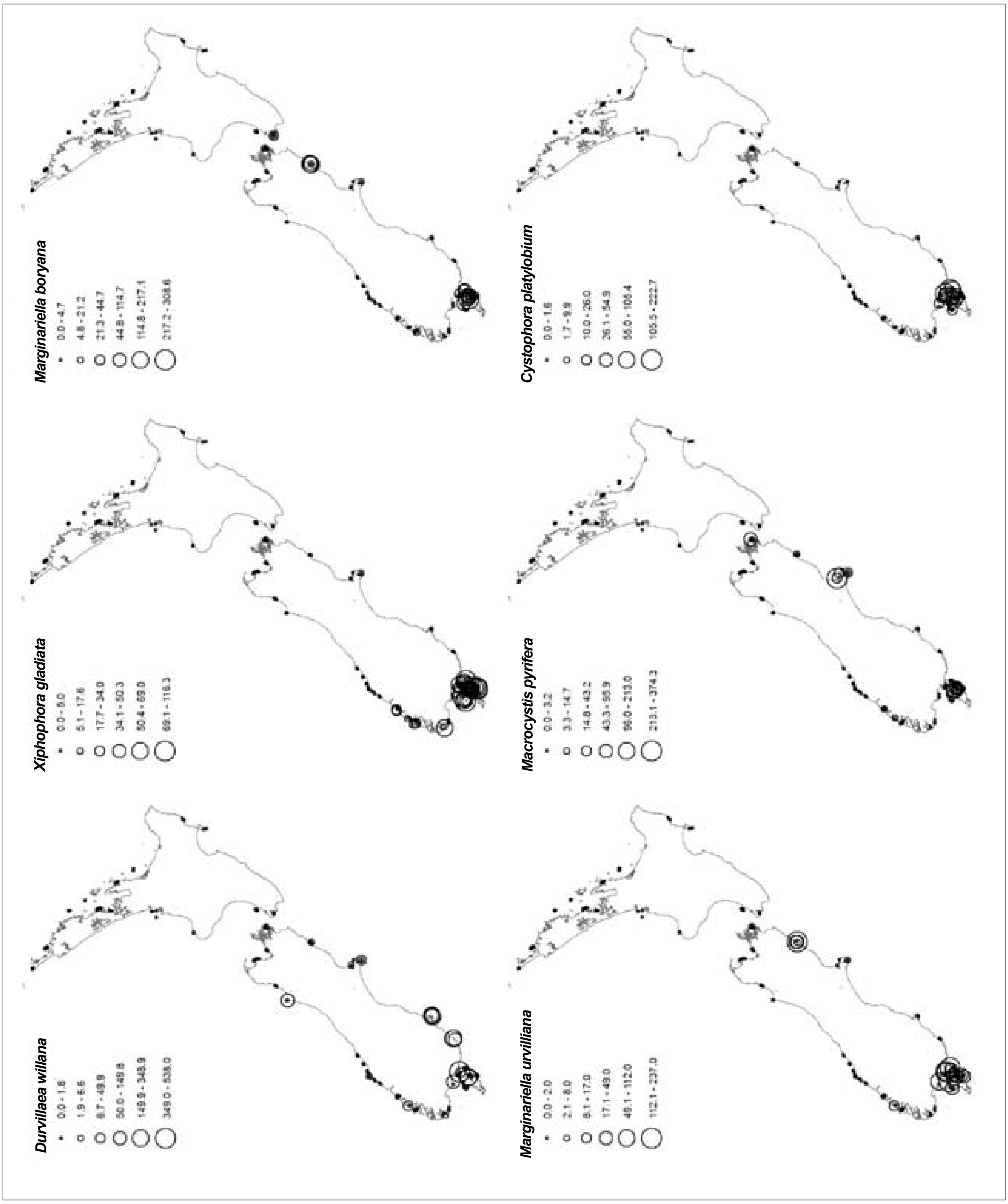


Figure 4B. Mean biomass (g AFDW/m^2) of other large brown macroalgal species at all sites, averaged across all depths sampled.

Durvillaea willana

Xiphophora gladiata

Marginariella boryana

Marginariella urvilliana

Macrocystis pyrifera

Cystophora platylobium

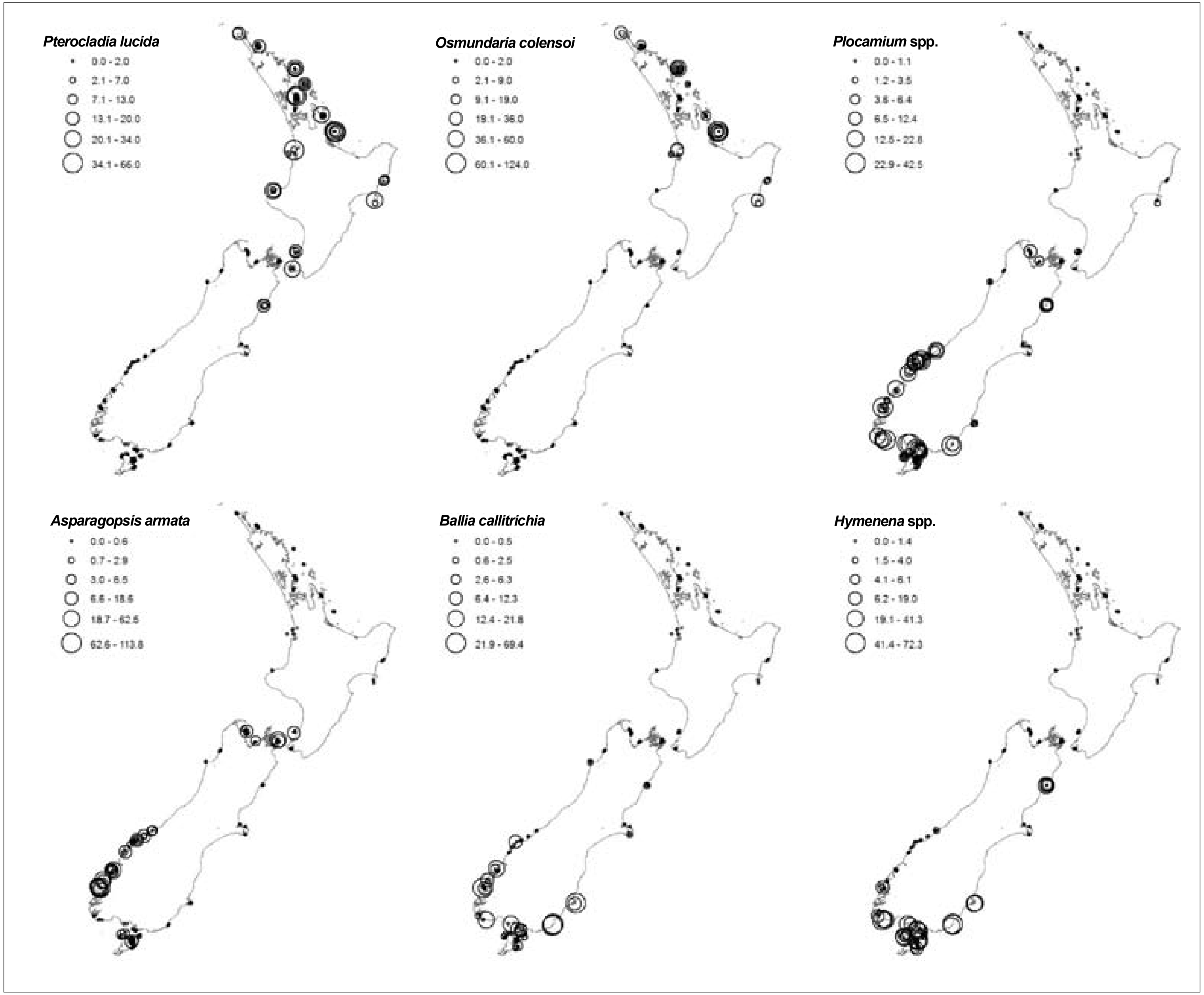


Figure 4C. Mean biomass (g AFDW/m^2) of dominant red macroalgal species at all sites, averaged across all depths sampled.

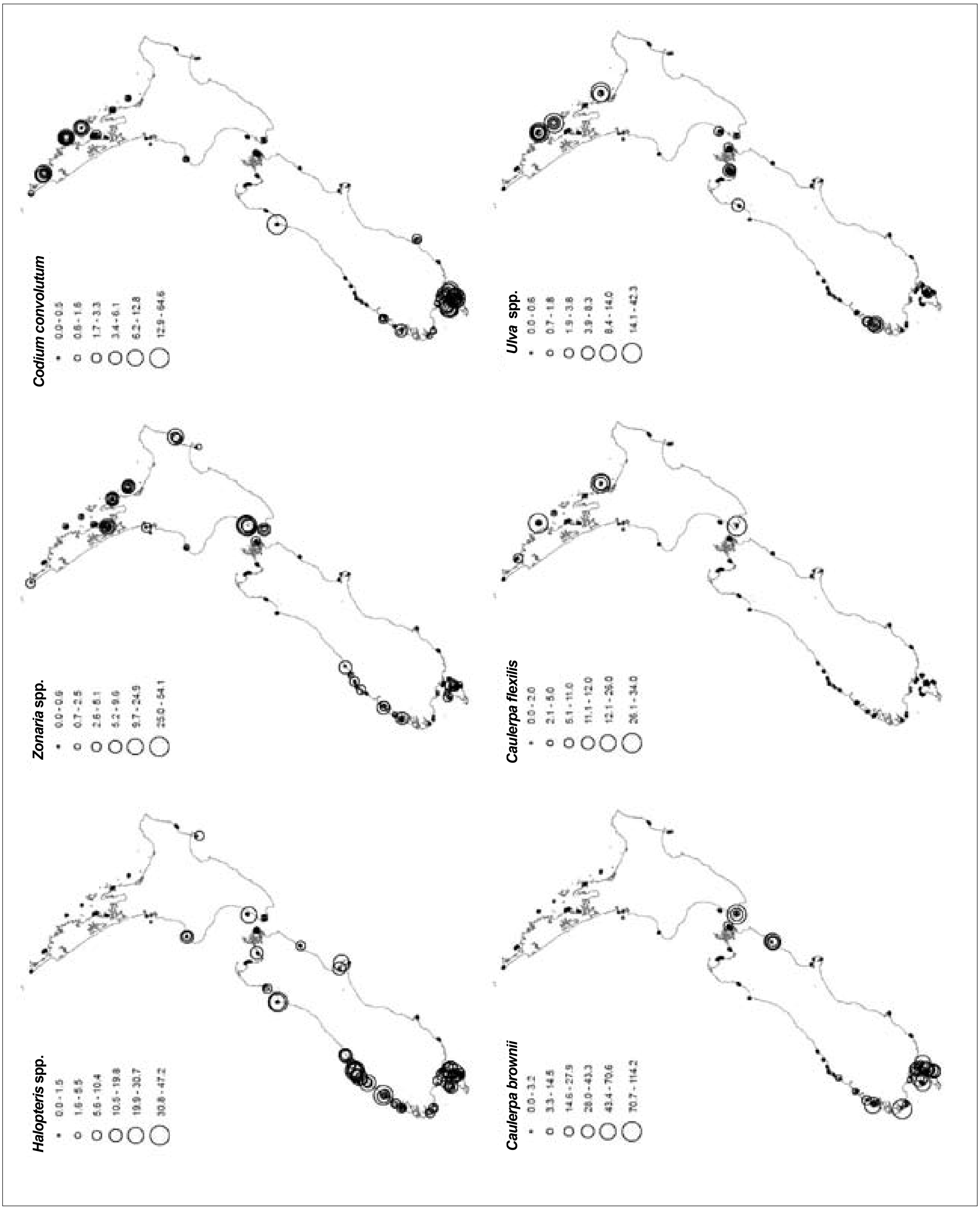


Figure 4D. Mean biomass (g AFDW/m^2) of dominant small brown and green macroalgal species at all sites, averaged across all depths sampled.

Red foliose algae were most abundant in the Cook, Chalmers and Stewart Island bioregions (Fig. 3B). Among the red foliose algae two Northern species were the greatest contributors to total algal biomass (*Pterocladia lucida* and *Osmundaria colensoi*) whereas a variety of red foliose algal species were important contributors at Southern locations, e.g. *Plocamium* spp., *Asparagopsis armata*, *Ballia callitrichia* and *Hymenena* spp (Table 3, Fig. 4C).

A variety of smaller brown algal species were found at low biomasses across all bioregions (Fig. 3B). Of these *Halopteris* spp. was the most abundant, particularly at Southern locations (Fig. 4D). *Zonaria* spp. were also common across many bioregions, but notably absent from Buller, Banks and Chalmers. Among the green algal species, *Caulerpa brownii* was the greatest contributor to overall biomass (1.2%), and was most common in Southern locations, particularly Wellington and Kaikoura. In contrast, *C. flexilis* was only found at North Island locations (Fig. 4D). Other green algal species such as *Ulva* spp. and *Codium convolutum* were common and found throughout New Zealand but were only small contributors to total algal biomass (Table 3).

3.1.3 Macroalgal species richness

There was a general trend of increasing macroalgal species richness (Chao 2 estimator, Estimate-S, Colwell & Coddington 1994) with latitude, with the highest algal diversity occurring at Southern locations (Fig. 5). There were, however, some Northern locations that had relatively high algal diversity, e.g. Cape Karikari and Northeastern offshore islands, and overall algal species richness was weakly correlated with northing ($r = -0.46$). Algal species richness was weakly positively correlated with water clarity (Secchi 0.37) and most of the locations with low species diversity were relatively turbid, e.g. Long Bay, Gisborne, Raglan, Cape Foulwind and Karamea.

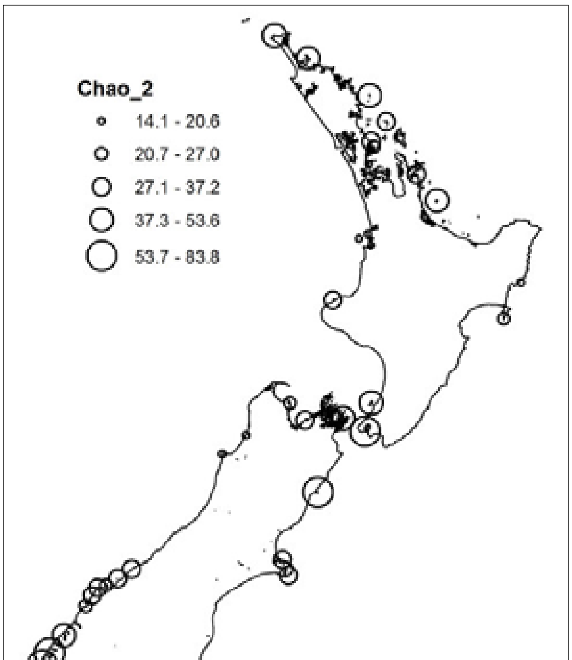


Figure 5. Predicted macroalgal species richness among locations (Chao 2 estimator, Estimate-S) (Colwell & Coddington 1994).

3.2 MOBILE MACROINVERTEBRATE ASSEMBLAGES

3.2.1 National variation in mobile macroinvertebrate assemblages

The number of mobile macroinvertebrate species (Table 5) was considerably lower than the number of macroalgal species recorded in this study. Despite notable variation in macroinvertebrate assemblages among locations within bioregions (e.g. Northeastern and Stewart Island), and among sites within locations (e.g. Open Bay Islands, Raglan and Mahia), there was a general north–south gradient in macroinvertebrate assemblages along PC1 (Fig. 6A). This was reflected by the strong correlation between PC1 and the spatial variables (Fig. 6B). As for macroalgal community structure, Banks Peninsula locations were most closely clustered with Northern locations, whereas Raglan and Kapiti were more similar to Southern locations. There was a particularly high level of variation among the two Preservation Inlet sites.

Several species were negatively correlated with PC1 and are generally more abundant at Northern locations, e.g. *Evechinus chloroticus*, *Trochus viridis*, *Cookia sulcata*, *Cantharidus purpureus* and *Dicathais orbita*, whereas the

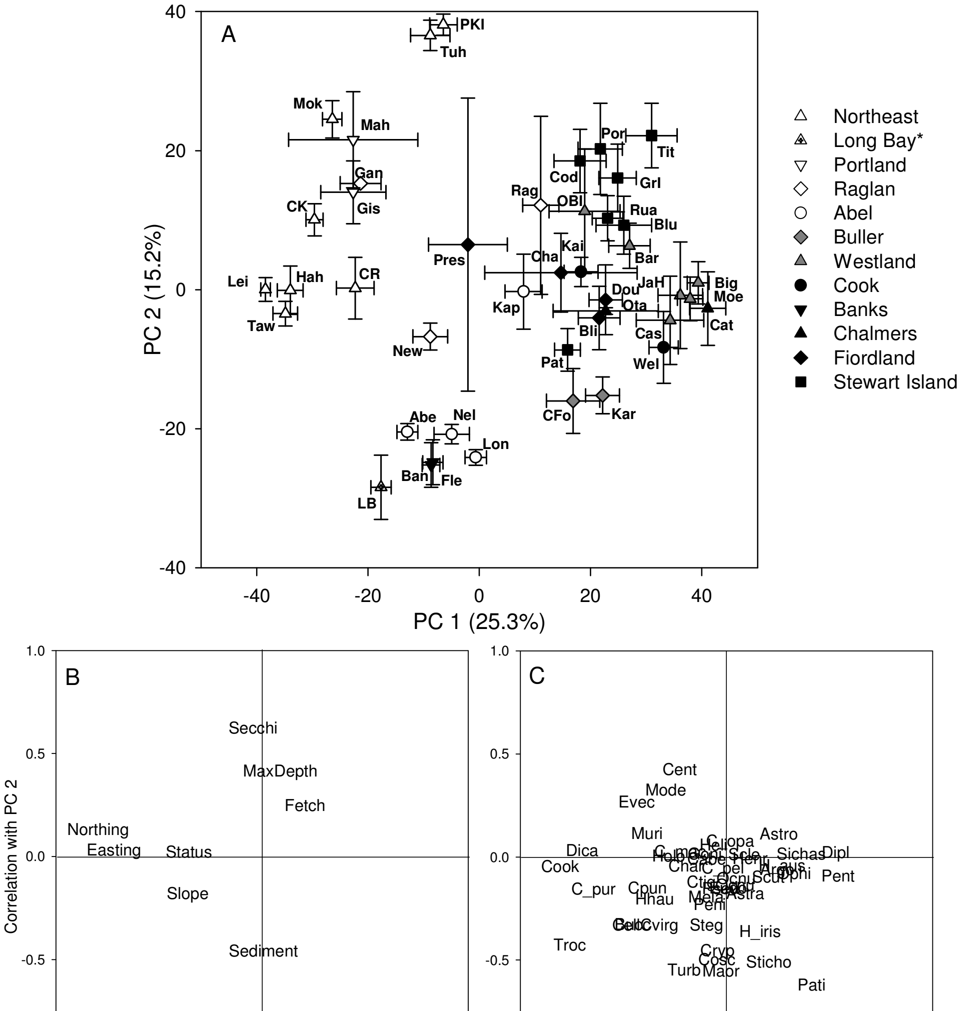


Figure 6. Mobile macroinvertebrate assemblages among sites from principal coordinates analysis based on fourth-root transformed count data of 47 species (A) (see Fig. 1 for location codes and Table 5 for species codes). Centroids are plotted for each location; standard error bars indicate the variation among sites at each location. Shaded symbols indicate bioregions in the Southern Province and open symbols indicate bioregions in the Northern Province. Bi-plots give correlations between principal coordinates axes and environmental variables (B) and original species (C). * Long Bay is distinguished from other Northeastern locations as it was not included in biogeographic analyses (Shears et al. in press).

TABLE 5. MEAN ABUNDANCE OF MOBILE MACROINVERTEBRATE SPECIES RECORDED. THE DISTRIBUTIONAL PATTERNS IN ABUNDANCE OF THE DOMINANT SPECIES ARE GIVEN IN FIG. 8. CODE INDICATES SPECIES ABBREVIATIONS USED IN FIG. 6.

NO.	SPECIES	CODE	CLASS	% OCC.	MEAN	%MEAN
1	*Evechinus chloroticus*	Evec	Echinoidea	85.02	1.341	17.59
2	*Trochus viridis*	Troc	Gastropoda	56.68	1.307	17.14
3	*Cookia sulcata*	Cook	Gastropoda	59.51	0.967	12.68
4	*Turbo smaragdus*	Turb	Gastropoda	21.05	0.881	11.55
5	*Cantharidus purpureus*	C_pur	Gastropoda	32.79	0.548	7.18
6	*Cellana stellifera*	Cell	Gastropoda	54.25	0.514	6.74
7	*Patiriella* spp.*	Pati	Asteroidea	54.25	0.464	6.09
8	*Maoricolpus roseus*	Maor	Gastropoda	23.48	0.370	4.85
9	*Dicathais orbita*	Dica	Gastropoda	34.41	0.211	2.76
10	*Stichopus mollis*	Sticho	Holothuroidea	38.06	0.124	1.63
11	*Ophiopsammus maculata*	Ophi	Ophiuroidea	29.15	0.118	1.55
12	*Haliotis australis*	H_aus	Gastropoda	46.96	0.082	1.08
13	*Cominella virgata*	Cvirg	Gastropoda	12.55	0.077	1.01
14	*Modelia granosa*	Mode	Gastropoda	29.15	0.077	1.01
15	*Stichaster australis*	Sichas	Asteroidea	19.84	0.063	0.82
16	*Haliotis iris*	H_iris	Gastropoda	19.84	0.060	0.78
17	*Buccinulum lineum*	Bucc	Gastropoda	27.53	0.054	0.71
18	*Pentagonaster pulchellus*	Pent	Asteroidea	37.25	0.052	0.68
19	*Calliostoma punctulatum*	Cpun	Gastropoda	24.29	0.047	0.61
20	*Eudoxochiton nobilis*	Eudo	Polyplacophora	36.44	0.040	0.52
21	*Cryptoconchus porosus*	Cryp	Polyplacophora	22.67	0.032	0.41
22	*Coscinasterias muricata*	Cosc	Asteroidea	21.86	0.029	0.38
23	*Diplodontias* spp.	Dipl	Asteroidea	20.24	0.025	0.33
24	*Haustrum haustorium*	Hhau	Gastropoda	14.17	0.022	0.29
25	*Astraea heliotropium*	Astra	Gastropoda	8.10	0.013	0.18
26	*Centrostephanus rodgersii*	Cent	Echinoidea	8.10	0.013	0.17
27	*Stegnaster inflatus*	Steg	Asteroidea	8.50	0.012	0.16
28	*Cantharidus opalas*	C_opa	Gastropoda	13.77	0.011	0.14
29	*Melagraphia aethiops*	Mela	Gastropoda	3.64	0.009	0.11
30	*Calliostoma tigris*	Ctig	Gastropoda	7.69	0.008	0.11
31	*Ocnus brevidentis*	O_brev	Holothuroidea	1.62	0.008	0.10
32	*Scutus breviculus*	Scut	Gastropoda	6.88	0.006	0.08
33	*Muricopsis* sp.	Muri	Gastropoda	8.10	0.006	0.08
34	*Pseudechinus* sp.	Pseu	Echinoidea	1.21	0.006	0.08
35	*Penion* sp.	Peni	Gastropoda	4.86	0.006	0.07
36	*Astrostole scabra*	Astro	Asteroidea	6.48	0.004	0.06
37	*Ocnus* sp. (white)	Ocnu	Holothuroidea	1.62	0.004	0.05
38	*Holopneustes* sp.	Holo	Echinoidea	4.45	0.004	0.05
39	*Cabestana spengleri*	Cabe	Gastropoda	5.67	0.004	0.05
40	*Argobuccinulum pustulosum*	Argo	Gastropoda	4.86	0.003	0.05
41	*Charonia lampas*	Char	Gastropoda	2.83	0.002	0.02
42	*Cominella maculosa*	C_mac	Gastropoda	2.43	0.001	0.02
43	*Goniocidaris tubaria*	Goni	Echinoidea	0.40	0.001	0.01
44	*Henricia* sp.	Henr	Echinoidea	1.21	0.001	0.01
45	*Sclerasterias mollis*	Scle	Echinoidea	0.40	0.001	0.01
46	*Calliostoma pellucida*	C_pel	Gastropoda	0.81	0.001	0.01
47	*Heliocidaris tuberculata*	Heli	Echinoidea	0.40	0.001	0.01

* Recorded as *Patiriella regularis* and was not distinquished from the new species of *Patiriella* described by O'Loughlin et al. (2002).

starfishes *Diplodontias* spp., *Pentagonaster pulchellus* and *Patiriella* spp. were positively correlated with PC1 and more typical of Southern bioregions (Figs 6C and 7). Secchi and Sediment were both correlated with PC2 (Fig. 6B), and this axis appeared to reflect an environmental gradient from more oceanic locations (e.g. Titi Islands and Northeastern offshore islands) to more sheltered and/or turbid coastal locations, such as the locations Long Bay, Abel Tasman, Nelson, Long Island and Banks Peninsula. Several species were correlated to PC2 and reflected this gradient; the sea urchin *Centrostephanus rodgersii* was positively correlated and only found at Northeastern offshore locations and Cape Karikari, whereas the sea cucumber *Stichopus mollis*, starfish *Patiriella* spp., and the gastropods *Turbo smaragdus*, *Trochus viridis* and *Maoricolpus roseus* were negatively correlated and more common at the more turbid coastal locations (Figs 6C and 8).

Environmental variables explained 24% of the variation in macroinvertebrate species composition at the national level (Table 6), with Secchi being the most strongly associated (7%). The relationship between explanatory variables and species composition varied with spatial scale and among bioregions (Table 6).

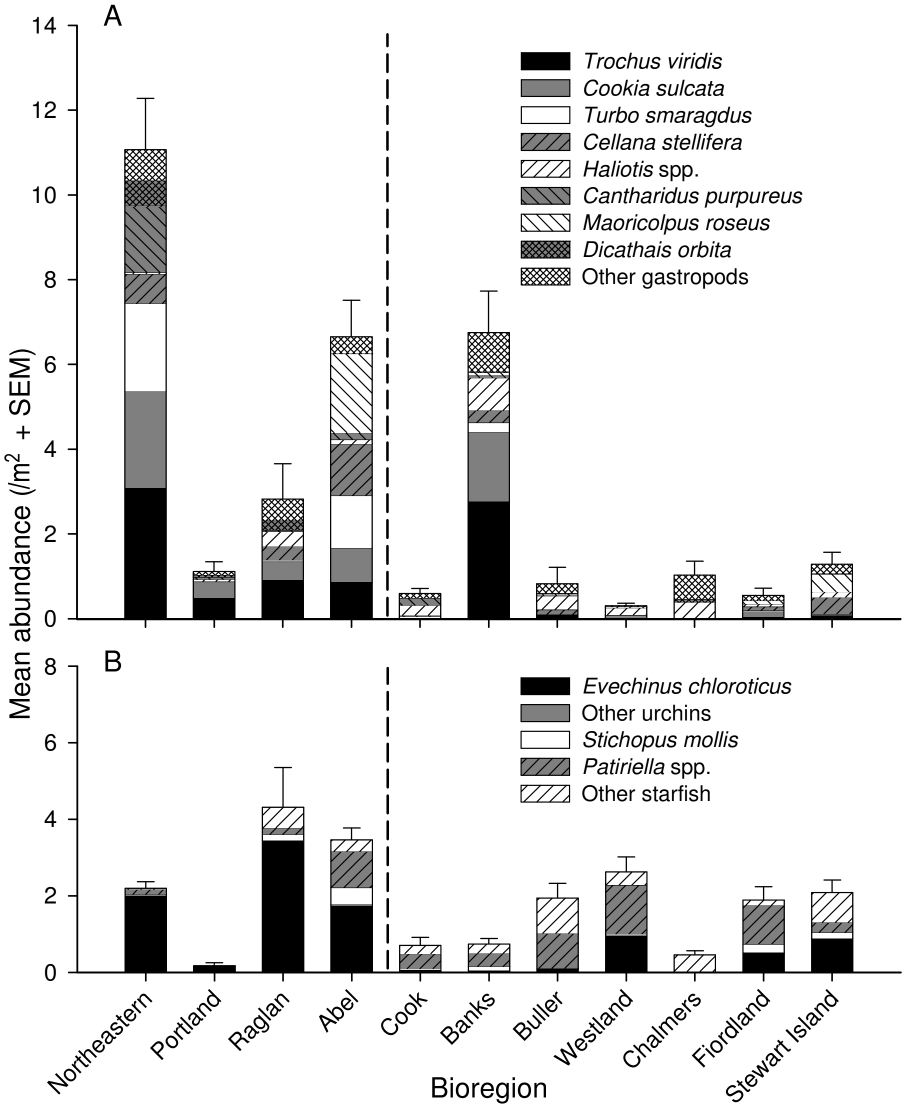


Figure 7. Mean abundance of the most common mobile macroinvertebrate species (gastropods, A, and echinoderms, B) for all bioregions. Dashed line indicates division between the Northern and Southern Provinces.

TABLE 6. RESULTS OF NON-PARAMETRIC MULTIVARIATE REGRESSION OF MOBILE MACROINVERTEBRATE ASSEMBLAGES (FOURTH-ROOT TRANSFORMED COUNT DATA), AND ENVIRONMENTAL AND SPATIAL VARIABLES AT DIFFERING BIOGEOGRAPHIC SCALES. THE PERCENTAGE VARIANCE EXPLAINED FOR EACH VARIABLE IS GIVEN (ns = NOT SIGNIFICANT), ALONG WITH THE CUMULATIVE FREQUENCY EXPLAINED FOLLOWING FORWARD SELECTION OF FACTORS (THE SIGNIFICANT FACTORS FROM THIS PROCEDURE ARE LISTED IN DESCENDING AMOUNT OF VARIATION EXPLAINED).

		BIOGEOGRAPHIC PROVINCES		BIOREGIONS		
	NZ	NORTHERN	SOUTHERN	NORTHEASTERN	ABEL	STEWART I
n	247	135	112	81	37	42
Local variables						
Fetch	5.9	5.9	11.8	6.6	9.3	20.0
Status	3.6	ns	3.3	3.5	ns	-
Slope	4.9	4.5	1.8	12.1	5.8	ns
MaxDepth	4.5	8.5	3.7	21.6	ns	5.7
Secchi	7.3	16.4	6.3	31.3	23.4	6.0
Sediment	4.0	8.0	4.6	4.8	12.1	19.7
Cumulative %	**24.0**	**30.6**	**28.7**	**48.2**	**36.7**	**31.1**
Significant factors	All	All	All	All, excl. Slope	Secchi, Fetch, Slope	Fetch. Sediment, MaxDepth
Spatial—Northing and Easting	19.3	20.8	18.7	30.7	31.3	16.8

Secchi explained the greatest variation for the Northeastern and Abel bioregions, while Fetch and Sediment were most important in the Stewart Island bioregion. The proportion of variation explained by environmental variables tended to increase with decreasing spatial scale.

3.2.2 National patterns in dominant mobile macroinvertebrate species

There was large variation in the total number of mobile invertebrates among bioregions (Fig. 7) and also among sites and locations within each bioregion (section 3.4). Total numbers were low ($< 2/m^2$) at Portland, Cook and Chalmers, whereas at Northeastern, Abel and Banks, herbivorous gastropods such as *Trochus viridis*, *Cookia sulcata* and *Turbo smaragdus* were common and total numbers exceeded $8/m^2$ (Figs 7A and 8A).

Evechinus chloroticus was the most commonly recorded mobile macroinvertebrate (Table 5), and was recorded at all locations except Karamea, Flea Bay and Catlins (Figs 7B and 8B). It was also particularly rare at several locations, e.g. Mahia, Kaikoura and Otago Peninsula. The abundance of *E. chloroticus* was generally highest in Northern bioregions (Fig. 7B) and, overall, was positively correlated with the Northing variable ($r = 0.36$). At the national level, Secchi explained the greatest variation (15%) in the abundance of *E. chloroticus* (Table 7) and was positively correlated across all sites ($r = 0.39$). Secchi also explained the greatest variation among sites in the Northeastern bioregion (28.5%), where *E. chloroticus* are rare at sheltered and turbid coastal sites (see section 3.4.1). In contrast, within the Abel bioregion, MaxDepth (23%) was found to be the

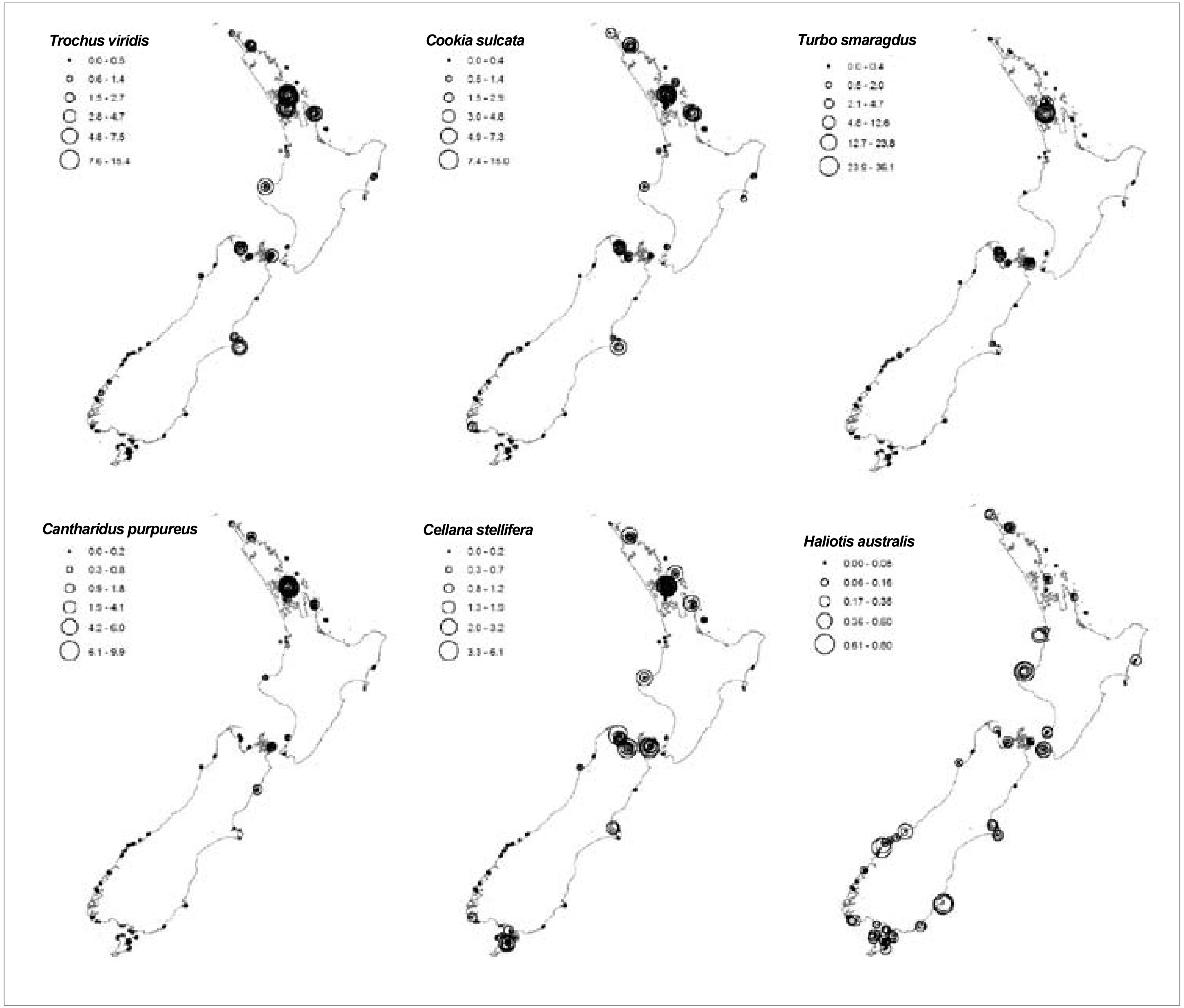
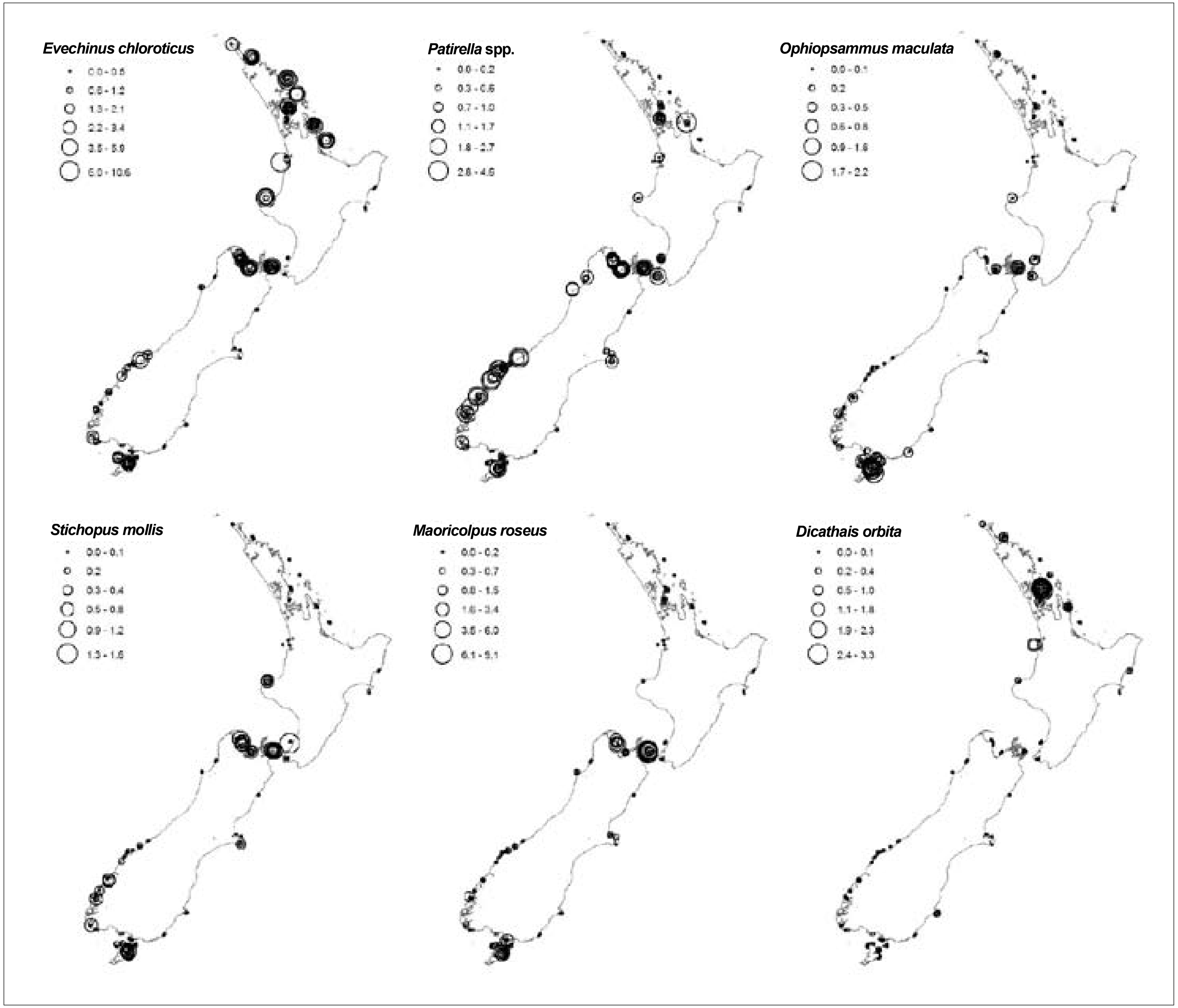


Figure 8A. Mean abundance (per m^2) of dominant mobile macroinvertebrates at all sampling sites: herbivorous gastropods.

Figure 8B. Mean abundance (per m^2) of dominant mobile macroinvertebrates at all sampling sites: echinoderms and other gastropods.



most important variable (Table 7). This was due to a few sites with shallow reefs (< 9 m depth) having high urchin densities. Fetch explained the greatest variation in the abundance of *E. chloroticus* among sites in the Stewart Island bioregion as the highest densities were recorded at sheltered sites in Paterson Inlet. For both Abel and Stewart Island there was no clear gradient in water clarity among sites or locations.

The size distributions of populations of *E. chloroticus* among the locations sampled exhibited some clear biogeographic patterns (Appendix 6). In most Northern bioregions, there were relatively high numbers of juveniles, most urchins were less than 100 mm TD, and the maximum size was c. 125 mm TD. One exception was Portland, where urchins occurred at low numbers and the population structure resembled Southern bioregions, with urchins generally larger than 100 mm TD and juveniles rare. At Open Bay Islands, Preservation Inlet and Paterson Inlet, where *E. chloroticus* was abundant, few individuals with a TD of less than 70 mm were recorded. Overall, *E. chloroticus* reached much greater sizes in Southern locations, with the maximum size recorded being 190 mm TD at Edwards Island (Titi Islands).

Trochus viridis and *C. sulcata* were the most common and abundant herbivorous gastropods nationwide (Table 5). Both species had similar distributions, being most abundant at locations in Northeastern, Abel and Banks bioregions (Fig. 8A). *Turbo smaragdus* was also one of the most abundant gastropods, but this was largely due to high densities at a number of sheltered locations, e.g. Nelson, Long Island and Long Bay. The limpet *Cellana stellifera* was generally most abundant in locations with high urchin abundances such as Northeastern and Abel locations, as well as New Plymouth and Paterson Inlet. The abalone *Haliotis australis* was also relatively common, but found at relatively low numbers throughout the country. A number of echinoderm species such as *Patiriella* spp., *Ophiopsammus maculata* and *Stichopus mollis* were found throughout the country, but tended to be more abundant on shallow reefs in southern regions (Figs 7B and 8B).

TABLE 7. RESULTS OF STEP-WISE MULTIVARIATE REGRESSION OF THE ABUNDANCE OF *Evechinus chloroticus*, AND ENVIRONMENTAL AND SPATIAL VARIABLES, AT DIFFERING BIOGEOGRAPHIC SCALES. THE F-VALUE AND PERCENTAGE VARIANCE EXPLAINED FOR EACH VARIABLE SELECTED FOR THE MODEL IS GIVEN. STATISTICALLY SIGNIFICANT VARIABLES ARE INDICATED BY: * = $P < 0.05$, ** = $P < 0.01$ AND *** = $P < 0.001$). THE R-SQUARED VALUE FOR EACH TEST IS ALSO GIVEN.

NZ			NORTHEASTERN			ABEL			STEWART I		
VARIABLE	F	%	VARIABLE	F	%	VARIABLE	F	%	VARIABLE	F	%
Local											
(R^2 = 0.17)			(R^2 = 0.33)			(R^2 = 0.33)			(R^2 = 0.40)		
Secchi	43.1***	15.0	Secchi	33.0***	28.5	MaxDepth	11.6**	23.0	Fetch	27.0***	40.3
Fetch	10.7**	4.2	Fetch	4.2*	5.0	Secchi	4.9*	9.7			
Spatial—Northing and Easting											
	19.4***	13.7		14.9***	27.7		12.0***	41.4		6.3**	24.3

3.3 BENTHIC COMMUNITY STRUCTURE

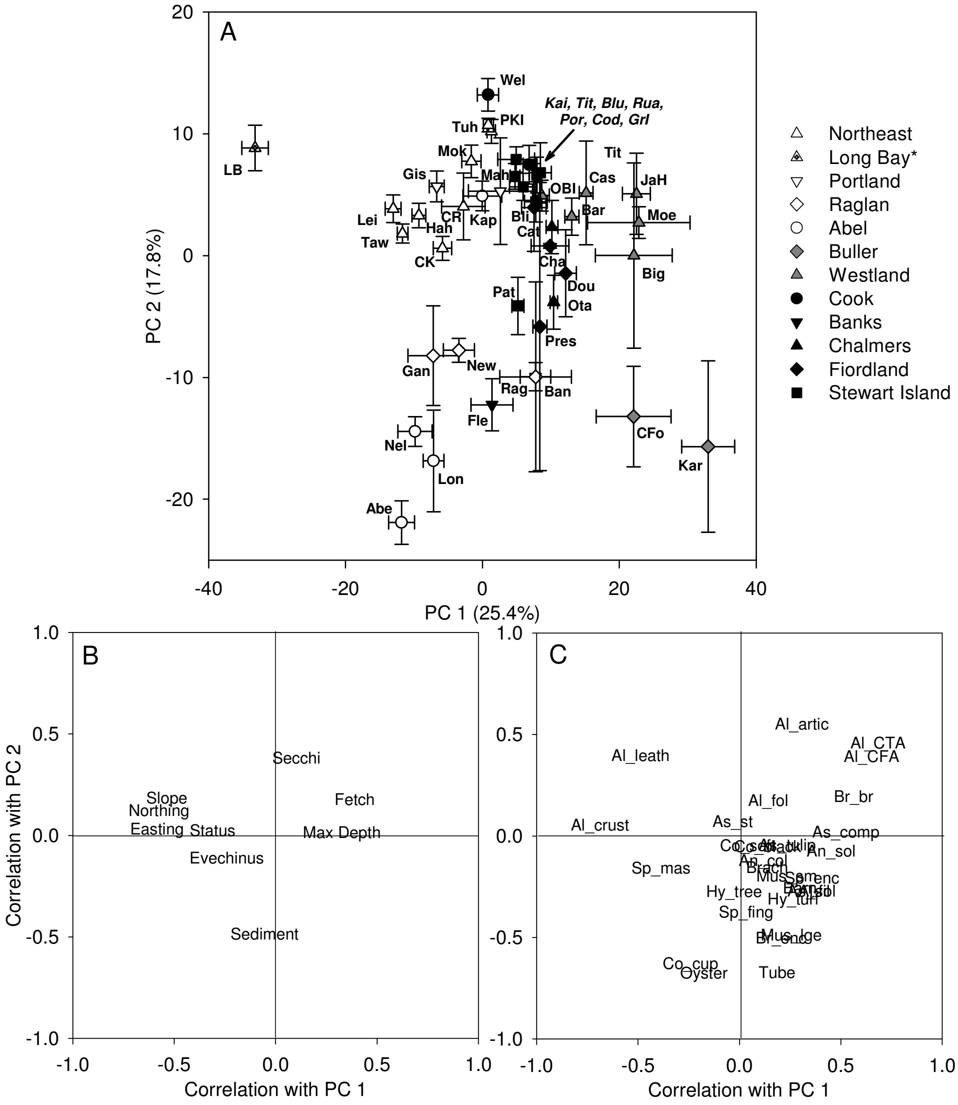
3.3.1 National variation in benthic community structure

There was a general gradient in the structure of benthic communities (biomass of algae and sessile invertebrates combined; Table 8) between Northern and Southern locations along PC1 (Fig. 9A). However, this axis of greatest variation (PC1) also appeared to more strongly reflect a gradient from sheltered Northern locations (Long Bay) to highly exposed West Coast locations at Buller and Westland. This was reflected by the correlation between PC1 and Fetch (Fig. 9B). Benthic community structure changed along this axis from being dominated by crustose and leathery algae to domination by corticated terete and corticated foliose algae, as indicated by the correlations between these groups and PC1 (Fig. 9C). PC2 was correlated with Secchi and Sediment. Therefore, it appears that PC2 reflects a gradient in community structure from turbid sites (bottom portion of ordination, Fig. 9A), where invertebrates (e.g. encrusting bryozoans, solitary ascidians, serpulid tube worms, mussels, oysters and cup corals) were

TABLE 8. CONTRIBUTION OF 29 STRUCTURAL GROUPS TO TOTAL BIOMASS (AFDW) OF BENTHIC COMMUNITIES AND THE PERCENTAGE OF ALL SITES AT WHICH EACH GROUP OCCURRED (% OCC.)

PHYLA	STRUCTURAL GROUP	MEAN (g/m^2)	% TOTAL	% OCC. (SITES)
Algae	Leathery macrophytes	286.45	66.91	95.55
Algae	Corticated terete algae	27.86	6.51	93.52
Algae	Corticated foliose algae	19.75	4.61	98.79
Porifera	Massive sponge	18.04	4.21	74.90
Porifera	Encrusting sponge	16.52	3.86	94.33
Algae	Crustose algae	14.64	3.42	100.00
Mollusca	Large mussels	12.33	2.88	23.89
Algae	Articulated algae	12.10	2.83	90.69
Ascidian	Solitary ascidian	5.67	1.32	88.66
Bryozoan	Branched bryozoan	2.30	0.54	54.66
Ascidian	Compound ascidian	1.94	0.45	83.81
Algae	Filamentous	1.68	0.39	88.66
Porifera	Finger sponge	1.59	0.37	22.67
Mollusca	Small mussels	1.17	0.27	2.02
Annellida	Serpulid tubeworms	1.12	0.26	21.86
Ascidian	Sea tulip	1.08	0.25	21.86
Algae	Foliose algae	0.92	0.21	38.06
Coelenterate	Colonial anemone	0.85	0.20	53.44
Hydrozoa	Hydroid turf	0.51	0.12	46.56
Crustacea	Barnacles	0.40	0.09	17.81
Ascidian	Stalked ascidian	0.35	0.08	40.08
Coelenterate	Cup coral	0.27	0.06	19.84
Mollusca	Oyster	0.20	0.05	16.60
Coelenterate	Large solitary anemone	0.18	0.04	32.79
Bryozoan	Encrusting bryozoan	0.17	0.04	41.30
Coelenterate	Black coral	0.01	0.00	2.02
Coelenterate	Soft coral	0.01	0.00	3.24
Hydrozoa	Hydroid tree	0.01	0.00	3.24
Brachiopod	Brachiopod	0.01	0.00	4.05

Figure 9. Structural patterns in reef communities among all locations from principal coordinates analysis based on fourth-root transformed AFDW of 29 algal and invertebrate structural groups (A) (see Fig. 1 for location codes and Table 2 for structural group codes). Centroids are plotted for each location; standard error bars indicate the variation among sites at each location. Shaded symbols indicate bioregions in the Southern Province and open symbols indicate bioregions in the Northern Province. Bi-plots give correlations between principal coordinates axes and environmental variables (B) and structural group variables (C). * Long Bay is distinguished from other Northeastern locations as it was not included in biogeographic analyses (Shears et al. in press).



more dominant, to more oceanic locations (top portion of ordination) with clearer water that are dominated by macroalgal groups.

The amount of variation explained by environmental variables (Table 9) tended to increase with decreasing spatial scale, explaining the most variation at the bioregional level (predominantly Secchi, Fetch and Evechinus). At the national level, Slope explained the greatest variation (8%), but at the provincial level Secchi (Northern: 12%) and Fetch (Southern 8%) explained the most variaiton. The abundance of *Evechinus chloroticus* was significantly related to benthic community structure at all spatial scales, accounting for only a small proportion of the variation at the national scale (3%), but 9–18% of the variation at the bioregional scale.

3.3.2 National patterns in dominant structural groups

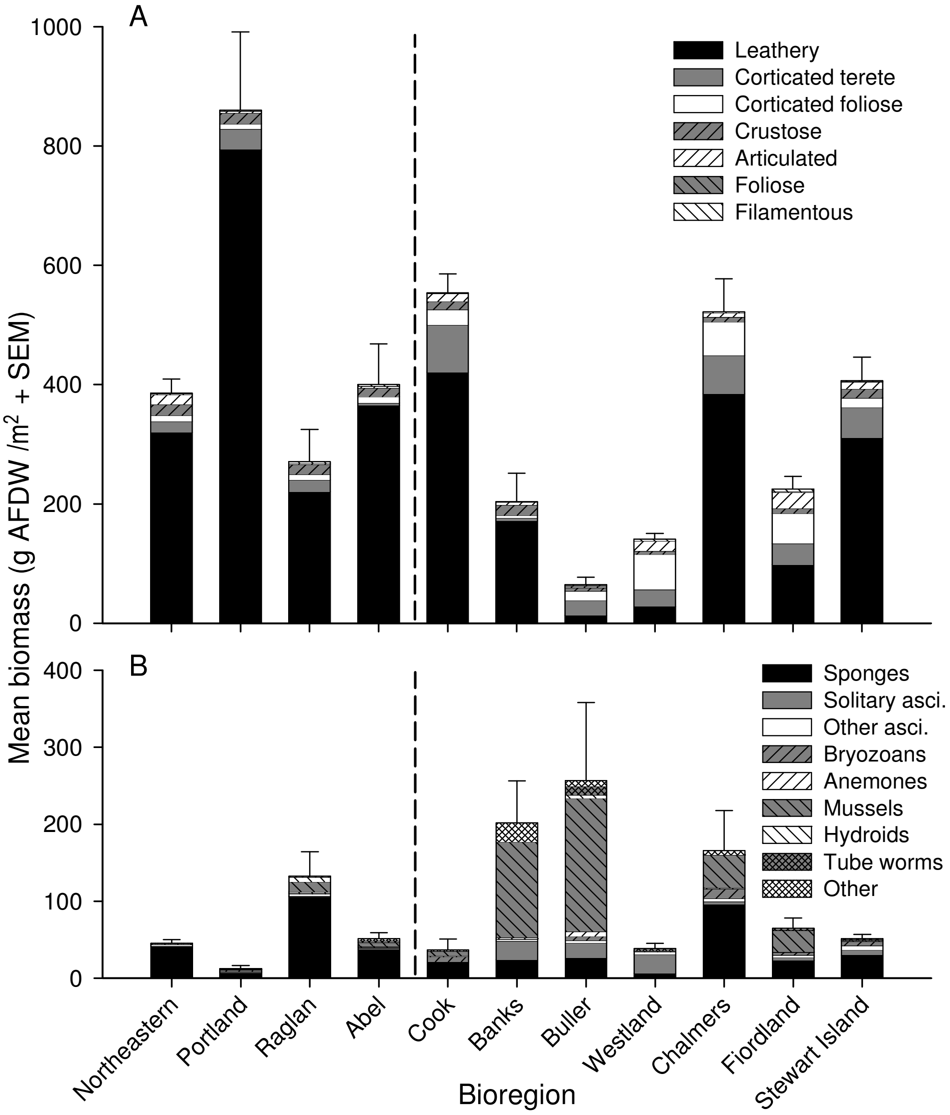
Leathery macrophytes made up 67% of the total biomass across all sites (Table 8) and dominated at all bioregions except Buller and Westland on the West Coast (Figs 10 and 11). In general, the biomass of leathery macrophytes was low at most west coast sites compared with sites on the east coast (Fig. 11A). The contribution of other structural groups was relatively small in Northern bioregions, with sponges, crustose algae and corticated terete algae being the largest contributors after leathery macrophytes. Overall, Southern bioregions tended to have a lower biomass of leathery macrophytes and a larger contribution from other groups such as corticated algae (Figs 10A and 11A) as well as mussels, solitary ascidians, other ascidians, sponges, and bryozoans (Fig. 10B). For the Buller bioregion, total biomass of algal groups was low and the structure of benthic communities was dominated by encrusting invertebrates (mussels, ascidians and sponges).

Among the encrusting invertebrate groups, sponges were the largest contributor to total biomass (9%; Table 8), particularly at Raglan and Chalmers locations (Figs 10B and 11B). Mussels were also a dominant structural component of benthic communities at Banks and Buller. Large mussels such as *Perna canaliculus* and *Mytilus* spp. were important at several locations (Raglan, Karamea, Banks Peninsula North, and those in Fiordland), whereas small mussels (*Xenostrobus pulex*) were an important component of the benthic communities at Cape Foulwind and Raglan. Solitary ascidians accounted for only 1% of the total biomass but were a major component of the benthic community at highly turbid locations where leathery macrophytes were reduced or restricted to shallow water, e.g. Buller, Westland and Banks locations (Figs 10B and 11B). Branching bryozoans were typically more abundant at Southern locations, whereas encrusting bryozoans were locally abundant at Cape Foulwind, Karamea, Abel Tasman, Nelson and New Plymouth. Cup corals (predominantly *Culicia rubeola*) were also locally abundant at Long Island and Abel Tasman (data not presented).

TABLE 9. RESULTS OF NON-PARAMETRIC MULTIVARIATE REGRESSION OF BENTHIC COMMUNITY STRUCTURE DATA (FOURTH-ROOT TRANSFORMED BIOMASS OF 29 STRUCTURAL GROUPS), AND ENVIRONMENTAL AND SPATIAL VARIABLES AT DIFFERING BIOGEOGRAPHIC SCALES. THE PERCENTAGE VARIANCE EXPLAINED BY EACH VARIABLE IS GIVEN (ns = NOT SIGNIFICANT), ALONG WITH CUMULATIVE FREQUENCY EXPLAINED FOLLOWING FORWARD SELECTION OF FACTORS (THE SIGNIFICANT FACTORS FROM THIS PROCEDURE ARE LISTED IN DESCENDING ORDER OF VARIATION EXPLAINED).

		BIOGEOGRAPHIC PROVINCES		BIOREGIONS		
	NZ	NORTHERN	SOUTHERN	NORTHEASTERN	ABEL	STEWARTI
n	247	135	112	81	37	42
Local variables						
Fetch	5.5	5.1	7.5	9.8	14.9	14.8
Status	2.9	1.5	5.4	ns	ns	-
Slope	8.3	7.6	3.9	16.0	5.4(0.08)	ns
MaxDepth	4.2	9.4	3.5	29.0	5.8(0.06)	4.9
Secchi	5.2	11.9	6.3	27.8	18.2	5.7
Evechinus	2.7	1.6	2.5	12.2	8.5	17.9
Sediment	5.6	9.1	6.1	5.9	14.6	13.0
Cumulative %	**27.6**	**32.0**	**35.7**	**43.9**	**39.0**	**31.0**
Significant factors	All	All, excl. Status	All	MaxDepth, Secchi, Fetch, Slope	Secchi, Fetch, MaxDepth	Evechinus, Fetch, Secchi
Spatial—Northing and Easting	14.8	21.9	20.3	43.9	34.1	17.5

Figure 10. Mean biomass of benthic structural groups (macroalgal groups, A, and other groups, B) for all bioregions. Dashed line indicates division between the Northern and Southern Provinces.



Other structural groups were locally abundant at specific locations, e.g. black coral at Fiordland locations; sea tulips at Banks Peninsula and Chalmers locations (data not presented).

3.4 BIOREGIONAL PATTERNS IN BENTHIC COMMUNITIES

3.4.1 Northeastern bioregion

There was large variation in algal community structure among sites within and between locations in the Northeastern bioregion (Fig. 12). However, consistent patterns were apparent among sites in relation to the environmental variables which explained 39% of the variation (Table 4). Hierarchical cluster analysis divided Northeastern sites into five groups at the 70% similarity level that broadly corresponded to large-scale differences in wave exposure (Fetch) among sites (Fig. 12A). PC1 was strongly correlated with several environmental variables (Fig. 12B) and reflected a gradient in algal community structure from exposed

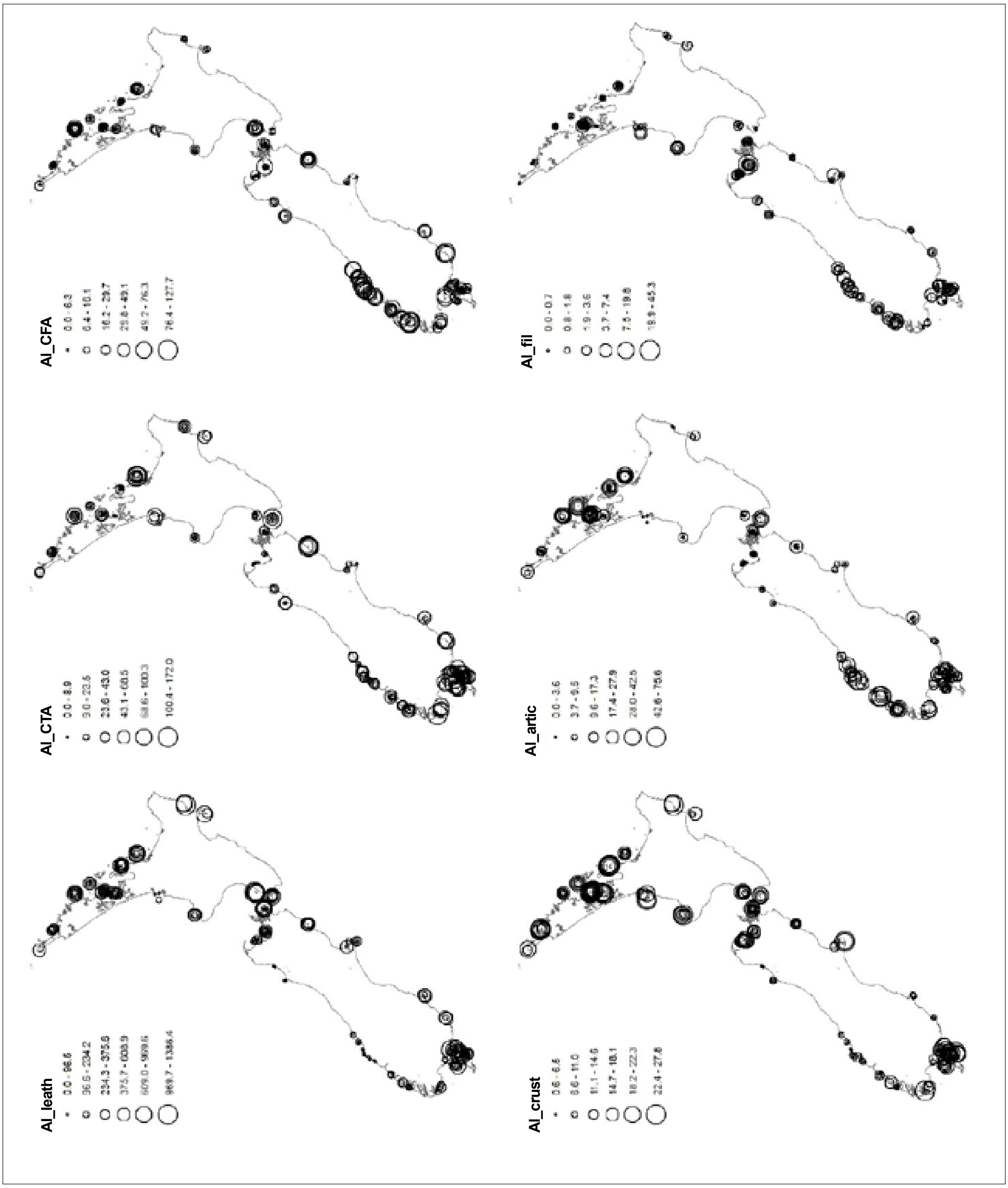
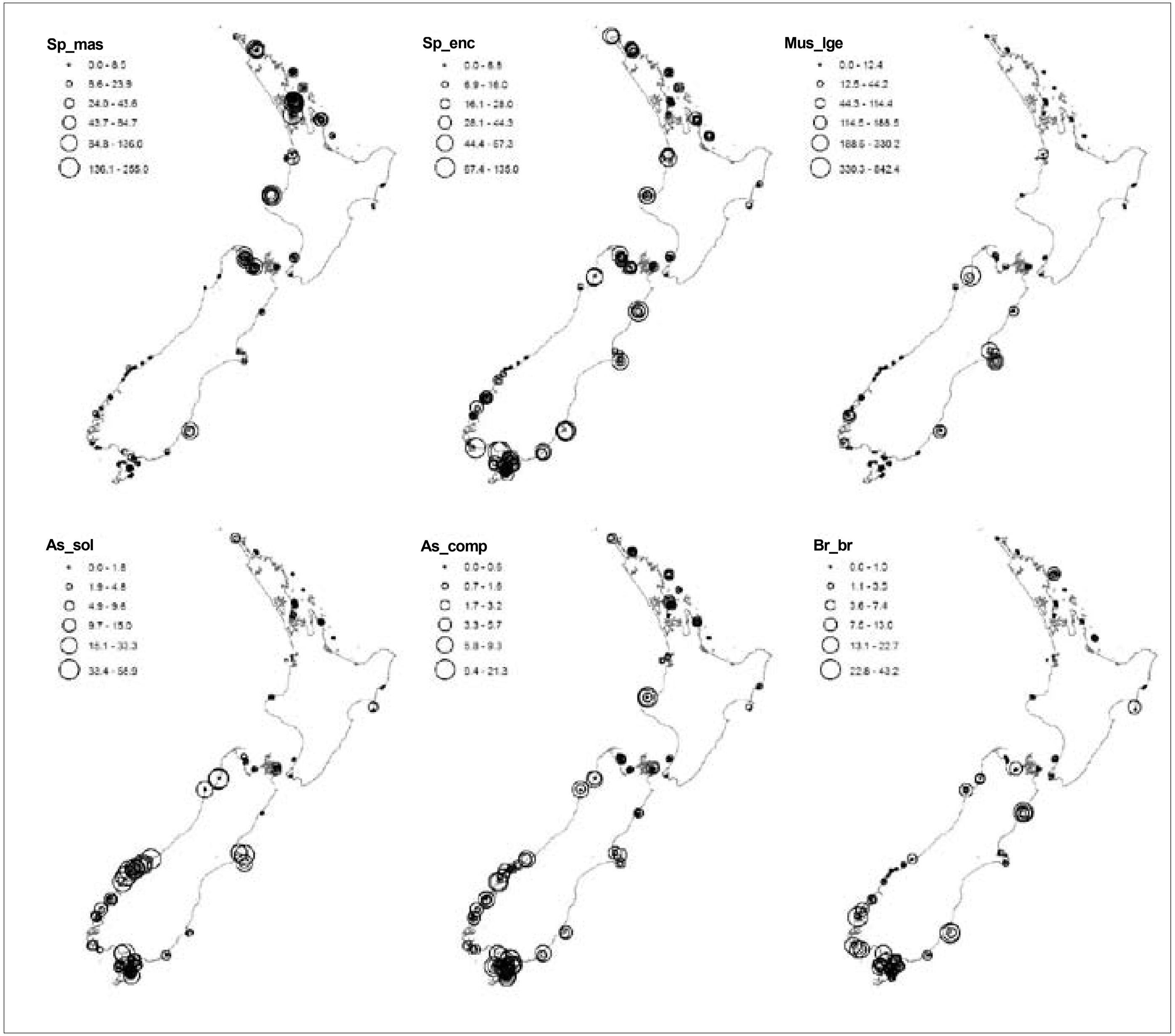


Figure 11A. Biomass of dominant structural groups (g AFDW/m^2) at all sites: algal groups. See Table 2 for structural group codes.

Figure 11B. Biomass of dominant structural groups (g AFDW/m^2) at all sites: sessile invertebrate groups. See Table 2 for structural group codes.



and offshore sites with steeply sloping reefs and clear water to more gradually sloping, sheltered coastal sites with high turbidity and a high percentage cover of sediment (e.g. Long Bay). Evechinus was also negatively correlated with PC1 and tended to be more common at exposed locations. There was a clear gradient in the organisation of algal communities across this large environmental gradient. *Carpophyllum flexuosum* was positively correlated with PC1 and was most abundant at sheltered sites, whereas *Lessonia variegata*, red turfing algae, coralline turf and green algae (e.g. *Ulva* spp.) were negatively correlated and were more characteristic of exposed and/or offshore sites (Fig. 12C). Similar groupings of Northeastern sites in relation to wave exposure were identified and described for each location in Shears & Babcock (2004b). Therefore, overall patterns in reef communities for each exposure group (Fig. 12) are summarised below for all locations combined.

Sheltered group

This group included all Long Bay sites and the most sheltered site from Hahei (Mussel Rock) (Fig. 12A). The shallow stratum (< 2 m) was characterised by high biomasses of *Carpophyllum maschalocarpum* and to a lesser extent *Ecklonia radiata* (Fig. 13A), while the 4–6 m depth range was dominated by *C. flexuosum*. A number of other brown algal species were also common at these sites, e.g. *C. plumosum*, *Cystophora retroflexa*, *Sargassum sinclairii* and *Zonaria* spp.

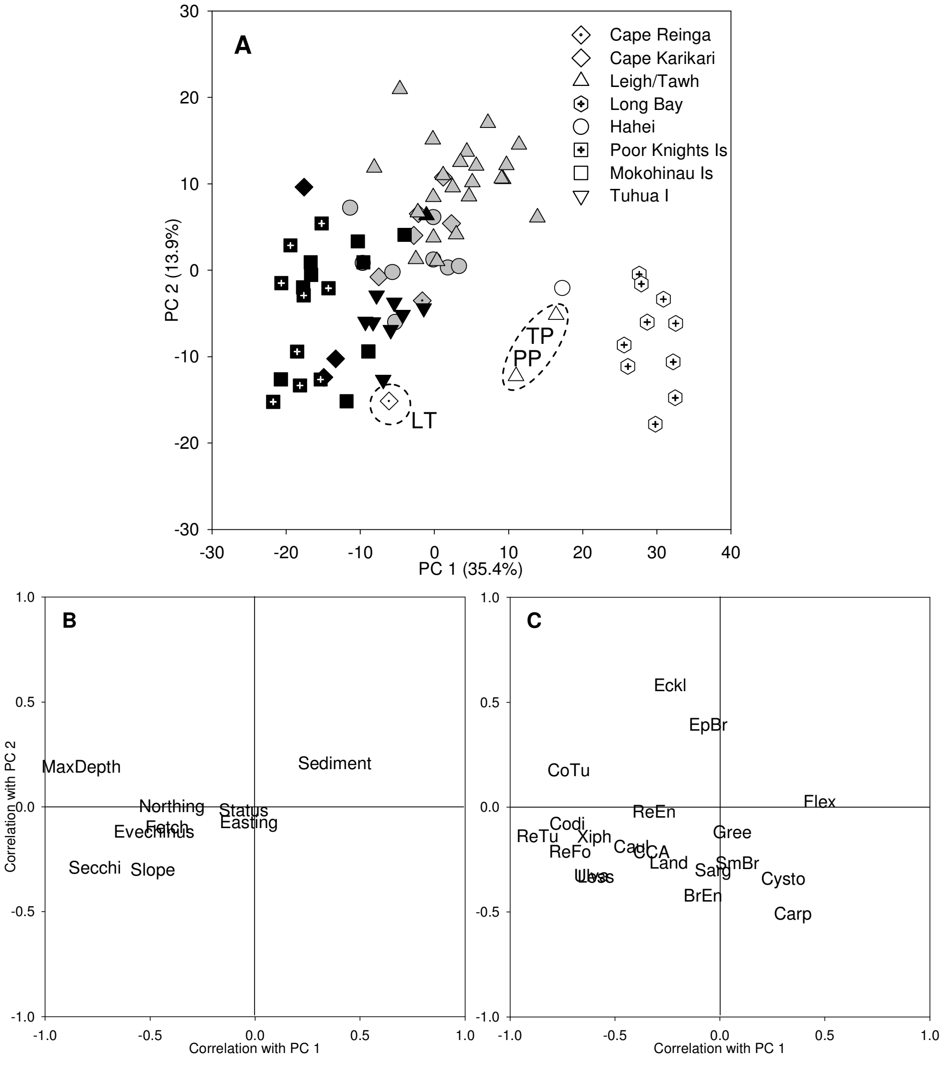


Figure 12. Principal coordinates analysis of sites sampled in the Northeastern bioregion, based on fourth-root transformed biomass of 23 macroalgal groups (A). Bi-plots give correlations between principal coordinates axes and environmental variables (B) and original macroalgal species groups (C) (see Table 1 for macroalgal group codes). Sites shaded according to groupings identified at the 70% similarity level. White = sheltered, grey = moderately exposed, black = exposed-offshore, LT = Lighthouse, PP and TP = P-Point and Ti Point, respectively.

(data not presented). Red foliose and turfing algae were rare across both depths. *Evechinus chloroticus* was rare at all sites, *Turbo smaragdus* occurred at high densities in the < 2 m stratum, and *Trochus viridis* was abundant at 4–6 m (Fig. 13B). Crustose coralline algae ('CCA') were the dominant substratum cover (> 70%), but sediment also covered a considerable proportion of reef (10–20%) (Fig. 13C).

Ti Point and P-Point

These two sites at Leigh and Tawharanui formed their own group at the 70% similarity level (Fig. 12A). Unlike other sites at these locations, the reef at both sites was inundated with sand at c. 5 m of depth. *Carpophyllum maschalocarpum* dominated the shallow stratum (< 2 m), whereas the reef at 4–6 m was relatively devoid of large brown macroalgae and sea urchins were common (Fig. 13A). Moderate numbers of *Turbo smaragdus* were recorded in the shallow stratum, whereas *Trochus viridis* and *Cellana stellifera* were most abundant at 4–6 m (Fig. 13B). Crustose coralline algae were the dominant substratum cover, but sediment covered a considerable proportion of reef at 4–6 m, and turfing and foliose algae were rare (Fig. 13C).

Moderately exposed group

The moderately exposed group included the remaining coastal sites, excluding Sunburn Point, Takini South and Pihoaka Point at Cape Karikari, Cape Rodney at Leigh and Tapotupotu at Cape Reinga, which were grouped in the Exposed-offshore group, as well as the highly exposed Lighthouse site (Cape Reinga), which formed its own group (Fig. 12A). Algal communities at these sites had a bimodal depth distribution with *Evechinus chloroticus* abundant in the 4–6 m depth stratum and peaks in algal biomass in the shallow (< 2 m) and deeper (7–9 m and 10–12 m) strata (Fig. 13A). *Carpophyllum maschalocarpum* dominated the < 2 m stratum, although *C. plumosum*, *Ecklonia radiata*, coralline turf, red turfing and red foliose algae were also abundant in the shallow stratum at some sites. *Carpophyllum angustifolium* and *Lessonia variegata* were common components of this shallow stratum at some of the more exposed sites in this group; however, *C. angustifolium* was not recorded at Cape Karikari or Cape Reinga. At some sites (e.g. sites in the following reserves: Cape Rodney-Okakari Point Marine Reserve, Tawharanui Marine Park, Te Whanagnui-a-Hei (Cathedral Cove) Marine Reserve), the 4–6 m depth stratum was dominated by a mixture of *E. radiata*, *C. maschalocarpum* and *C. flexuosum*. At Koware South (Cape Karikari), *C. flexuosum* (sheltered morphology) dominated the 4–6 m stratum. For the remaining sites, *Evechinus chloroticus* was common and macroalgal biomass reduced at this depth. *Evechinus chloroticus* was rare in the deeper strata (7–9 m, 10–12 m) across all sites in this group and forests of *Ecklonia radiata* dominated. The understorey was dominated by crustose coralline algae, coralline turf, and to a lesser extent sponges, ascidians and small brown algae such as *Zonaria* spp. and *Distromium scottsbergii* (Fig. 13C). The percentage cover of sediment tended to increase with depth, on average covering c. 30% of the substratum at 10–12 m. Herbivorous gastropods occurred at relatively high densities at sites within this group (Fig. 13B). *Cookia sulcata* was the most abundant in the 0–2 m and 4–6 m strata, whereas *Trochus viridis* and *Cantharidus purpureus* were most abundant in the deeper strata and associated with *E. radiata*. *Cellana stellifera* was most abundant at 4–6 m and associated with *Evechinus chloroticus*, whereas the predatory gastropod *Dicathais orbita* occurred across all depths.

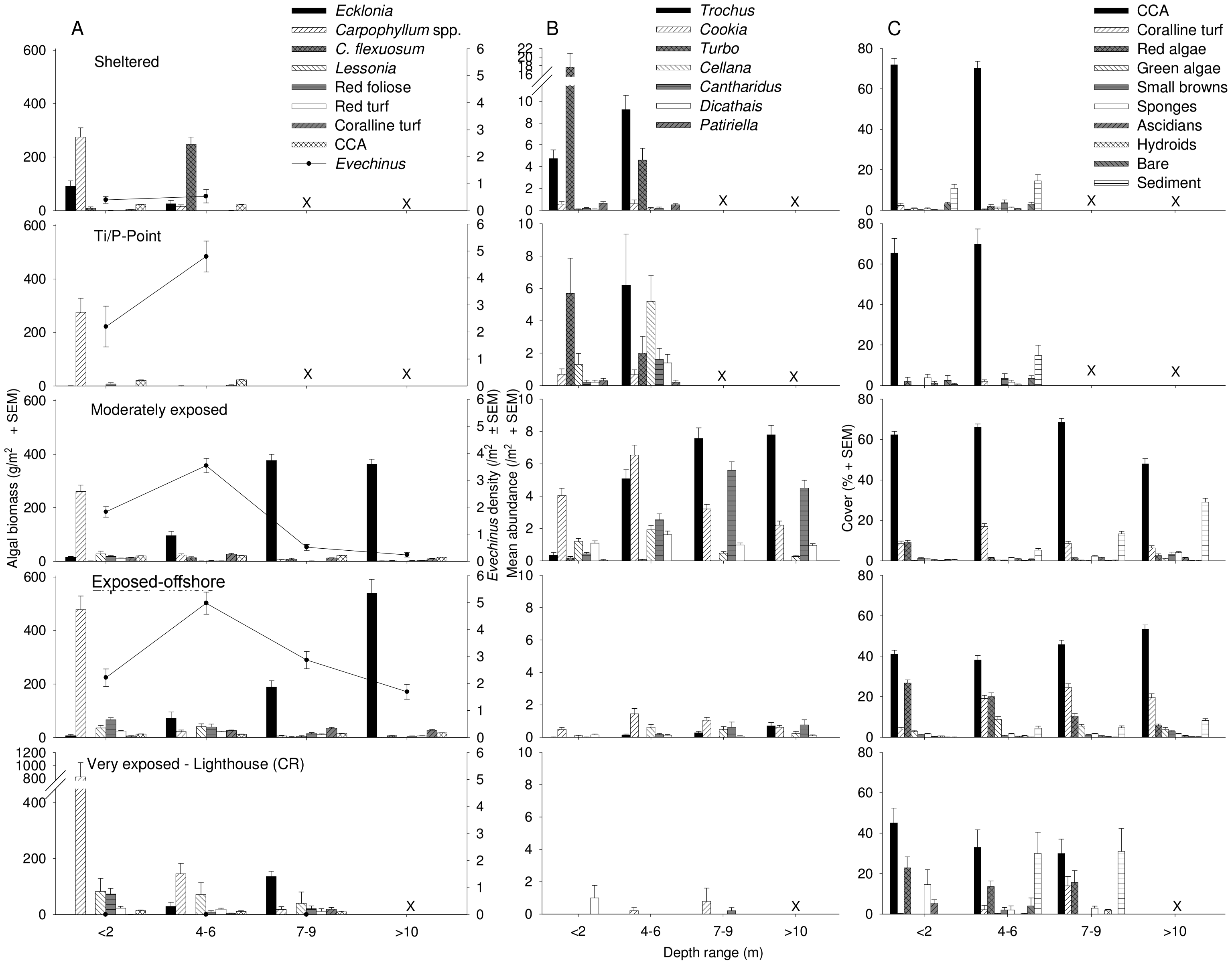


Figure 13. Depth-related patterns in biomass (g AFDW/m^2) of dominant macroalgal groups and density of *Evechinus chloroticus* (A), density of common mobile invertebrates (B) and cover of common encrusting forms (C) for site groups within the Northeastern bioregion. See Shears & Babcock (2004b) for description of groups within each location for the Northeastern bioregion.

Exposed-offshore group

This group included all offshore island sites, and four of the most exposed coastal sites (Sunburn Point, Takini South, Pihoaka Point and Cape Rodney) (Fig. 12A). Algal community structure at sites in the exposed-offshore group also had a bimodal depth distribution, although sea urchins were abundant to depths of c. 8 m and the biomass of *Ecklonia radiata* was generally reduced (Fig. 13A). The shallow stratum (< 2 m) was dominated by *Carpophyllum angustifolium* and/or *C. maschalocarpum* with *Lessonia variegata*, red foliose and red turfing algae also common. The mid-depth ranges (4–6 m and 7–9 m) were characterised by mixed large brown algae (*L. variegata*, *C. maschalocarpum* and *E. radiata*) interspersed with sea urchins, and patches of coralline turf, red turf, red foliose algae and green algae, mainly *Ulva* spp. and *Caulerpa flexilis*. *Ecklonia radiata* dominated the 10–12 m stratum at most sites in this group, although at some sites sea urchins were abundant and macroalgal biomass reduced to depths of c. 12 m. Crustose coralline algae were the dominant cover at all depths, however, coralline turf, red foliose algae and green algae covered a considerable proportion of the reef at all depths (Fig. 13C). Herbivorous gastropods occurred in only low numbers (Fig. 13B), with *Cookia sulcata*, *Trochus viridis* and *Cellana stellifera* being the most common. The sea urchin *Centrostephanus rodgersii* and herbivorous gastropod *Modelia granosa* were also common in the deeper strata (7–9 m and 10–12 m) at some sites (data not presented).

Very exposed: Lighthouse (Cape Reinga)

The organisation of algal communities at this site was considerably different to that of the other Northeastern bioregion sites. Lighthouse was the most exposed Northeastern site (based on fetch estimates), but the reef was relatively gradually sloping and inundated by sand at c. 9 m. *Evechinus chloroticus* was rare and restricted to crevices at all depths, and algal biomass tended to decline with depth (Fig. 13A). *Carpophyllum maschalocarpum* dominated the immediate subtidal, whereas at greater depths mixed stands of large brown algae (e.g. *C. maschalocarpum*, *Lessonia variegata*, *Ecklonia radiata*, *C. plumosum*, *Landsburgia quercifolia*) and patches of red foliose algae (e.g. *Osmundaria colensoi*, *Pterocladia lucida*) occurred. All gastropod species were rare (Fig. 13B). Crustose coralline algae were the dominant cover at shallow depths but there was a high percentage cover of sediment (mainly coarse sand) in the deepest strata (Fig. 13C).

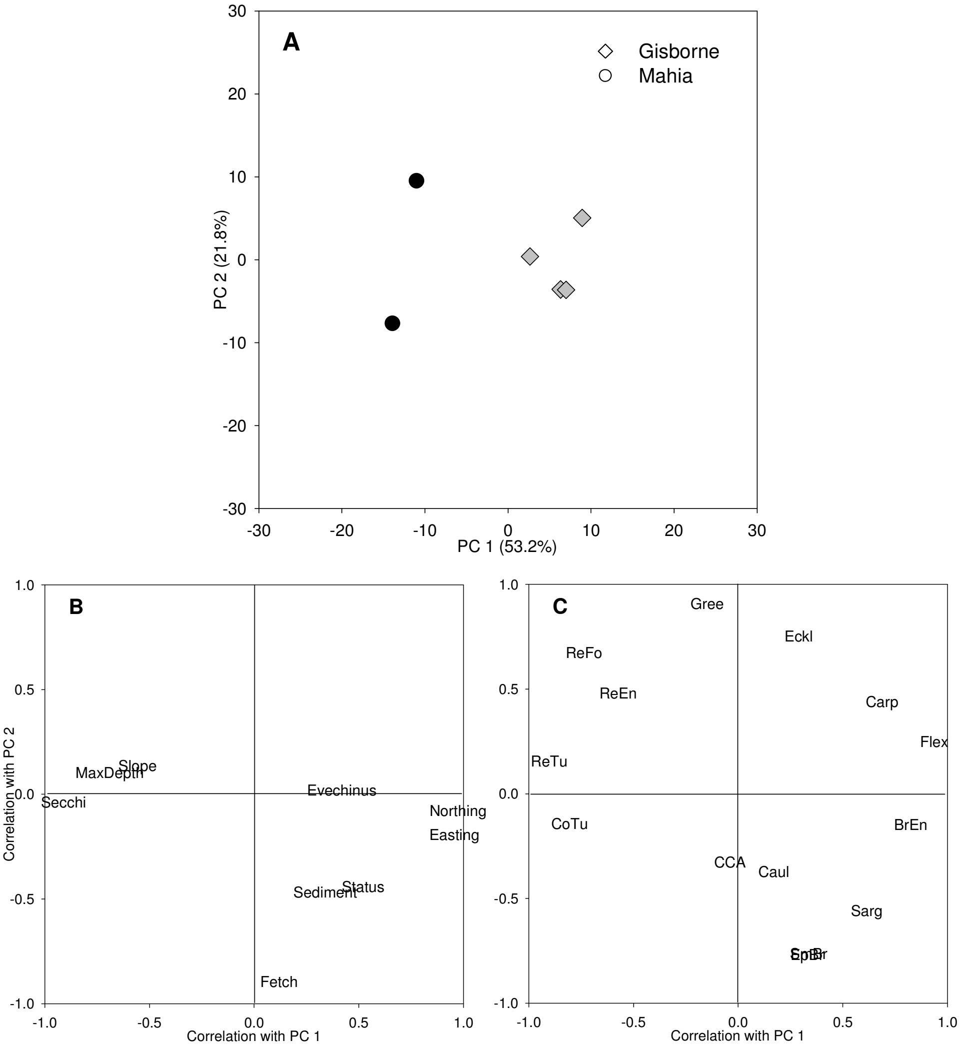
3.4.2 Portland bioregion

Sites from Gisborne and Mahia were clustered among Northeastern localities for all datasets (Figs 2, 6 and 9), and their algal communities were typically dominated by the same few species (*Ecklonia radiata*, *Carpophyllum maschalocarpum*, *C. flexuosum*). Algal community structure was relatively similar between sites from Gisborne and Mahia (Fig. 14), with sites from the two locations being separated at only the 77% similarity level. The correlation between environmental variables and principal coordinates axes (Fig. 14B) gives some indication of factors that may explain the differences between these locations. Sites from Gisborne and Mahia were separated along PC1 (Fig. 14A), which was strongly correlated with Secchi, MaxDepth and Slope (Fig. 14B). Gisborne sites were more turbid, had shallower, more gradually sloping reefs, and a higher biomass of *C. flexuosum*

(Figs 14C and 15A). In contrast, Mahia had clearer water and a greater biomass of coralline turf, red turf and red foliose algae (Figs 14C and 15C). All the sites sampled in this bioregion were highly exposed compared to most Northeastern locations, with similar wave exposure estimates to the Cape Reinga sites. Fetch was negatively correlated with PC2, and the biomass of *E. radiata* was positively correlated with it, with the most wave-exposed sites (Portland Island, Pouawa Reef North and Pouawa Reef South) having reduced biomass of *E. radiata*.

Algal biomass declined with depth at Gisborne and Mahia, and *Evechinus chloroticus* was rare at all depths (Fig. 15A). *Carpophyllum maschalocarpum* dominated shallow depths down to c. 6 m at Gisborne, and to c. 9 m at the more exposed Mahia sites. *Ecklonia radiata* dominated the deepest stratum at Mahia, but was mixed with *C. flexuosum* and the green algae *Caulerpa articulata* at Gisborne sites. *Landsburgia quercifolia*, *Lessonia variegata* and *Cystophora* spp. were not recorded at any of the sampling sites in this region. *Durvillaea antarctica* was common in the intertidal at both Mahia and Gisborne and in some cases small plants did extend into the shallow subtidal. The small brown algal species *Zonaria* spp. and *Carpomitra costata* were common at Gisborne, whereas *Halopteris* spp. were also common at Mahia (Appendix 5: Table A5.1). Several red foliose algal species were found in both areas, but were more common at Mahia, e.g. *Osmundaria colensoi*, *Pterocladia*

Figure 14. Principal coordinates analysis of sites sampled in the Portland bioregion, based on fourth-root transformed biomass of 23 macroalgal groups (A). Bi-plots give correlations between principal coordinates axes and environmental variables (B) and original macroalgal species groups (C) (see Table 1 for macroalgal group codes). Sites shaded according to grouping at 77% similarity level.



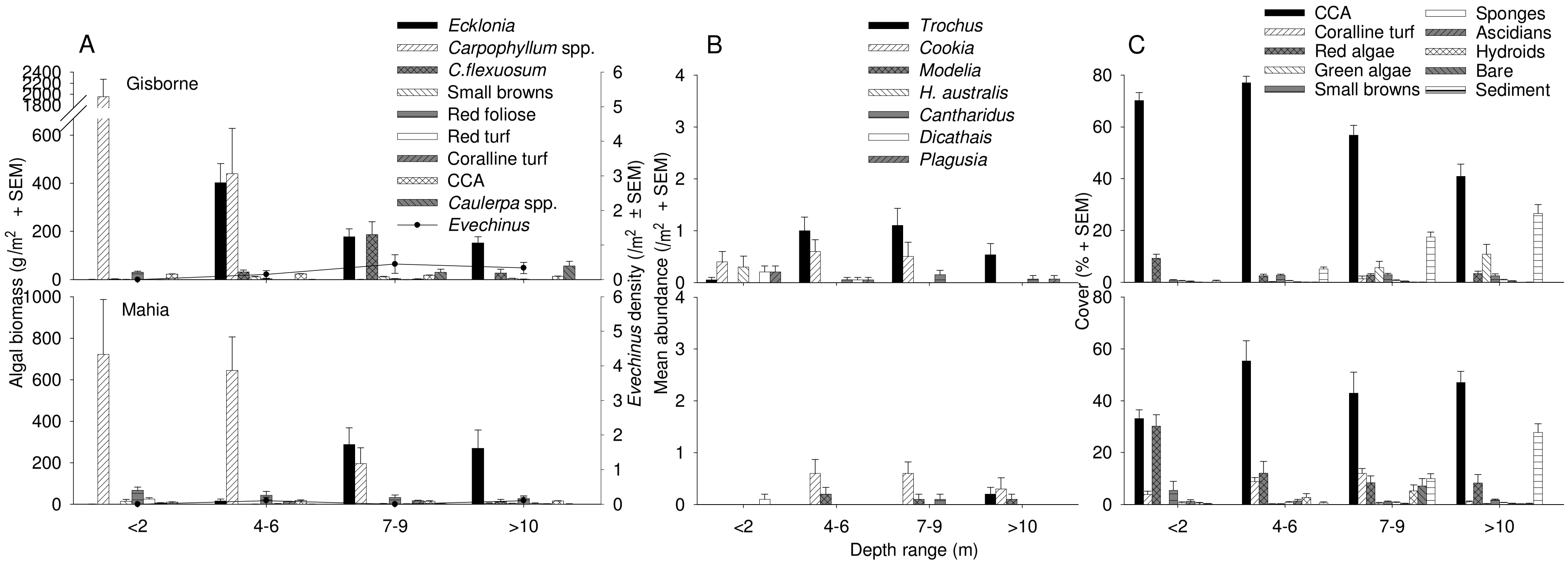


Figure 15. Depth-related patterns in biomass (g AFDW/m^2) of dominant macroalgal groups and density of *Evechinus chloroticus* (A), density of common mobile invertebrates (B) and cover of common encrusting forms (C) for site groups within the Portland bioregion.

lucida and *Plocamium* spp. The substratum was dominated by crustose coralline algae at both locations and the percentage cover of sediment increased with depth (Fig. 15C). Few mobile macroinvertebrates were recorded at both locations (Fig. 15B), with only low numbers of *Haliotis australis*, *Cantharidus purpureus*, *Cookia sulcata*, *Trochus viridis* and *Modelia granosa* being present. *Haliotis iris* was not recorded at the sites surveyed.

3.4.3 Raglan bioregion

Algal communities at all Raglan, Gannet Rock and New Plymouth sites were characterised by a shallow band of *Carpophyllum maschalocarpum* and a general lack of deeper macroalgal forests. These sites were divided into three groups at the 65% similarity level: Raglan sites, offshore island sites (including both Gannet Rock sites and one site from New Plymouth (Seal East)), and the remaining New Plymouth sites (Fig. 16A). These groupings generally reflected the large-scale differences in environmental conditions among the three locations. Raglan sites were located on the mainland coast, had shallow reefs (maximum depth of c. 6 m) that were highly exposed and were turbid, whereas Gannet Rock is located c. 28 km offshore, has steep, sloping reefs and is bathed in clear oceanic water. New Plymouth sites were somewhat intermediate along this onshore–offshore gradient, being located on

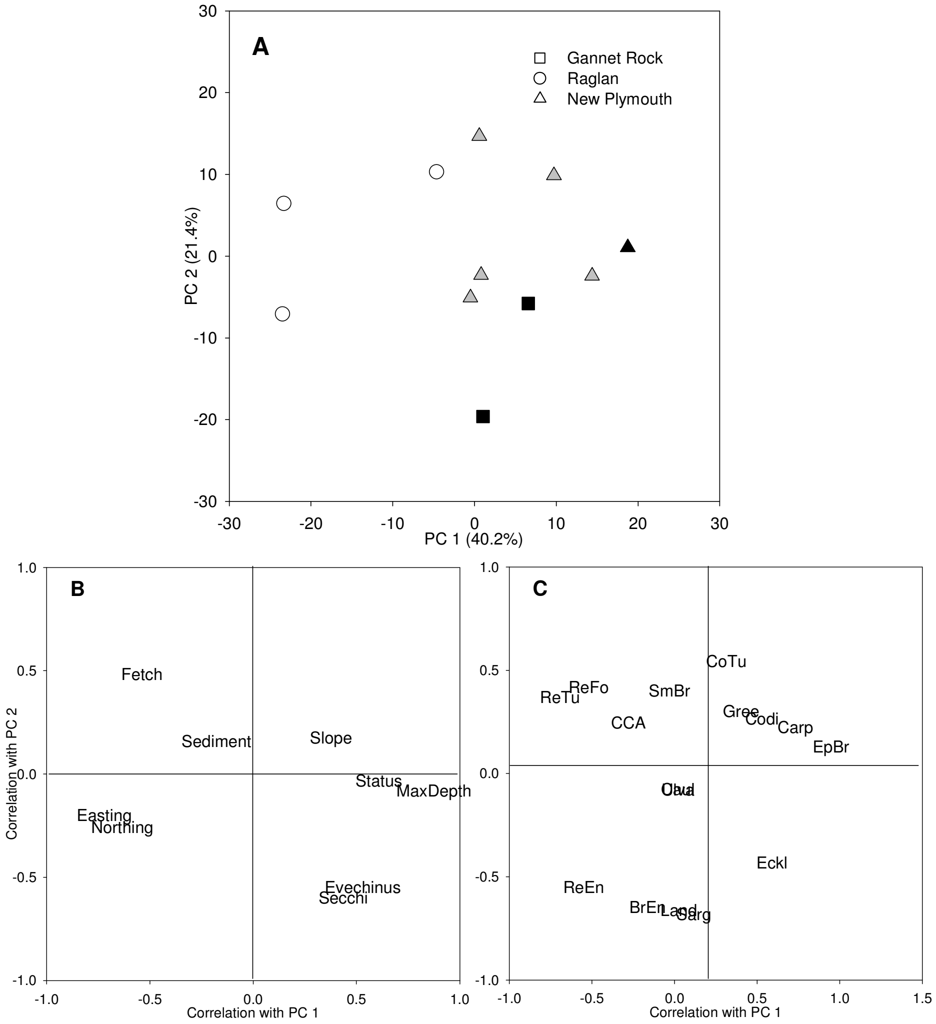


Figure 16. Principal coordinates analysis of sites sampled in the Raglan bioregion, based on fourth-root transformed biomass of 23 macroalgal groups (A). Bi-plots give correlations between principal coordinates axes and environmental variables (B) and original macroalgal species groups (C) (see Table 1 for macroalgal group codes). Sites shaded according to groupings identified at the 65% similarity level.

rockstacks located 1–2 km offshore. The associated gradient in algal community structure was reflected by strong correlations between Fetch, Secchi and MaxDepth, and PC1 (Fig. 16B). Algal species variables that were strongly correlated with PC1 include red turf and red foliose algae, which dominated Raglan sites, and *Carpophyllum maschalocarpum* and ephemeral brown algae (e.g. *Glossophora kunthii* and *Dictyota* spp.), which were more common at New Plymouth sites (Fig. 16C). The abundance of *Evechinus chloroticus* was low at coastal sites and high at offshore sites. PC2 also reflected a gradient from coastal (Raglan) to offshore locations (Gannet Rock). *Ecklonia radiata*, *Landsburgia quercifolia* and *Sargassum sinclairii* were more common at Gannet Rock (Appendix 5) and negatively correlated with PC2.

Raglan

The shallow reefs at Raglan were relatively devoid of large brown algae except for small amounts of *Carpophyllum maschalocarpum* interspersed with red foliose algae (*Pterocladia lucida*, *Osmundaria colensoi* and *Melanthalia abscissa*) in the shallow stratum (Fig. 17A). *Zonaria* spp. and *Endarachne binghamiae* were also common (Appendix 5). At 4–6 m crustose coralline, red foliose and red turfing algae dominated and there was a relatively high percentage cover of sponges, bryozoans, mussels (*Xenostrobus pulex*, *Perna canaliculus*), bare rock and sediment (Fig. 17C). The red algal species *Gymnogongrus humilis* and *Lophurella hookeriana* were also present. Mobile macroinvertebrates such as *Evechinus chloroticus* and *Haliotis iris* occurred in low numbers, but the starfish *Stichaster australis* was relatively abundant (Fig. 17B).

Gannet Rock

The two sites sampled at Gannet Rock were located on the eastern side and somewhat protected from large breaking southwesterly swells. *Evechinus chloroticus* was extremely abundant at both Gannet Rock sites (Fig. 17A), and occurred to depths greater than 25 m. *Carpophyllum maschalocarpum* was restricted to depths less than 4 m; crustose coralline algae dominated below this (Fig. 17A, C). Low numbers of *Landsburgia quercifolia* (not presented, Appendix 5) and *Ecklonia radiata* occurred amongst the *C. maschalocarpum*, along with *Osmundaria colensoi*, *Pterocladia lucida*, *Pterocladiella capillacea* and *Melanthalia abscissa*. On the exposed side of Gannet Rock, *C. maschalocarpum* and *Landsburgia quercifolia* extended to depths of c. 9 m before giving way to urchin barrens (NS, pers. obs.). *Cookia sulcata* and *Dicathais orbita* were common at all depths (Fig. 17B).

New Plymouth

The shallow band of *Carpophyllum maschalocarpum* extended to depths of 3–4 m, beyond which large brown algae were rare (Fig. 17A). Sea urchins were abundant at 4–6 m, and declined with depth. Crustose coralline algae were the dominant substratum cover but also declined with depth (Fig. 17C). At depths greater than 5 m there was a relatively high percentage cover of sediment, turfing algae, sponges, bryozoans and ascidians. The small cup coral *Culicia rubeola* was also common (c. 2% cover per m^2) at 7–12 m. The Seal East site was grouped separately (with Gannet Rock sites), the main differences being the occurrence of low numbers of small *Ecklonia radiata* in deeper areas (> 11 m) and the high

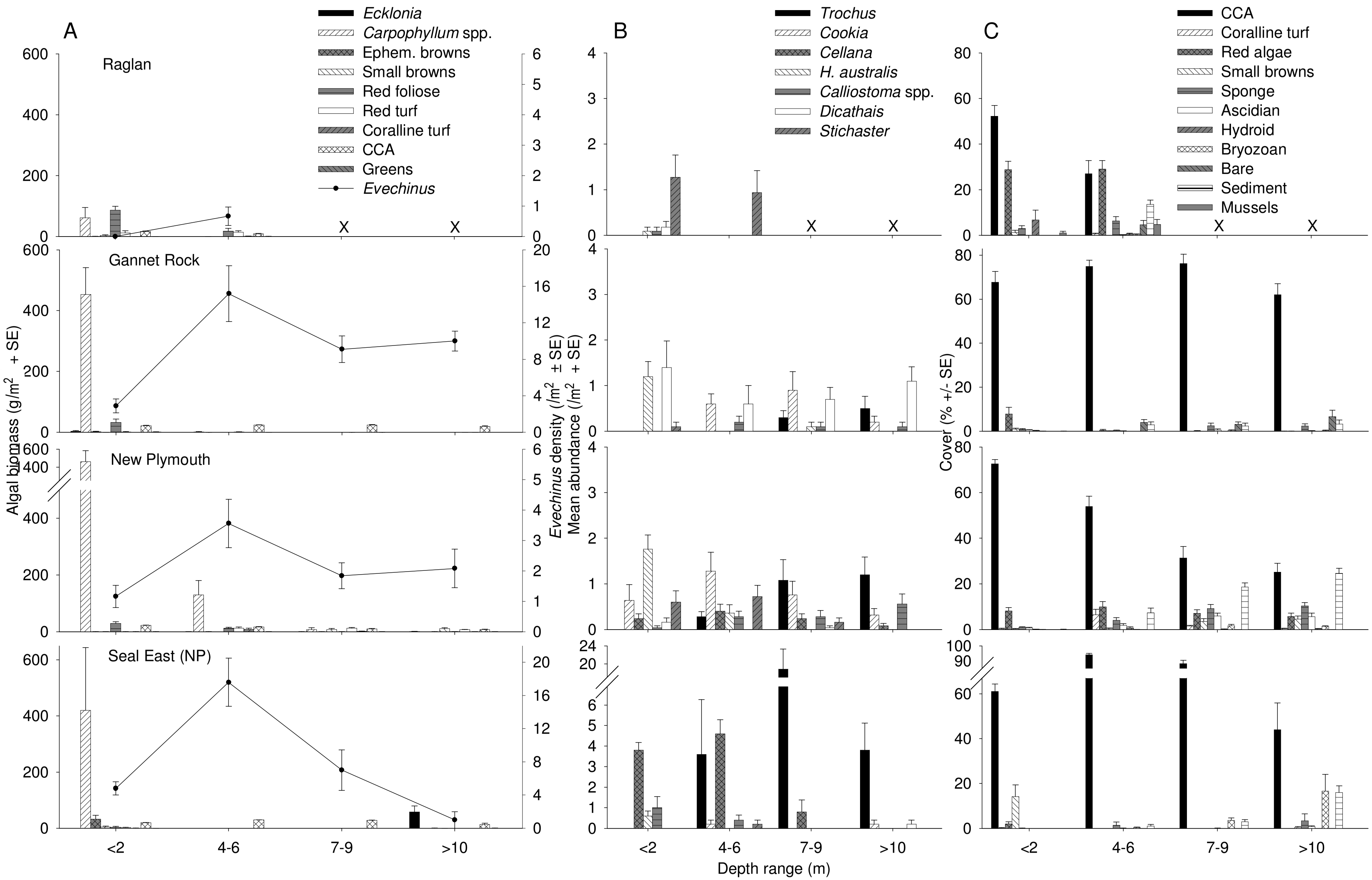


Figure 17. Depth-related patterns in biomass (g AFDW/m^2) of dominant macroalgal groups and density of *Evechinus chloroticus* (A), density of common mobile invertebrates (B) and cover of common encrusting forms (C) for site groups within the Raglan bioregion.

cover of crustose coralline algae at all depths. Seal East also had higher densities of *Evechinus chloroticus*, *Trochus viridis* and *Cellana stellifera* (Fig. 17B). Whereas the algal community structure analysis did not separate out the three offshore sites at New Plymouth (Seal East, Seal West, Saddleback SW), these sites had higher densities of *E. chloroticus*, higher cover of crustose coralline algae and a lower cover of sediment compared to inshore sites which were dominated by turfing algae, encrusting invertebrates and sediment.

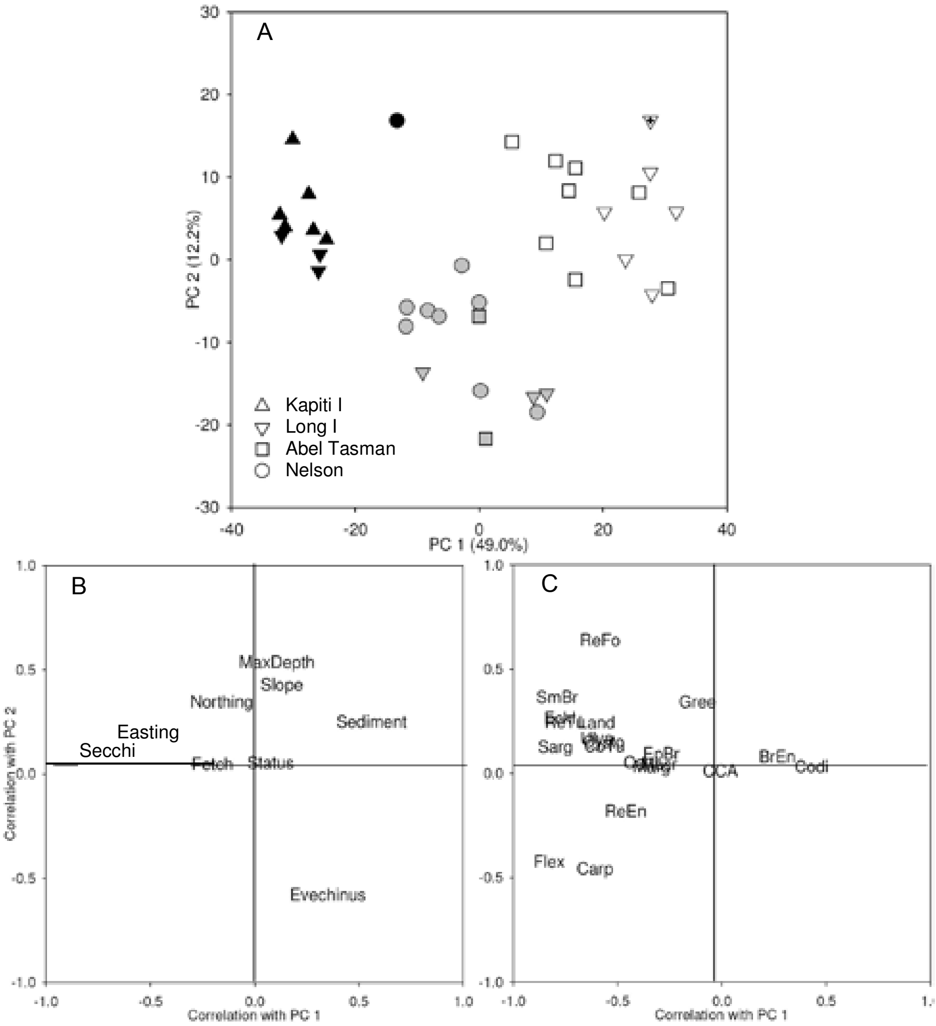
3.4.4 Abel bioregion

There was large variation in algal community structure among the locations within this bioregion at the national level (Fig. 2), with Long Island, Nelson and Abel Tasman being clustered most closely to Raglan locations, and Kapiti being more like Northeastern and Portland locations. Site-level cluster analysis based on algal community structure divided Abel sites into four groups at the 60% similarity level that broadly reflected an inshore–offshore gradient along PC1 (Fig. 18). These groups were subjectively termed 'exposed-offshore', 'moderately exposed', 'sheltered' and 'very sheltered' (Blumine Island) to aid in describing the patterns within each location. Environmental variables explained 42% of the variation in algal community structure (Table 4), with Secchi (21%) and Sediment (19%) being strongly correlated with PC1 (Fig. 18B). Fetch was not strongly correlated with PC1 and only explained 7% of the variation across all sites in this bioregion; however, this was largely due to all of the sites from Kapiti (both sheltered and exposed) being grouped together (see below). Most algal species (excluding brown encrusting algae and *Codium* spp.) were negatively correlated with PC1 (Fig. 18C), which reflects their higher biomass at more exposed and offshore sites. PC2 was correlated with MaxDepth, Slope and Evechinus, and appears to reflect a gradient from deep, steeply sloping sites (e.g. Maheipuku at Nelson) with a higher biomass of red foliose algae to more gradually sloping sites with higher abundances of *Evechinus chloroticus* and higher biomasses of *Carpophyllum flexuosum* and *C. maschalocarpum* (e.g. Foul Point at Abel Tasman).

Kapiti Island

All sites from Kapiti Island were grouped into the exposed-offshore group (Fig. 18); however, there were clear differences between the sites on the northwestern side of the island and the more sheltered sites on the east (Fig. 19A). Algal community structure at Kapiti was similar to that seen at Gisborne, with *Carpophyllum maschalocarpum* dominating the immediate subtidal, *Evechinus chloroticus* being rare, and extensive forests of *Ecklonia radiata* and *C. flexuosum* occurring at greater depths. At the more sheltered eastern sites *C. maschalocarpum* was restricted to the shallow depth stratum. *Ecklonia radiata* was also abundant at shallow depths, but its biomass declined markedly with depth. *Carpophyllum flexuosum* was dominant at 7–9 m, although its biomass was also reduced at 10–12 m, where the small brown algae *Halopteris* sp. (Southeast Point only), *Ulva* spp. and the red algal species *Plocamium* spp., *Rhodophyllis gunnii* and *Asparagopsis armata* were common. Crustose coralline algae were the dominant substratum cover at shallow depths but sediment dominated the deeper strata (7–9 m, 10–12 m) (Fig. 19C). Encrusting invertebrates such as sponges and ascidians covered only a small fraction of the substratum and mobile invertebrates were rare at all sites (Fig. 19B).

Figure 18. Principal coordinates analysis of sites sampled in the Abel bioregion, based on fourth-root transformed biomass of 23 macroalgal groups (A). Bi-plots give correlations between principal coordinates axes and environmental variables (B) and original macroalgal species groups (C) (see Table 1 for macroalgal group codes). Sites shaded according to groupings identified at the 60% similarity level. Black = exposed-offshore, grey = moderately exposed, white = sheltered and cross symbol indicates very sheltered (Blumine Island).



The more exposed western sites at Kapiti had a distinct pattern in algal community structure in that *E. radiata* was abundant, and achieved high biomasses at 4–12 m of depth (Fig. 19A). The biomass of *E. radiata* was reduced in the shallow stratum (< 2 m), where *C. maschalocarpum* dominated, but co-occurred with *C. maschalocarpum* and *Cystophora retroflexa* at 4–6 m, and with *C. flexuosum* at 7–9 m and 10–12 m depths. Low numbers of *Landsburgia quercifolia* also occurred at some of these sites and the red algal species *Plocamium* spp., *Anotrichium crinitum*, *R. gunnii* and *Asparagopsis armata* were common. Crustose coralline algae were the dominant substratum cover at all depths, although small brown algae (*Zonaria* spp., *Carpomitra costata* and *Halopteris* spp.) dominated the understorey (Fig. 19A). Red algae, predominantly *Pterocladia lucida* and red turfing algae, were abundant in the shallow stratum, and *Ulva* spp. were also common. The cushion star *Patiriella* spp. was the most abundant mobile macroinvertebrate and low numbers of *Cookia sulcata*, *Trochus viridis* and *Cantharidus purpureus* were recorded (Fig. 19B).

Long Island

The sites sampled at Long Island spanned a large gradient from inner Queen Charlotte Sound to more exposed outer parts of the Sound and the sites fell into all of the exposure groups identified for the Abel bioregion (Fig. 18). The inner-

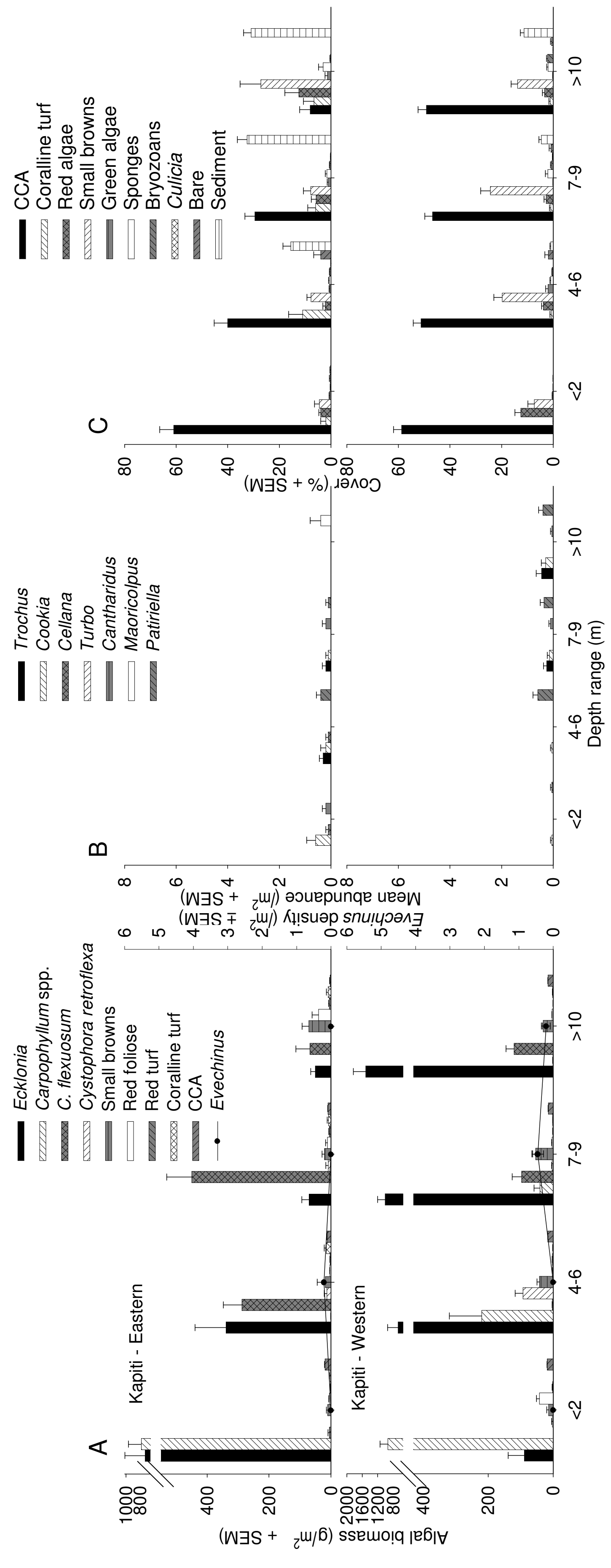


Figure 19. Depth-related patterns in biomass (g AFDW/m^2) of dominant macroalgal groups and density of *Evechinus chloroticus* (A), density of common mobile invertebrates (B) and cover of common encrusting forms (C) for sites on the eastern and western side of Kapiti Island sites (Abel bioregion). Note: all Kapiti sites were grouped in the Exposed-offshore group (Fig. 18).

most site, Blumine Island, formed its own very sheltered group and was the only site sampled in the entire Northern Province that completely lacked a shallow band of *Carpophyllum maschalocarpum* (Fig. 20A). Large brown algae were absent at this site and crustose coralline algae were the dominant algal group at all depths. Small amounts of filamentous and turfing algae (e.g. *Polysiphonia* sp. and *Chondria* sp.) were present at shallow depths. *Evechinus chloroticus* occurred at moderately low densities (c. 1/m^2) across all depths. *Turbo smaragdus* occurred at high densities in the shallow stratum (< 2 m), *Cellana stellifera* was abundant at mid-depths, and *Maoricolpus roseus* was abundant in the deepest strata (4–12 m) (Fig. 20B). Crustose coralline algae dominated the shallow stratum, but at greater depths sediment was the dominant cover (Fig. 20C). Bare rock also made up an important component of the substratum.

Large brown algae were also scarce at sites in the sheltered group, except for *C. maschalocarpum* in the immediate subtidal (< 2 m deep). Moderate densities of *E. chloroticus* occurred at shallow depths and densities tended to decline with depth (Fig. 20A). Mobile macroinvertebrates and substratum cover showed similar patterns to those of Blumine Island, although the numbers of *Patiriella* spp. and percentage cover of the cup coral *Culicia rubeola* were higher (Fig. 20B, C). Moderately exposed sites mainly differed in the occurrence of *C. flexuosum* at 4–6 m. The numbers of *E. chloroticus*, *Trochus viridis*, *Cantharidus purpureus*, *Cookia sulcata* and *Patiriella* spp. also tended to be higher than at the sheltered sites. Consistent with increasing wave exposure and/or water movement, the percentage cover of crustose coralline algae was higher in the deepest strata, and the cover of sediment was lower, compared to the more sheltered sites (Fig. 20C).

At the exposed-offshore sites, *Carpophyllum flexuosum* stands were present at depths of 4–9 m, and sea urchins were abundant only in the deepest stratum (10–12 m) (Fig. 20A). *Carpophyllum flexuosum* exhibited a sheltered morphology (Cole et al. 2001) and formed forests typical of sheltered sites in other parts of the country, e.g. Long Bay. *Ecklonia radiata* was also present at 10–12 m interspersed with *C. flexuosum*. *Macrocystis pyrifera*, *Marginariella urvilliana* and tall *Sargassum sinclairii* plants (> 2 m length) also occurred at the Motuara Island site, which was subject to strong currents. In general, the biomass of red foliose algae, e.g. *Rhodymenia* sp. and *Asparagopsis armata*, increased with depth. Crustose coralline algae dominated the substratum at shallow depths and declined with depth. Coralline turf was also a dominant cover at shallow depths, whereas sediment dominated the deepest stratum (Fig. 20C). Mobile macroinvertebrate species were not as common as at the other sites (Fig. 20B), although *Cantharidus purpureus* tended to be more abundant, possibly associated with the higher biomass of *E. radiata.*

Abel Tasman

Two sites at Abel Tasman (Foul Point and Isol Rock) were grouped in the moderately exposed group whereas the others were classified as sheltered (Fig. 18). Algal and invertebrate assemblages were similar to those seen in equivalent groups at Long Island. At sheltered sites, the shallow band of *Carpophyllum maschalocarpum* extended to depths less than 2 m and *Evechinus chloroticus* occurred at moderate–low densities across all depths (Fig. 21A). Intermediate exposure sites were characterised by stands of *C. flexuosum* at mid-depths

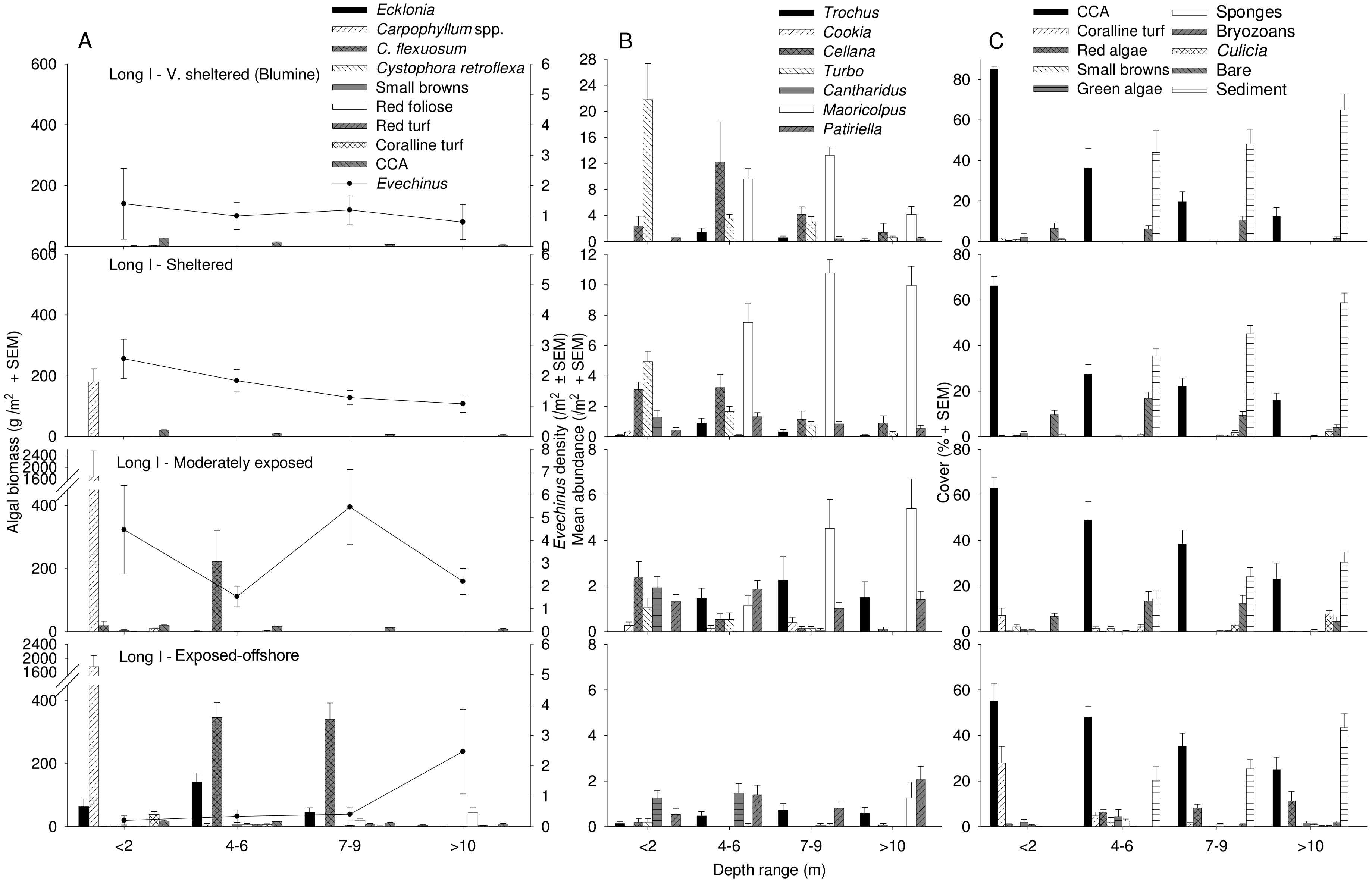


Figure 20. Depth-related patterns in biomass (g AFDW/m^2) of dominant macroalgal groups and density of *Evechinus chloroticus* (A), density of common mobile invertebrates (B) and cover of common encrusting forms (C) for Long Island sites (Abel bioregion). Sites are grouped according to the exposure groups identified in Fig. 18.

(4–6 m and 7–9 m) and variable densities of *E. chloroticus*. *Ecklonia radiata* was absent from all Abel Tasman sites (but see Davidson & Chadderton 1994). There was little difference in mobile macroinvertebrates between the two groups (Fig. 21B), except *Turbo smaragdus* was more abundant at the sheltered sites. *Cookia sulcata*, *Trochus viridis* and *Maoricolpus roseus* were common at all sites. Crustose coralline algae were the dominant substratum cover at all depths, except for at 10–12 m, where sediment was the dominant cover (Fig. 21C). The percentage cover of sponges and bryozoans was notably higher than that recorded at Long Island sites.

Nelson

All of the Nelson sites were grouped into the moderately exposed group, except for Maheipuku (exposed-offshore group). *Carpophyllum maschalocarpum* was the dominant large brown algae at all the sites sampled and was generally restricted to the shallow depth stratum (< 2 m), where it formed dense stands (Fig. 21A). *Glossophora kunthii*, *Sargassum sinclairii*, *C. flexuosum*, *Cystophora retroflexa* and *C. torulosa* were also occasionally found in this shallow zone. *Ecklonia radiata* was absent from all sites. For the moderately exposed sites, depth distributions of large browns and *Evechinus chloroticus* were consistent with those seen for this group at Long Island. *Carpophyllum flexuosum* and *Sargassum sinclairii* were common at 4–6 m, although most of the *C. flexuosum* was short (< 0.5 m long) and appeared to be grazed by sea urchins. With increasing depth (7–9 m and 10–12 m), the density of *E. chloroticus* tended to decline and large brown algae became rare, with the exception of a few sparsely distributed *C. flexuosum*. The substratum was dominated by crustose coralline algae at all depths, but the percentage cover of sediment, sponges and bryozoans increased with depth (Fig. 21C). Mobile macroinvertebrates were present in moderate numbers, with *Cellana stellifera* and *Patiriella* spp. being the most abundant at all depths (Fig. 21B). The ambush star *Stegnaster inflatus* was also common at some sites.

Algal community structure at Maheipuku was considerably different from that of other sites within the exposed-offshore group. The reef at this site consisted of a relatively steep wall sloping to 13 m deep. *Carpophyllum maschalocarpum* dominated the shallow depth stratum and large brown algae were rare at greater depths where red foliose and red turfing algae dominated (e.g. *Asparagopsis armata*, *Anotrichium crinitum* and *Plocamium* spp.) (Fig. 21A). *Carpophyllum flexuosum* was not recorded at this site, but other brown algae including *Sargassum sinclairii*, *Demarestia ligulata*, *Carpomitra costata* and *Halopteris* sp. were common. *Evechinus chloroticus* occurred at lower numbers compared with other Nelson sites, and the percentage cover of crustose coralline algae was low. Dominant percentage cover categories were red turfing and foliose algae, sediment, bryozoans and sponges (Fig. 21C). Mobile macroinvertebrates were rare, except for *Patiriella* spp., which was found at all depths (Fig. 21B).

3.4.5 Cook bioregion

All sites sampled at Wellington and Kaikoura were relatively exposed to the open sea and there was little variation in algal community structure, with sites from the two locations separated at the 75% similarity level (Fig. 22A). There

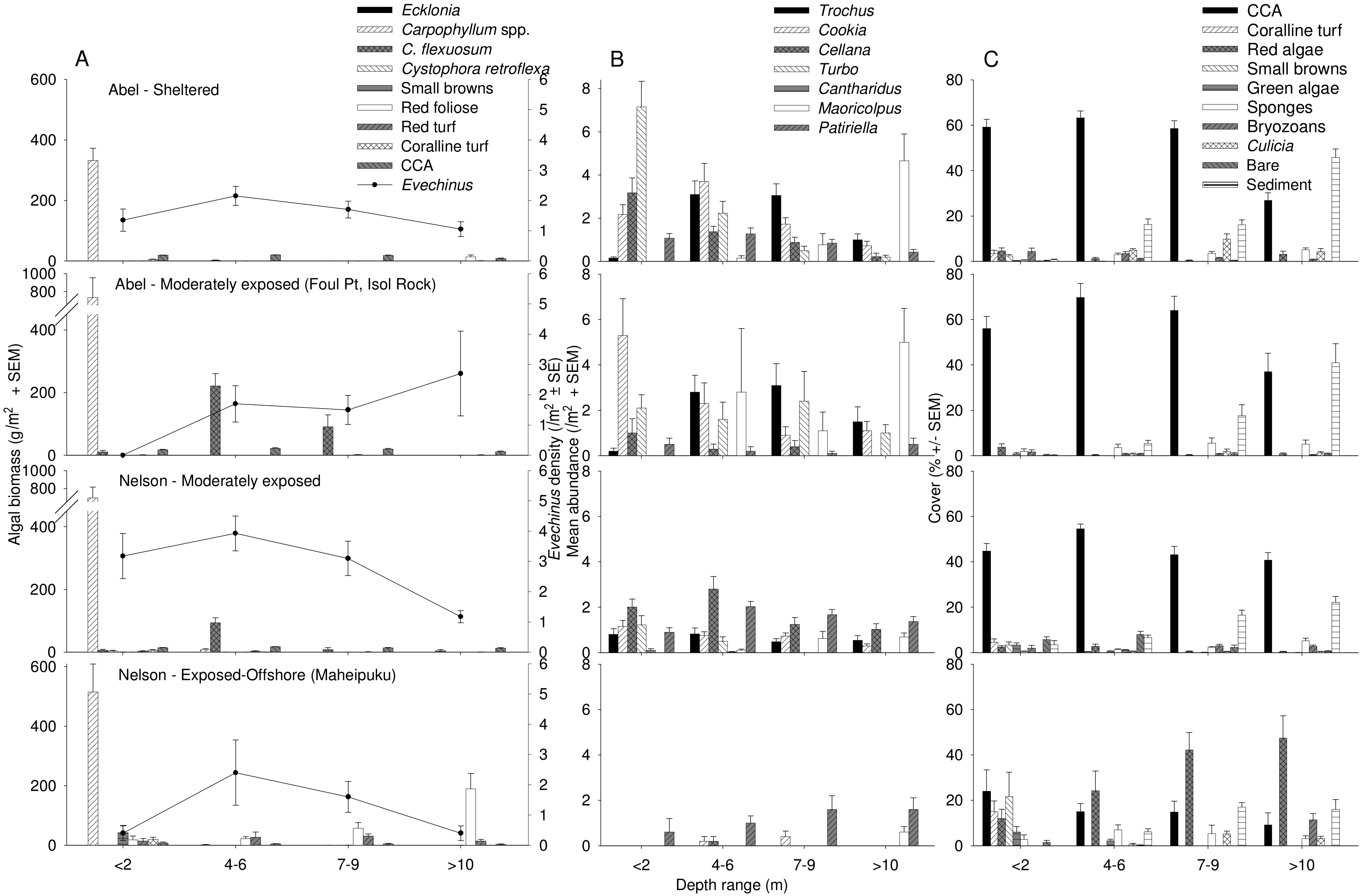


Figure 21. Depth-related patterns in biomass (g AFDW/m^2) of dominant macroalgal groups and density of *Evechinus chloroticus* (A), density of common mobile invertebrates (B) and cover of common encrusting forms (C) for Abel Tasman and Nelson sites (Abel bioregion). Sites from each location are grouped according to the exposure groups identified in Fig. 18.

was no clear division between sites sampled on the northern and southern side of the Kaikoura Peninsula, or among sites at Wellington associated with any clear geographic or environmental gradients. The environmental variables Slope, Secchi and MaxDepth were strongly correlated with PC1 (Fig. 22B). Wellington sites tended to have more gently sloping reefs and clearer water than the Kaikoura sites. Differences in the dominant species between the two locations are reflected in the correlations with PC1. *Carpophyllum maschalocarpum* and *C. flexuosum* were more abundant at Wellington, whereas *Landsburgia quercifolia*, *Marginariella* spp. and red foliose algae were more abundant at Kaikoura (Fig. 22C).

Wellington

Algal community structure on Wellington's south coast shared several similarities with both Northern and other Southern locations (Fig. 2). As in Northern locations, the immediate subtidal was dominated by *Carpophyllum maschalocarpum*, and *Pterocladia lucida* was also abundant, but species more typical of Southern locations were also abundant in this zone at some sites, e.g. *Marginariella urvilliana*, *Landsburgia quercifolia* and *Lessonia variegata* (Fig. 23A, Appendix 5). *Lessonia variegata* was dominant at greater

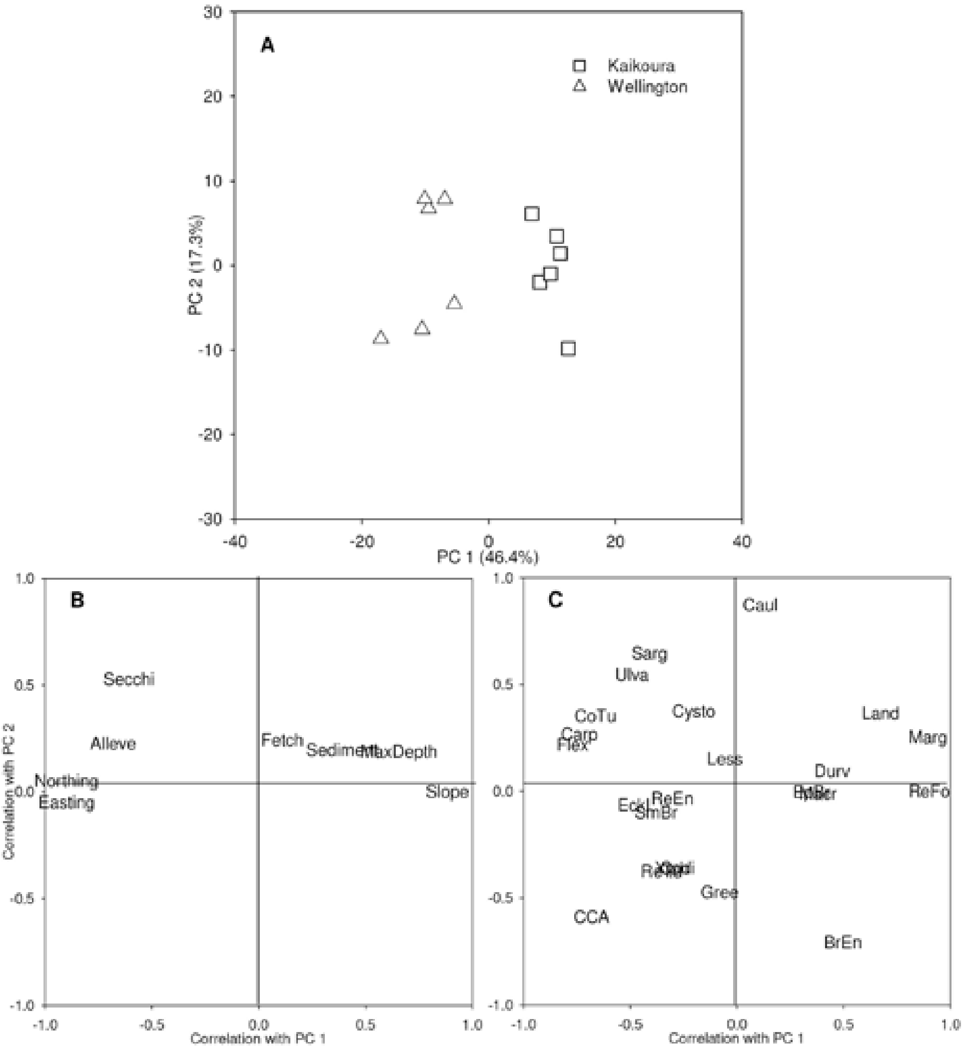


Figure 22. Principal coordinates analysis of sites sampled in the Cook bioregion, based on fourth-root transformed biomass of 23 macroalgal groups (A). Bi-plots give correlations between principal coordinates axes and environmental variables (B) and original macroalgal species groups (C) (see Table 1 for macroalgal group codes). Sites from both locations were separated at the 75% similarity level.

depths but formed mixed algal assemblages with *Ecklonia radiata*, *Landsburgia quercifolia* and *M. urvilliana*. There was a diverse understorey of red algae, including *Euptilota formosissima*, *Callophyllis* spp., *Craspedocarpus erosus*, *Plocamium* spp. and *Rhodophyllis gunnii*. Large areas were also dominated by the green algae *Caulerpa brownii*, and to a lesser extent *C. flexilis* and *C. articulata*. *Carpophyllum flexuosum* was common at the most sheltered site, at the entrance to the Wellington Harbour (Palmer Head), and low numbers of both *Macrocystis pyrifera* and the exotic *Undaria pinnatifida* were recorded at this site. *Evechinus chloroticus* and other mobile invertebrates were rare, although *Haliotis australis* was common in the shallow depth stratum, and *Patiriella* spp. were common across deeper strata (Fig. 23B). Crustose coralline algae were the dominant substratum cover at all depths but coralline turf was also important in the shallow stratum, whereas the green algae *Caulerpa* spp. and also *Ulva* spp. were important at greater depths (Fig. 23C).

Kaikoura

Algal assemblages at Kaikoura were dominated by a mixture of large brown and red foliose algae at all depths (Fig. 23A). *Carpophyllum maschalocarpum* was found only in the shallow stratum and mixed with *Landsburgia quercifolia*, *Lessonia variegata*, *Marginariella urvilliana* and red foliose algae. *Ecklonia radiata* was abundant in mixed stands with *L. variegata* and *M. boryana* at 4–8 m at the northern sites but was rare at southern sites, which are more exposed to the prevailing southerly swell. *Marginariella boryana* dominated the deepest strata at the northern sites, whereas *Landsburgia quercifolia* was the dominant large brown alga at these depths for the southern sites. *Sargassum sinclairii* and *Macrocystis pyrifera* were present in low biomasses at sites on the northern side of the peninsula. Some *Durvillaea willana* plants occurred in the shallow stratum at the southern sites. The Kaikoura sites had a diverse red algal flora that achieved high biomasses across all depths. At shallow depths the red algal species *Pterocladia lucida*, *Hymenocladia sanguinea*, *Cladhymenia oblongifolia* and *Rhodymenia* spp. were most common, whereas for the deeper strata *Euptilota formosissima*, *Hymenena palmata*, *Craspedocarpus erosus*, *Plocamium* spp., *Rhodophyllis gunnii*, *Schizoseris* spp., *Streblocladia glomerulata* and *Rhodymenia obtusa* were most common (Appendix 5). The green alga *Caulerpa brownii* was also common in the deepest strata (7–9 m and 10–12 m) (Fig. 23A). Mobile macroinvertebrates, e.g. the two starfish species *Diplodontias* sp. and *Pentagonaster pulchellus*, occurred in low numbers (Fig. 23B). Crustose coralline algae were the dominant substratum cover (Fig. 23C), but there was a relatively high percentage cover of other encrusting forms, in particular red foliose algae and the green algae *Caulerpa brownii*. Sites at Kaikoura generally had higher percentages cover for sponges, bryozoans and sediment than Wellington sites, which is consistent with the higher turbidity recorded at Kaikoura.

3.4.6 Banks bioregion

Algal community structure at Banks Peninsula North and Flea Bay were similar to those of Northern locations (Fig. 2), largely owing to the predominance of *Carpophyllum maschalocarpum* in the shallow subtidal and *C. flexuosum* at greater depths. The Banks bioregion sites were divided into three groups at the 60% similarity level (Fig. 24A). The relationship between these groupings and

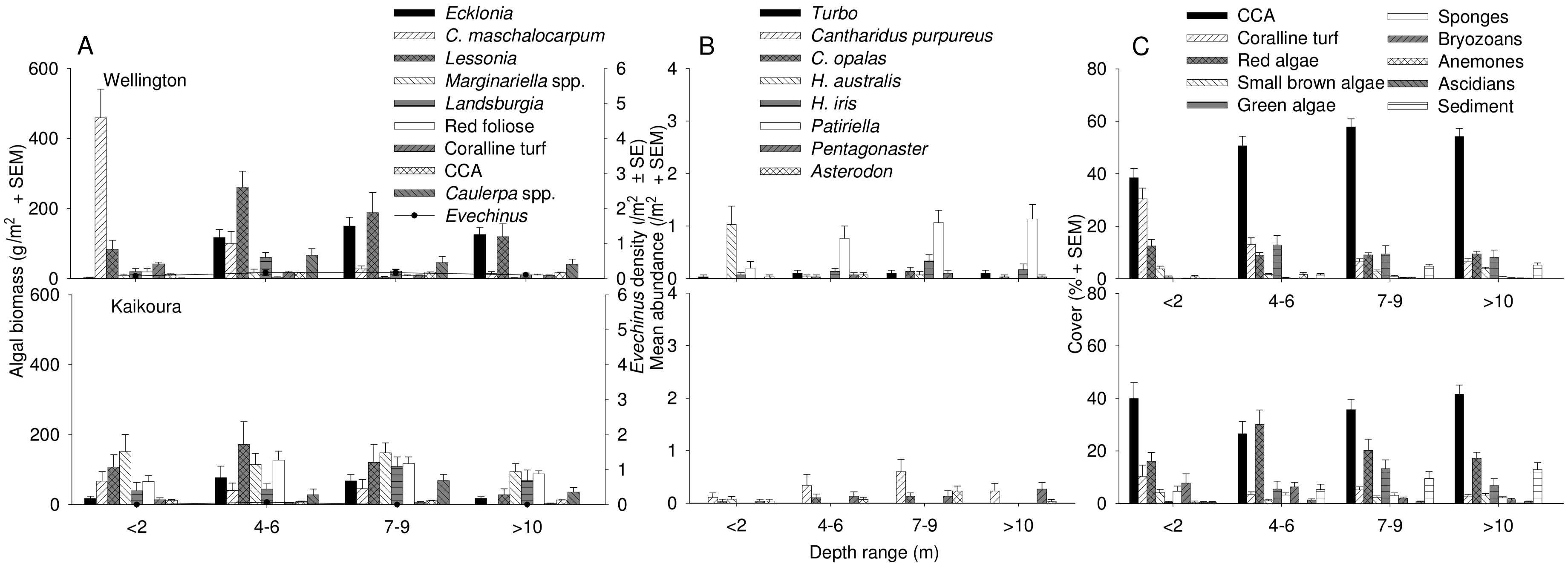


Figure 23. Depth-related patterns in biomass (g AFDW/m^2) of dominant macroalgal groups and density of *Evechinus chloroticus* (A), density of common mobile invertebrates (B) and cover of common encrusting forms (C) for site groups within the Cook bioregion.

environmental variables was not clear (Fig. 24B), most likely because of the low number of sites sampled. However, differences in algal community structure among groups were broadly consistent with a wave-exposure gradient and groups were subjectively named according to their relative exposure levels. The Banks Peninsula North sites and the two sites from the eastern side of Flea Bay (Hectors Wall and Flea East) made up the moderately exposed group, whereas the sites on the western side of Flea Bay were divided into two groups; the most sheltered site (Rockpool Point) formed one group, whereas the more exposed outer sites (Outer West and Tern Rock) formed the other. Secchi and Sediment were correlated with PC1 (Fig. 24B) which corresponded to the higher turbidity and higher percentage cover of sediment at the Banks Peninsula North sites. There was a general gradient in species composition along PC1, from moderately exposed sites with *Macrocystis pyrifera* and *Ecklonia radiata* to exposed sites dominated by *Lessonia variegata* (Fig. 24C). However, Fetch was strongly correlated with PC2 and reflected the differences between the sheltered site (Rockpool Point) and the other sites. The species most strongly correlated with PC2 included *C. flexuosum* and *Xiphophora gladiata*, which were more abundant at Rockpool Point, and *Durvillaea willana*, which was more abundant at the exposed western sites at Flea Bay.

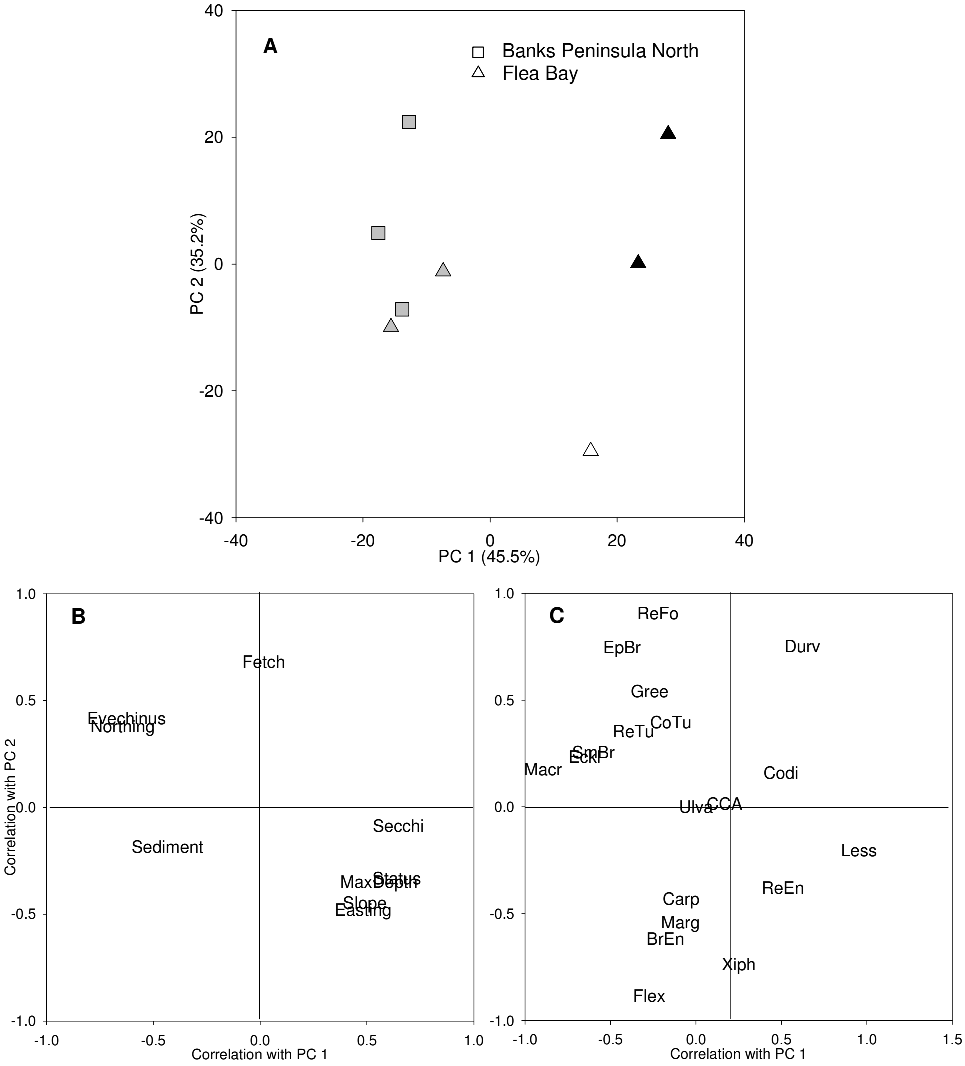


Figure 24. Principal coordinates analysis of sites sampled in the Banks bioregion, based on fourth-root transformed biomass of 23 macroalgal groups (A). Bi-plots give correlations between principal coordinates axes and environmental variables (B) and original macroalgal species groups (C) (see Table 1 for macroalgal group codes). Sites shaded according to groupings identified at the 75% similarity level. Black = exposed, grey = moderately exposed, white = sheltered.

Banks Peninsula North

Large brown algae extended to a maximum depth of 8 m at Banks Peninsula North sites and all fleshy macroalgae were rare in the deepest stratum (10–12 m). *Carpophyllum maschalocarpum* formed a patchy band in the shallow depth stratum, with *Marginariella urvilliana*, *D. antarctica* and *Macrocystis pyrifera* also occurring (Fig. 25A). At this depth *Haliotis iris* was abundant ($3.5 \pm 2.0/m^2$), along with the stalked ascidian *Pyura pachydermatina* ($16 \pm 7.0/m^2$) and the mussel *Perna canaliculus* (Fig. 25B,C). The brown algal species *Glossophora kunthii*, *Desmarestia ligulata*, *Halopteris* sp. and *Microzonia velutina* were also common in the shallow subtidal. *Macrocystis pyrifera* and *C. flexuosum* were the dominant macroalgal species at 4–6 m of depth and *Ecklonia radiata* also occurred at this depth. Below 6 m, large brown algae were rare and the substratum was mainly covered by sediment and solitary ascidians (Fig. 25C). Red foliose and red turfing algae were rare at all sites and only small amounts of *Rhodophyllis gunnii*, *Anotrichium crinitum* and *Plocamium* spp. were found at 4–6 m and 7–9 m. Low numbers of *Evechinus chloroticus* were recorded at all depths; however, patches of *E. chloroticus* were common in the shallow subtidal at c. 3 m of depth (NS, pers. obs.). Similarly, patches of *H. iris* (< 125 mm shell length) were also observed at this depth. *Trochus viridis* occurred at moderate numbers at mid-depths, whereas low numbers of *Cellana stellifera*, *Cookia sulcata* and *Turbo smaragdus* were also found at depths down to 9 m (Fig. 25B).

Flea Bay

Algal community structure at the sheltered site (Rockpool Point) was comparable to that at sheltered sites in Northern locations (e.g. Long Bay) with low algal diversity, a shallow band of *Carpophyllum maschalocarpum*, and *C. flexuosum* forests dominating the deeper strata (Fig. 25A). One exception was the occurrence of *Lessonia variegata* in the shallow subtidal. No red foliose, red turfing or green algal species were recorded at this site and coralline turf was relatively rare. *Cookia sulcata* and *Trochus viridis* were abundant across all depths and *Haliotis iris* was common in the deepest strata (7–9 m and 10–12 m) (Fig. 25B). Crustose coralline algae were the dominant encrusting form at all depths; however, the percentage cover of sediment was high in the deepest strata (Fig. 25C). Moderately exposed sites (eastern Flea Bay) had relatively low biomass of macroalgae at all depths, which may be due to shading effects as both sites were south facing with steeply sloping reefs. *Carpophyllum maschalocarpum*, *Durvillaea willana* and *Marginariella urvilliana* dominated the shallow stratum, whereas *C. flexuosum* and *Macrocystis pyrifera* dominated at 4–6 m. Low numbers of *Ecklonia radiata* and *Marginariella urvilliana* (sheltered morphology; Adams 1994) were present at 10–12 m. Red foliose, red turfing and green algal species were rare at all depths, and the percentage cover of crustose coralline algae declined with depth and that of sediment increased (Fig. 25C). *Perna canaliculus* and *Pyura pachydermatina* were abundant at shallow depths. *Trochus viridis* was abundant at all depths and low numbers of *Cookia sulcata*, *Haliotis iris* and *Calliostoma punctulatum* also occurred (Fig. 25B). Exposed western Flea Bay sites (Tern Rock and Outer West) were dominated by *Carpophyllum maschalocarpum*, *L. variegata* and *D. willana* at 0–2 m, and *C. maschalocarpum* at 4–6 m, whereas all fleshy macroalgae were rare at greater depths (Fig. 25A). Crustose coralline

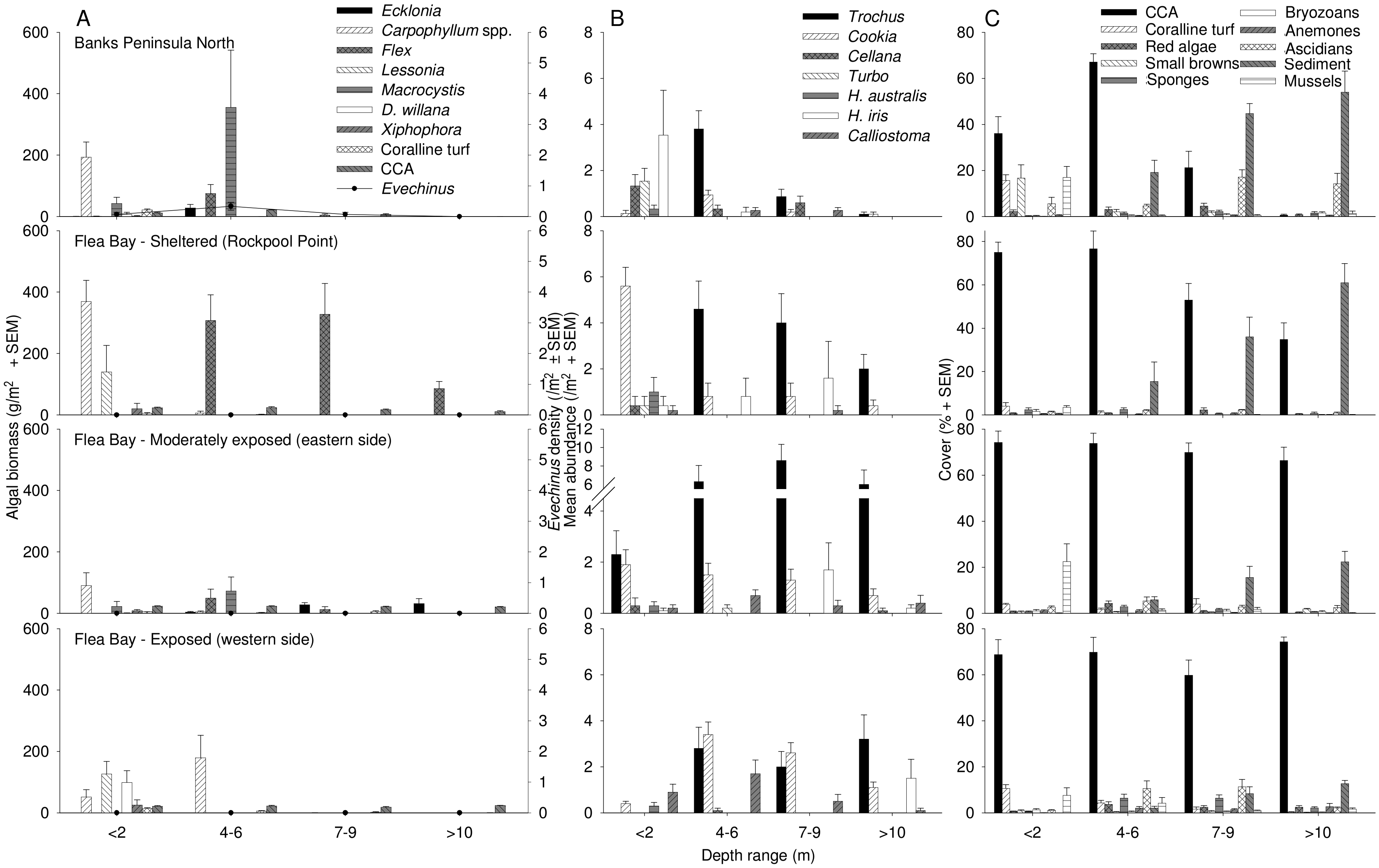


Figure 25. Depth-related patterns in biomass (g AFDW/m^2) of dominant macroalgal groups and density of *Evechinus chloroticus* (A), density of common mobile invertebrates (B) and cover of common encrusting forms (C) for site groups within the Banks bioregion. Sites from each location are grouped according to the exposure groups identified in Fig. 24 (see section 3.4.6 for explanation of groupings).

algae were the dominant substratum cover at all depths although sponges and solitary ascidians had a relatively high percentage cover in the deeper strata (Fig. 25C). *Pyura pachydermatina* was abundant at 4–6 m (28.2 ± 11.9/m^2) and 7–9 m (13.3 ± 7.2/m^2). Red foliose algae were more common at these sites, particularly as epiphytes on *P. pachydermatina*, e.g. *Callophyllis hombroniana* and *Hymenocladia sanguinea*. Large specimens of *H. iris* (up to 145 mm shell length) were common at 10–12 m.

3.4.7 Buller bioregion

All sites at Cape Foulwind and Karamea were highly exposed to large southwesterly swells, and had shallow reefs (< 11 m maximum depth) with high sandscour and turbidity. Algal and benthic community structure at these locations was unique at the national scale (Figs 2 and 9). Most key habitat-forming species were absent (e.g. *Ecklonia radiata*, *Carpophyllum* spp.) and the reefs were dominated by encrusting invertebrates (Fig. 10). Cluster analysis revealed no clear site groupings associated with any clear spatial or environmental gradients (Fig. 26A). However, several environmental variables were correlated with PC1, and suggested a gradient in community structure between inshore sites and two sites (Fishing Rod Reef and South Seal Rocks) located on offshore rockstacks (known as 'Three Steeples') at Cape Foulwind, which are surrounded by clearer, deeper water and have lower wave-exposure estimates as they have some protection from the prevailing southwesterly swell (Fig. 26B). Secchi was negatively correlated with PC1, whereas Fetch was positively correlated with it, being higher at inshore sites. Evechinus was also negatively correlated with PC1 and was only recorded at the two offshore sites. The algal groups responsible for this pattern appeared to be red turfing algae, ephemeral brown algae (e.g. *Endarachne binghamiae* and *Glossophora kunthii*) and brown encrusting algae, which were more common at offshore sites, whereas *Durvillaea willana*, red foliose algae and crustose coralline algae were more common at the inshore sites (Fig. 26C). Additional information on the reef communities and habitat types found at these sites is given in Shears (2007).

Karamea

Large brown macroalgae were absent from all the Karamea sites and the shallow stratum (< 2 m) was dominated by the mussel *Perna canaliculus*, crustose coralline algae, red foliose and red turfing algae (e.g. *Ballia callitrichia* and *Echinothamnion* sp.) (Fig. 27A). The brown algae *Glossophora kunthii*, *Halopteris* sp. and *Endarachne binghamiae* were also present (Appendix 5). *Ulva* spp. were also common on mussels at Little Wanganui Inlet. At greater depths, macroalgae were rare except for a low percentage cover of crustose coralline algae. Instead the substratum was dominated by encrusting invertebrates (sponges, ascidians and bryozoans), bare rock and sediment (Fig. 27C). At 10–12 m, the majority of the substratum was bare rock, most likely owing to high levels of sandscour. Mobile macroinvertebrates were rare at Karamea sites, with *Stichaster australis* and *Patiriella* spp. being the most common (Fig. 27B).

Cape Foulwind

The sites at Cape Foulwind exhibited a similar pattern in algal community structure to that of Karamea sites, except that *Durvillaea willana* occurred in the shallow stratum at Granite Spot, and crustose coralline algae and red turfing algae extended to greater depths (Fig. 27A). A short turfing *Halopteris* species (probably *H. congesta*) dominated the shallow stratum at most sites. *Gymnogongrus humilis* and *Ballia callitrichia* were the dominant red foliose algal species in the shallow stratum, although *Plocamium* spp., *Echinothamnion* sp. and *Lophurella hookeriana* were also common (Appendix 5). *Sargassum sinclairii* and *Codium convolutum* were locally abundant at South Seal Rocks. The deeper strata were dominated by sediment, bare rock, the mussel *Xenostrobus pulex*, bryozoans and ascidians (Fig. 27C). Barnacles extended into the shallow subtidal and the hydroid *Amphisbetia bispinosa* ('mussel beard') was relatively common across all depths. *Haliotis iris* was abundant in the deepest stratum, occurring in patches on bare rock. The starfish species *Stichaster australis* (> 1/m^2) and *Patiriella* spp. occurred at relatively high densities across all depths (Fig. 27B).

3.4.8 Westland bioregion

There was a clear distinction in algal community structure between the sites at Open Bay Islands and sites at the mainland locations (Fig. 8A). Algal community structure at the mainland locations in Westland was broadly similar to that of the Buller locations, with stands of large brown algae being rare and short red foliose and turfing algae dominating (Fig. 3). In contrast, large brown algae were

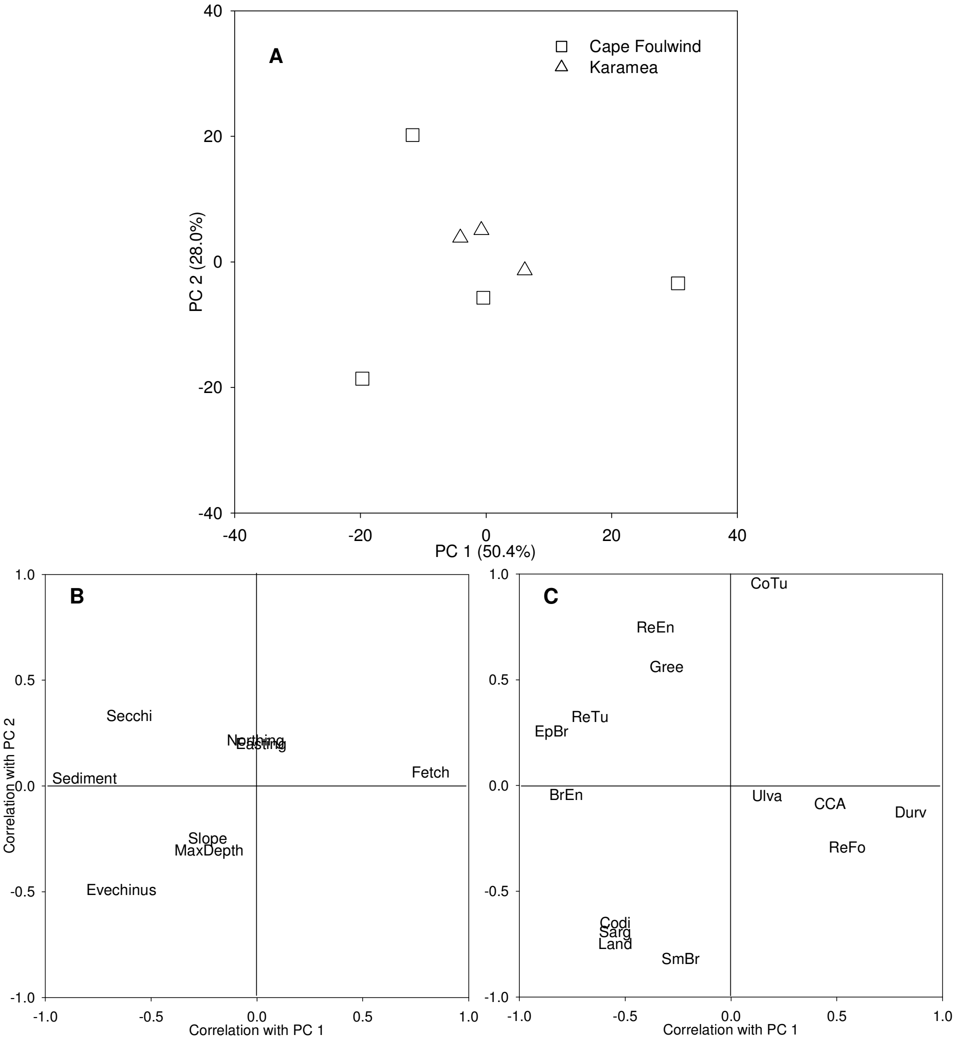


Figure 26. Principal coordinates analysis of Buller sites based on fourth-root transformed biomass of 23 macroalgal groups (A). Bi-plots give correlations between principal coordinates axes and environmental variables (B) and original macroalgal species groups (C) (see Table 1 for macroalgal group codes).

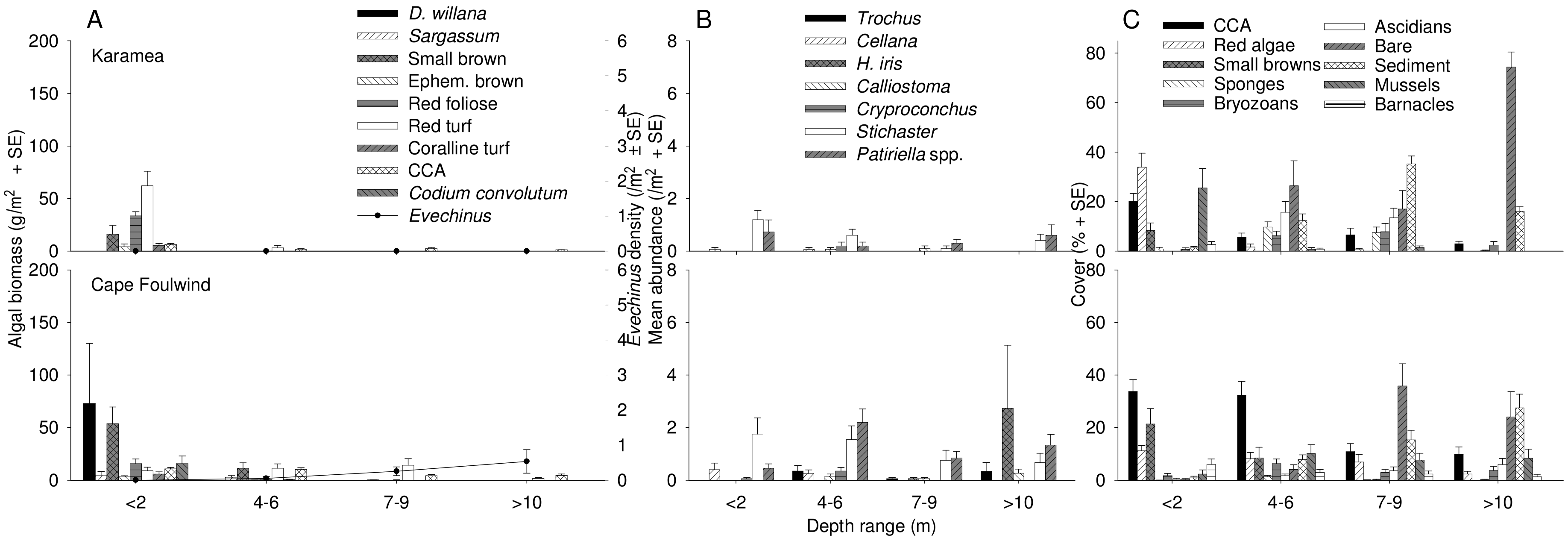


Figure 27. Depth-related patterns in biomass (g AFDW/m^2) of dominant macroalgal groups and density of *Evechinus chloroticus* (A), density of common mobile invertebrates (B) and cover of common encrusting forms (C) for locations within the Buller bioregion.

abundant at Open Bay Islands, and these sites were more closely grouped to Fiordland sites (Fig. 2). There was a strong negative correlation between PC1 and Secchi, which reflected the coastal–offshore gradient between locations (Fig. 28B). Evechinus was also negatively correlated with PC1 owing to its higher abundances at Open Bay Islands. The higher abundances of *Ecklonia radiata*, *Landsburgia quercifolia*, *Carpophyllum flexuosum* and *Sargassum sinclairii* at Open Bay Islands was reflected by their negative correlation with PC1 (Fig. 28C). Red turfing algae and small brown algae were positively correlated with PC1 and these generally were recorded at higher biomasses at the mainland locations. Additional information on the reef communities and habitat types found at these sites is given in Shears (2007).

Open Bay Islands

The organisation of algal assemblages at Open Bay Islands differed considerably from the other highly exposed West Coast locations, with *Ecklonia radiata* and *Landsburgia quercifolia* dominating at shallow depths (Fig. 29A). However, the sites sampled were located in small embayments or areas where there was some shelter from the large southwesterly swell, particularly the NE Taumaka site. *Ecklonia radiata* and *L. quercifolia* had a short (< 50 cm total length), leathery wave-adapted morphology at SE Popotai. *Carpophyllum flexuosum* and *Sargassum sinclairii* were common at 4–6 m,

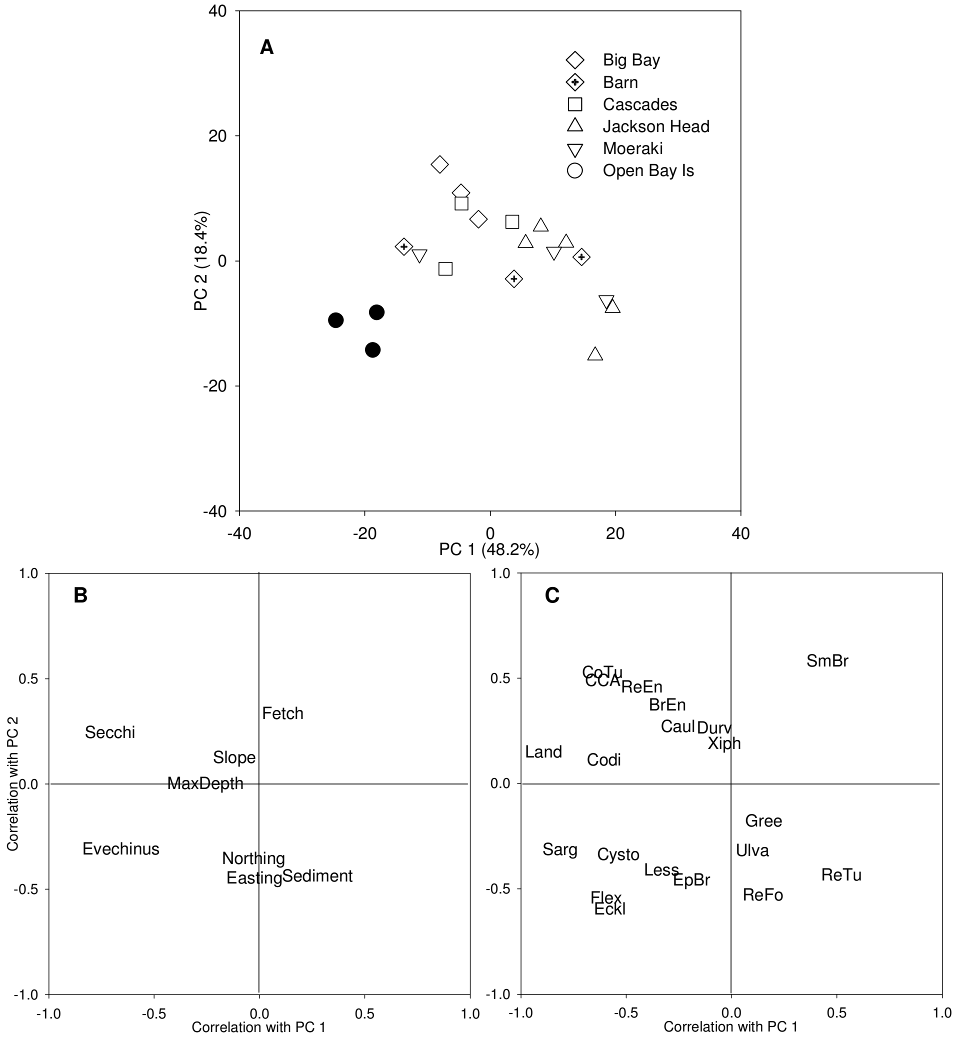


Figure 28. Principal coordinates analysis of Westland sites based on fourth-root transformed biomass of 23 macroalgal groups (A). Bi-plots give correlations between principal coordinates axes and environmental variables (B) and original macroalgal species groups (C) (see Table 1 for macroalgal group codes). Sites shaded according to grouping at the 65% similarity level.

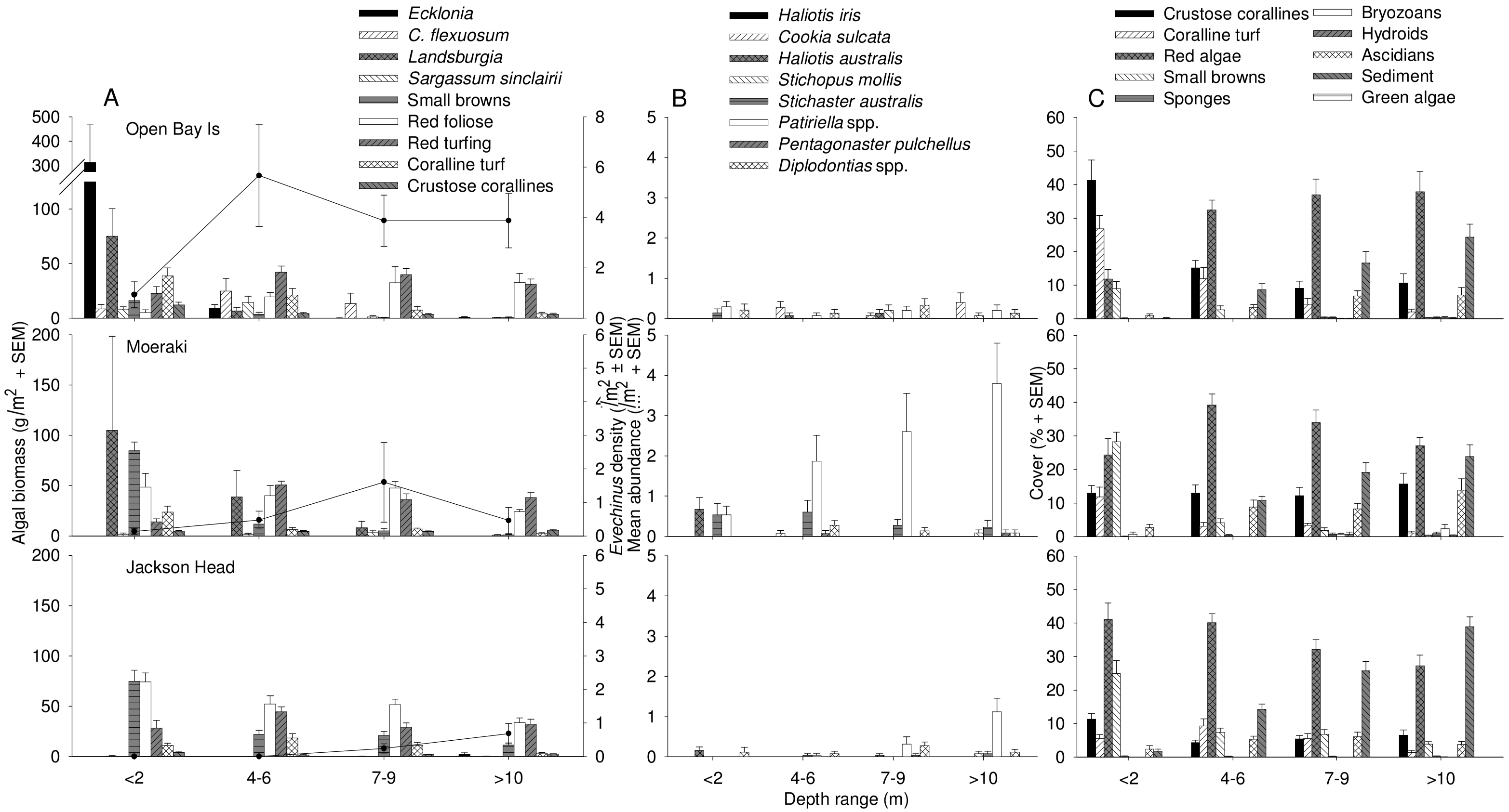


Figure 29. Depth-related patterns in biomass (g AFDW/m^2) of dominant macroalgal groups and density of *Evechinus chloroticus* (A), density of common mobile invertebrates (B) and cover of common encrusting forms (C) for sites at Open Bay Islands, Moeraki and Jackson Head within the Westland bioregion. Note: Open Bay Islands sites were distinct from sites in all other Westland locations at the 65% similarity level (Fig. 28).

red foliose (predominantly *Asparagopsis armata*, *Rhodophyllis gunnii* and *Anotrichium crinitum*) and red turfing algae were abundant at all depths, and *Evechinus chloroticus* occurred in dense patches in the deeper strata (7–9 m and 10–12 m). Mobile macroinvertebrates occurred at low numbers (Fig. 29B), although *Turbo smaragdus* was common in the < 2 m depth stratum at NE Taumaka ($2.4 \pm 2.2/m^2$), suggesting this site is relatively protected from large swells. Numerous *Astrostole scabra* were observed feeding on *E. chloroticus* at 10–12 m. The dominant substratum covers were crustose coralline algae, coralline turf, red algae and, to a lesser extent, small brown algae (predominantly *Microzonia velutina*) at shallow depths, and red algae, ascidians (mostly solitary species) and sediment in the deeper strata (Fig. 29C).

Moeraki and Jackson Head

Depth-related patterns in algal community structure and substratum cover were similar for Moeraki and Jackson Head sites (Fig. 29). Large brown algae were rare (although *Landsburgia quercifolia* and *Sargassum sinclairii* were common at Arnott Point) and the reef was covered by a diverse foliose and turfing algal community (Fig. 29A). The immediate subtidal was dominated by a short algal turf assemblage, predominantly *Echinothamnion* sp., *Lophurella hookeriana*, *Halopteris* sp., with coralline turf, crustose coralline algae and red turfing algae. *Glossophora kunthii*, *Microzonia velutina*, *Plocamium* spp., *Asparagopsis armata*, *Codium convolutum* and *Colpomenia sinuosa* were also common (Appendix 5). At greater depths, the percentage cover of coralline turf declined, and sediment and solitary ascidians covered most of the substratum (Fig. 29C). The dominant red foliose algae were *Plocamium* spp., *Euptilota formosissima*, *Anotrichium crinitum*, *Lophurella hookeriana, Rhodophyllis gunnii* and *Ballia callitrichia*. The small browns *Carpomitra costata*, *Halopteris* spp. and *Microzonia velutina* were common, and *Spatoglossum chapmanii* and a *Dictyota* sp. were also present. Individual *Evechinus chloroticus* were large (> 100 mm TD, Appendix 6) and most abundant in the deeper strata (Fig. 29A). *Patiriella* spp. was the most abundant mobile macroinvertebrate species, particularly at Moeraki sites (Fig. 29B). Other mobile macroinvertebrates occurred at low numbers, e.g. *Stichopus mollis*, *Pentagonaster pulchellus*, *Diplodontias* spp., *Coscinasterias muricata* and *Stichaster australis*.

Cascades, Barn and Big Bay

Algal community structure at these locations was generally similar to that of Moeraki and Jackson Head (Fig. 30A), although *L. quercifolia* and *S. sinclairii* tended to be more common, particularly at Crayfish Rocks (Big Bay). In general, the biomass of *L. quercifolia* tended to be highest at locations with greater water clarity, e.g. Crayfish Rocks and Barn Island. Small brown algae and red foliose algae dominated the < 2 m depth stratum at most sites, while red turfing algae, crustose corallines, coralline turf and sediment dominated at greater depths (Fig. 30B). *Evechinus chloroticus* was most abundant in the deepest strata and formed patches of urchin barrens habitat (areas up to 10–30 m^2) at Crayfish Rocks. A number of algal species were particularly abundant at the Crayfish Rocks site, e.g. *Caulerpa brownii* and *Dictyota* spp. As for Moeraki and Jackson Head sites, *Patiriella* spp. was the most abundant mobile macroinvertebrate, although *Haliotis australis* was common in the < 2 m depth strata at Barn sites, and patches of *Haliotis iris* were recorded in the 7–9 m depth stratum at the Cascades sites (Fig. 30A).

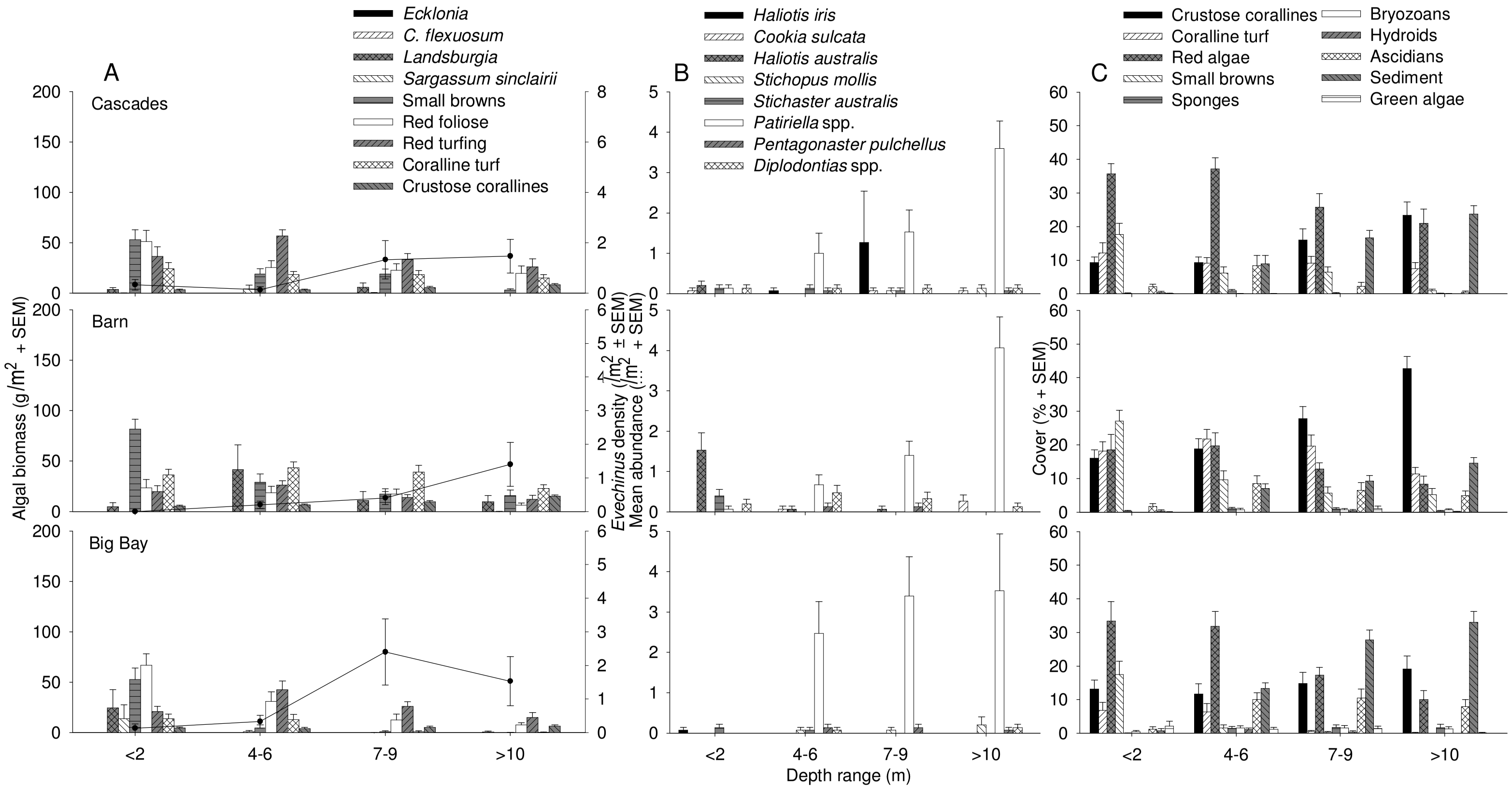


Figure 30. Depth-related patterns in biomass (g AFDW/m^2) of dominant macroalgal groups and density of *Evechinus chloroticus* (A), density of common mobile invertebrates (B) and cover of common encrusting forms (C) for sites at Cascades, Barn and Big Bay within the Westland bioregion.

3.4.9 Chalmers bioregion

Algal community structure at Otago Peninsula and Catlins was distinctive from other locations (Fig. 2), and several large brown algal species common in Southern locations were notably absent, e.g. *Ecklonia radiata*, *Carpophyllum flexuosum*, *Marginariella* spp. and *Macrocystis pyrifera*. All sites sampled in this bioregion were relatively steeply sloping and highly exposed to southerly swells. There was little variation in algal community structure among sites (Fig. 31A) and there were no clear patterns associated with environmental variables (Fig. 31B). The Tuhawaiki site (far left of ordination) had the lowest wave exposure and highest percentage cover by sediment, and had several species that were not found at other sites, e.g. *Caulerpa flexilis*, *Cystophora platylobium*, *Xiphophora gladiata* and *Landsburgia quercifolia*, which were negatively correlated with PC1 (Fig. 31C).

The immediate subtidal (< 2 m) was dominated by a forest of *Durvillaea willana* (Fig. 32A), consisting of plants up to 3 m tall with stipes up to 150 mm in diameter. The forests extended to depths of c. 3 m and had a unique understorey assemblage dominated by mats of *Ballia callitrichia*, coralline turf and crustose coralline algae. Several other red algal species were common in this habitat, including *Camontagnea hirsuta*, *Plocamium cirrhosum*, *Callophyllis calliblepharoides*, *Heterosiphonia concinna*, *Lophurella hookeriana* and *Hymenena durvillaei*.

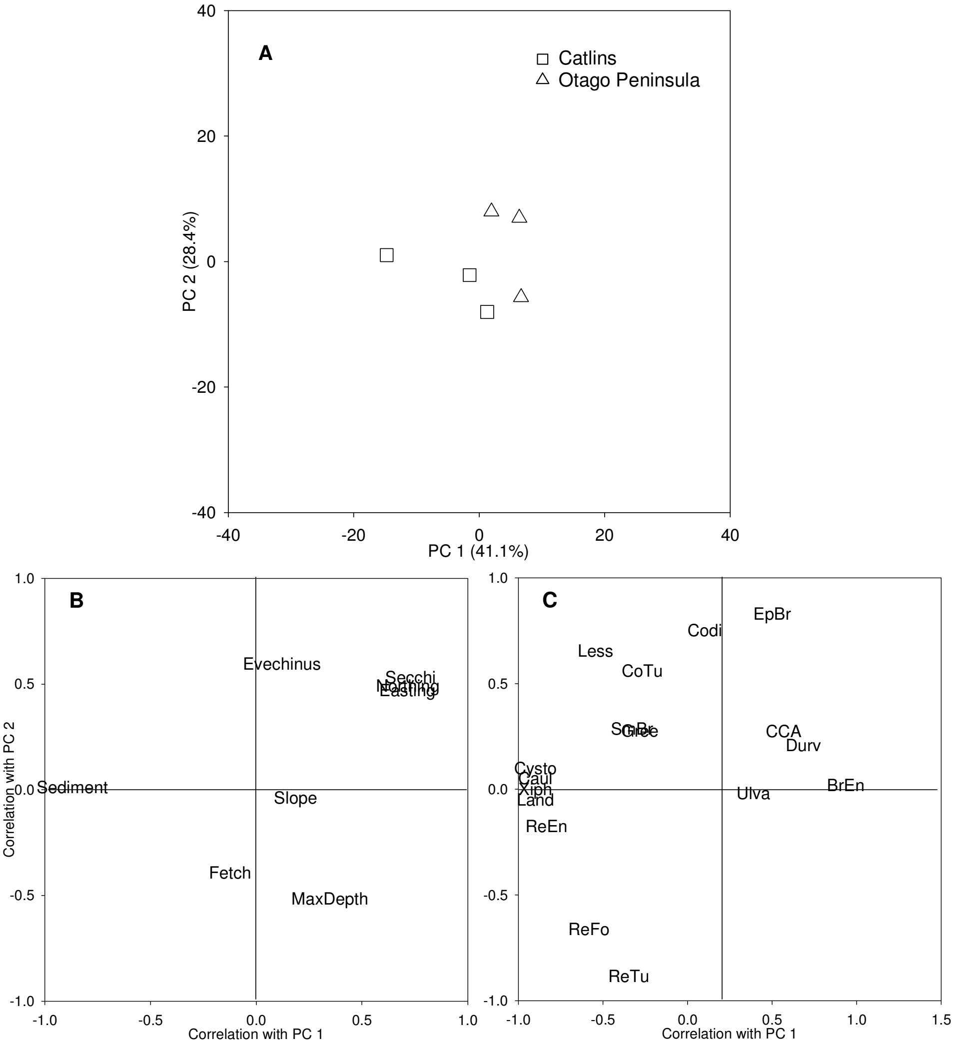


Figure 31. Principal coordinates analysis of sites sampled in the Chalmers bioregion, based on fourth-root transformed biomass of 23 macroalgal groups (A). Bi-plots give correlations between principal coordinates axes and environmental variables (B) and original macroalgal species groups (C) (see Table 1 for macroalgal group codes).

Mussels (predominantly *Perna canaliculus*) were also common in this stratum (Fig. 32C), along with *Haliotis australis* and *Cryptoconchus porosus* (Fig. 32B). At greater depths, *Lessonia variegata* was the dominant large brown alga, and co-occurred with a diverse assemblage of red foliose algal species including *Callophyllis hombroniana*, *C. ornata*, *Cladhymenia oblongifolia*, *Curdiea flabellata*, *Euptilota formosissima*, *Hymenena palmata*, *Laingia hookeri*, *Rhodymenia obtusa*, *Schizoseris dichotoma* and *Streblocladia glomerulata* (Appendix 5: Table A5.2). Very low numbers of *Landsburgia quercifolia* and *Cystophora platylobium* were recorded. Green algae such as *Ulva* spp., *Caulerpa flexilis* and *Cladophora* spp. were occasionally recorded and *Codium convolutum* was common at Otago Peninsula sites. *Evechinus chloroticus* was rare (only one recorded), and other grazing invertebrates including *Haliotis australis*, *H. iris* and *Scutus breviculus* occurred in low numbers (Fig. 32B). *Haliotis australis* was the most common grazing invertebrate, and was found at all depths sampled. Starfishes, including *Pentagonaster pulchellus*, *Diplodontias* spp., *Stichaster australis* and the ophiuroid *Ophiopsammus maculata*, were found at low numbers (< 1/m^2). The percentage cover of crustose coralline algae was relatively low at these locations, with the substratum being covered largely by red algae, sediment and a suite of encrusting invertebrates, in particular sponges, bryozoans and solitary ascidians (Fig. 36C). The percentage cover of red foliose algae tended to be higher at the Catlins, whereas the percentages cover of crustose coralline algae, sponges and ascidians were higher at Otago Peninsula. The ascidian *Pyura pachydermatina* was abundant at depths greater than 4 m.

3.4.10 Fiordland bioregion

Sites from Fiordland locations were divided into four groups at the 70% similarity level (Fig. 33A), although Weka Point (Preservation Inlet) was separated from all other sites at the 55% similarity level. There were no clear differences in algal community structure among Fiordland locations; instead, groupings broadly corresponded to the position of sites in each fiord (outer, mid and inner), which was correlated with Slope, Sediment, Fetch and Evechinus along PC1 (Fig. 33B). Inner-fiord sites were more steeply sloping and had higher percentages cover of sediment, whereas outer-fiord sites had more gradually sloping reefs, and higher wave exposure and abundances of *Evechinus chloroticus. Landsburgia quercifolia*, *Lessonia variegata*, *Xiphophora gladiata* and *Carpophyllum flexuosum* were positively correlated with PC1 and had higher biomasses at outer-fiord sites, whereas *Ecklonia radiata*, *Macrocystis pyrifera*, red foliose algae, *Ulva* spp. and coralline turf were more typical of mid- and inner-fiord sites (Fig. 33C). Weka Point was grouped separately from other Fiordland sites, largely due to low biomasses of all macroalgal groups except *C. flexuosum*.

Bligh Sound

The inner-fiord sites at Bligh Sound had low algal biomass across all depths (Fig. 34A). Coralline turf dominated all depths (Fig. 34A, C). Red turfing algae also dominated the shallow stratum (< 2 m), and *Sargassum sinclairii*, *Cystophora retroflexa*, *Pterocladiella capillacea*, *Adamsiella angustifolia* and *Hormosira banksii* were also present. In the deeper strata, *Ecklonia radiata*, *S. sinclairii*, *C. retroflexa*, *Codium gracile*, *Asparagopsis armata*, *Dictyota papenfussii* and *Caulerpa brownii* were common. *Evechinus chloroticus* was not recorded, and

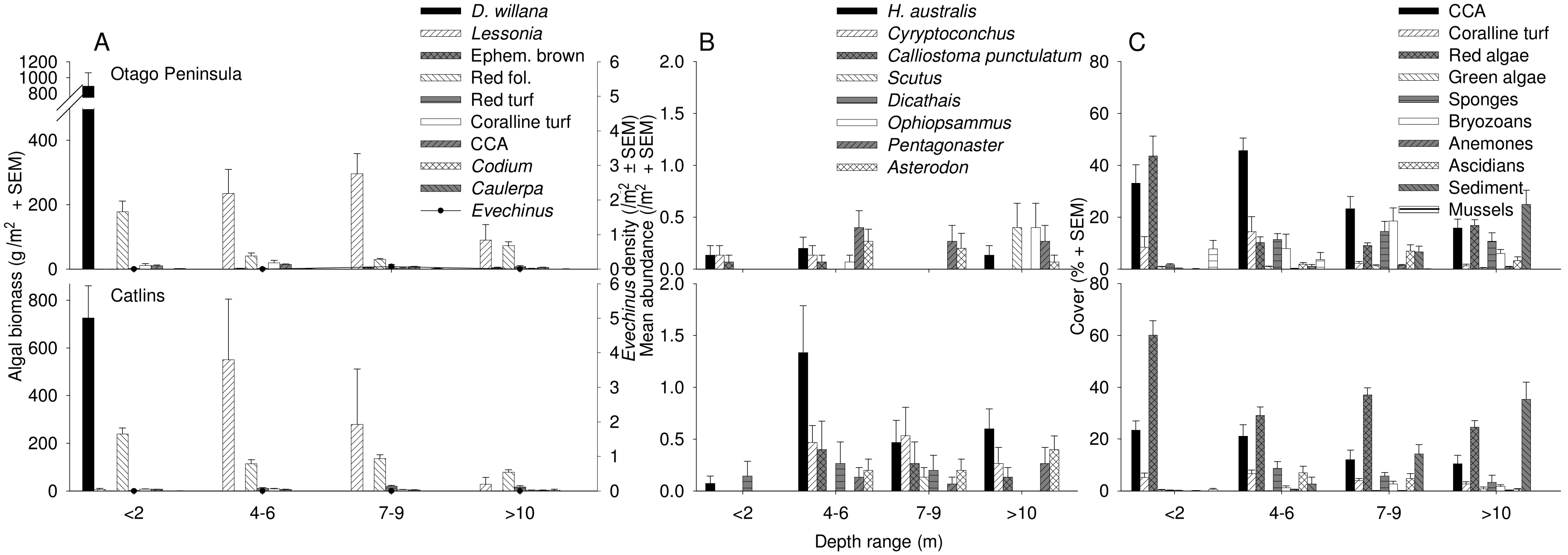
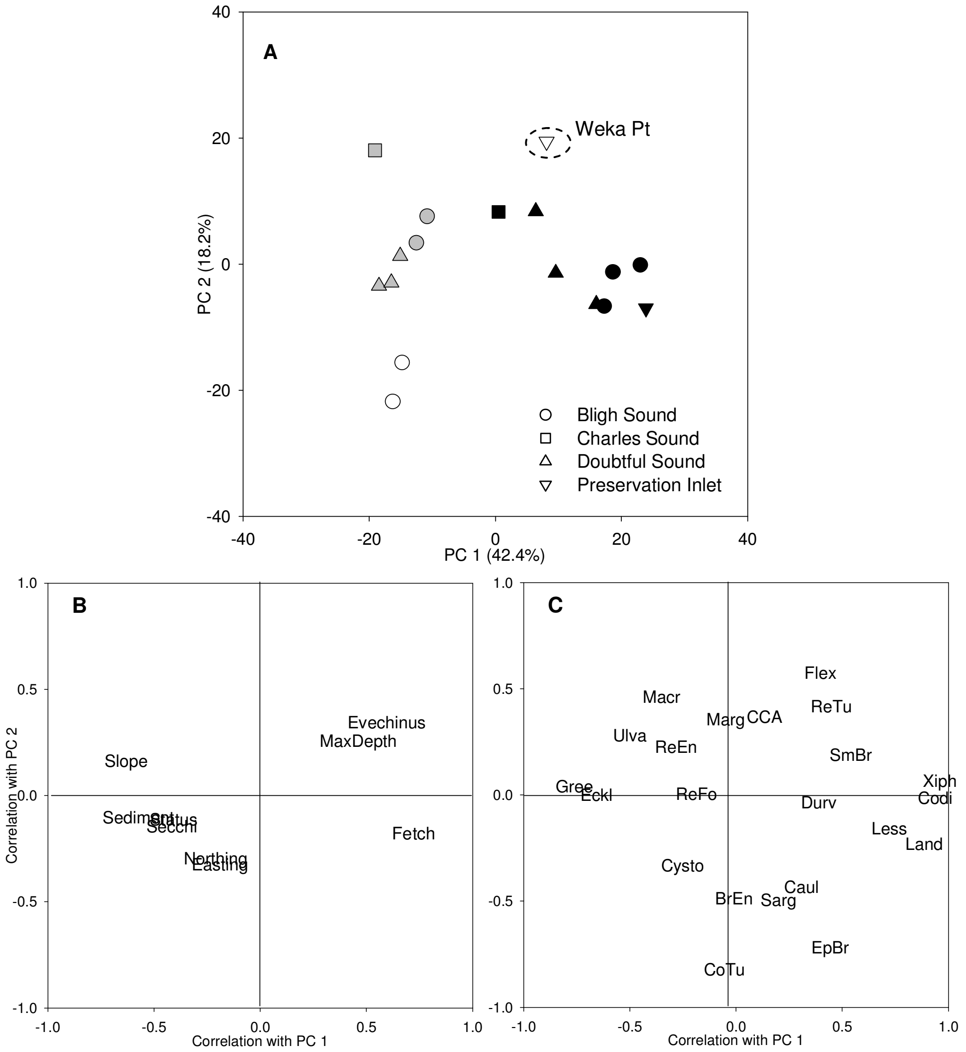


Figure 32. Depth-related patterns in biomass (g AFDW/m^2) of dominant macroalgal groups and density of *Evechinus chloroticus* (A), density of common mobile invertebrates (B) and cover of common encrusting forms (C) for locations within the Chalmers bioregion.

Figure 33. Principal coordinates analysis of sites sampled in the Fiordland bioregion, based on fourth-root transformed biomass of 23 macroalgal groups (A). Bi-plots give correlations between principal coordinates axes and environmental variables (B) and original macroalgal species groups (C) (see Table 1 for macroalgal group codes). Weka Point was distinct from other sites at the 55% similarity level. Remaining sites are shaded according to groupings identified at the 70% similarity level and reflect their relative positions in each fiord. Inner = white, mid = grey, outer = black.



Stichopus mollis was the only common mobile macroinvertebrate (Fig. 34B). Encrusting invertebrates were rare in the shallow stratum, but sponges and ascidians were common in the deepest strata (Fig. 34C).

The mid-fiord sites also had relatively low algal biomass across all depths (Fig. 34A). Large brown algae were rare in the 0–2 m stratum, except for the occasional patch of plants of *Macrocystis pyrifera* ($0.8 \pm 0.5/m^2$), and the substratum was dominated by crustose corallines, coralline turf, red algae (e.g. *P. capillacea*) (Fig. 34C). *Perna canaliculus* also covered a small proportion of the substratum (< 5%). At greater depths, *Ecklonia radiata* and *Carpophyllum flexuosum* formed a sparse assemblage and *Evechinus chloroticus* was present in low numbers. Red foliose algal species were also common in the deeper strata, e.g. *Asparagopsis armata*, *Anotrichium crinitum*, *Plocamium* spp., *Rhodophyllis gunnii* and *Euptilota formosissima*. The green algae *Codium gracile* and *Caulerpa brownii*, and the small brown algae *Zonaria* spp. and *Halopteris* sp., were also common. *Marginariella urvilliana* occurred at low numbers at 10–12 m and had a distinct sheltered morphology, with broad fronds (Adams 1994). Coralline turf, red foliose algae and sediment dominated the substratum in the

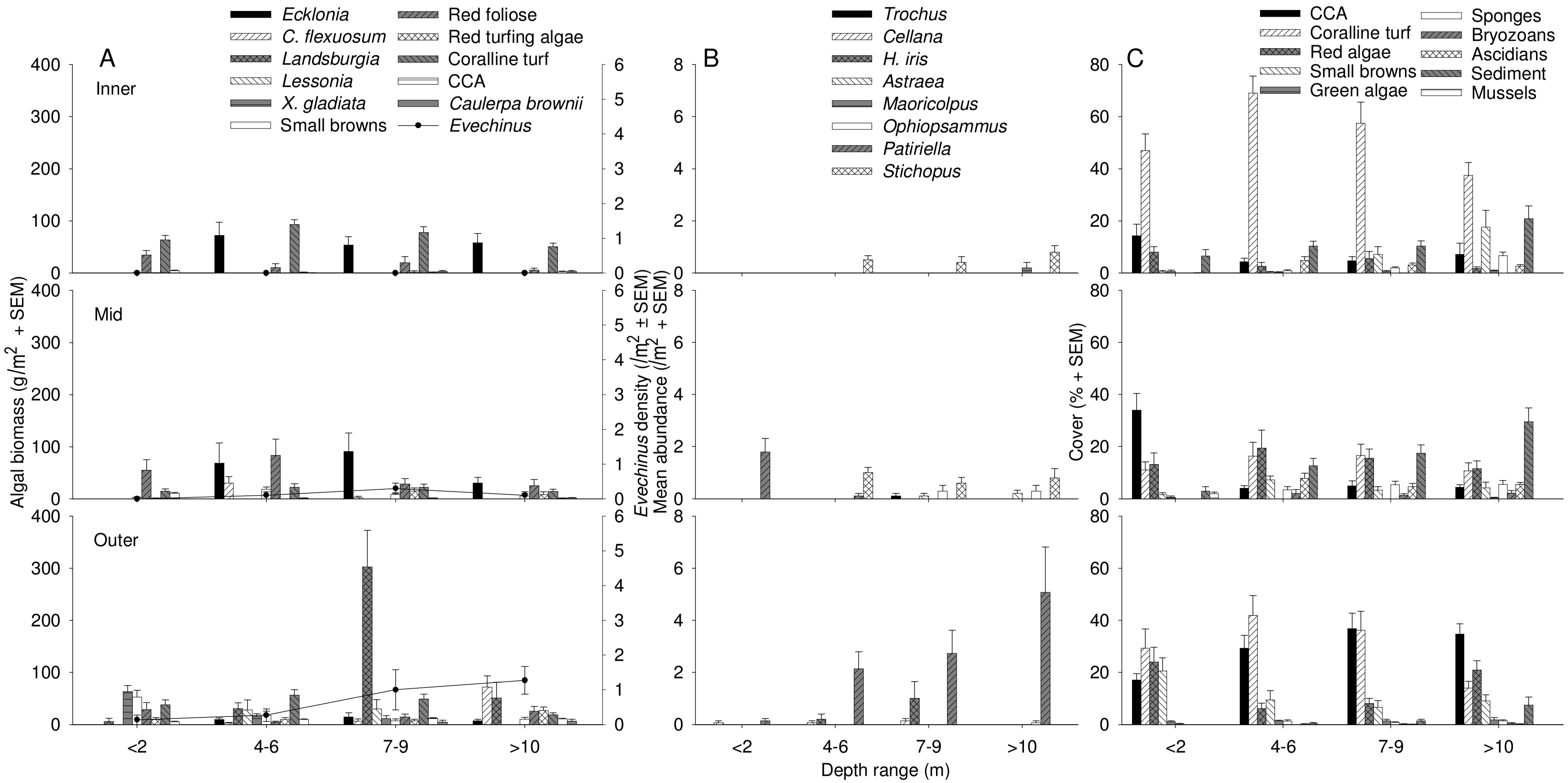


Figure 34. Depth-related patterns in biomass of (g AFDW/m^2) of dominant macroalgal groups and density of *Evechinus chloroticus* (A), density of common mobile invertebrates (B) and cover of common encrusting forms (C) for site groups at Bligh Sound within the Fiordland bioregion.

deepest strata, although sponges, ascidians and bryozoans were also common (Fig. 34C). *Patiriella* spp. occurred at shallow depths, whereas *Stichopus mollis* and *Ophiopsammus maculata* were common in the deeper strata (Fig. 34B).

The outer, coastal sites at Bligh Sound had extensive stands of large *Xiphophora gladiata* (up to 80 cm total length) in the shallow stratum and extending down to c. 4 m depth (Fig. 34A). *Durvillaea willana* was also present in low numbers in the immediate subtidal, along with a variety of red turfing and smaller brown algal species (e.g. *Camontagnea hirsuta*, *Lophurella hookeriana*, *Plocamium* spp., *Halopteris* sp., *Colpomenia sinuosa*, *Microzonia velutina* and *Glossophora kunthii*). At 4–6 m, *X. gladiata* was interspersed with *Lessonia variegata*, *Landsburgia quercifolia*, *Ecklonia radiata*, red foliose algae (e.g. *Asparagopsis armata*, *Plocamium* spp., *R. gunnii*), small brown algae (e.g. *Halopteris* sp., *Dictyota papenfussii*, *Carpomitra costata*, *Zonaria* spp.), green algae (*Caulerpa brownii*, *Codium convolutum*) and coralline turf. The morphology of *E. radiata* was characteristic of highly wave exposed sites, having short stipes and long primary laminae. *Landsburgia quercifolia* dominated at 7–9 m and co-occurred with short *Carpophyllum flexuosum* plants (< 50 cm total length) at 10–12 m. The substratum was dominated by crustose corallines, coralline turf, red algae, small brown algae and the green alga *Caulerpa brownii* (Fig. 34C). Encrusting invertebrates and sediment covered a small proportion of the reef (< 1%). Individual *Evechinus chloroticus* were large and they increased in abundance with depth, typically being found around the base of large boulders or rocky outcrops. *Haliotis iris* also occurred in isolated patches at some sites (Fig. 34B). *Patiriella* spp. was the most common mobile invertebrate and its abundance also increased with depth.

Charles Sound

At the mid-fiord site (Charles inner), large brown algae were absent from the shallow stratum and a mixture of red (*Gigartina livida*, *Polysiphonia* spp., *Pterocladiella capillacea*) and green (*Ulva* spp., *Cladophora* sp.) algae dominated (Fig. 35A). Mussels (*Mytilus* sp.) were also recorded in this stratum, but they covered only a small proportion of the reef (< 5%). At 4–6 m, crustose coralline algae and coralline turf dominated, with small amounts of *Ecklonia radiata*, *Carpophyllum flexuosum* and *Macrocystis pyrifera* present. In the deeper strata (7–9 m and 10–12 m), *E. radiata* dominated. Plants of *E. radiata* were large (up to 100 cm total length) and they resembled a forest more typical of Northern locations. Crustose coralline algae were the dominant substratum cover in the deeper strata, and sponges, bryozoans and ascidians covered a small percentage of the substratum (Fig. 35A). Mobile macroinvertebrates were absent from the shallow stratum, but at greater depths *Trochus viridis*, *Astraea heliotropium* and *Stichopus mollis* were common (Fig. 35C). At the outer Charles Sound site (Charles outer), *Durvillaea willana* and *Xiphophora gladiata* dominated the 0–2 m depth stratum (Fig. 35A). Crustose corallines were the dominant cover beneath the *D. willana*, and *Ballia callitrichia*, *Camontagnea hirsuta* and *Ulva* spp. were also common. *Ecklonia radiata* and *Carpophyllum flexuosum* were the dominant large brown algal species at greater depths, forming a sparse assemblage interspersed with *Caulerpa brownii* and red foliose algal species (e.g. *Euptilota formosissima*, *Rhodymenia* sp., *Plocamium* spp., *Rhodophyllis gunnii*, *Asparagopsis armata*). *Marginariella urvilliana* was also common at

4–6 m. The substratum in the deepest strata was covered by a mixture of crustose corallines, coralline turf, red algae, sponges, ascidians, bryozoans and sediment (Fig. 35C). *Patiriella* spp. was the only commonly recorded mobile invertebrate species across all depths (Fig. 35B).

Doubtful Sound

Three sites were sampled in outer Doubtful Sound, and three in the mid-fiord area at the intersection between Thompson and Doubtful Sounds. At mid-fiord sites, the shallow zone was comparable to the mid-fiord site in Charles Sound, with an absence of large brown algae, a dominance of red foliose algae (*Polysiphonia* spp., *Gigartina* spp., *Gracilaria chilensis*, *Delisea elegans*), and green algae (*Chaetomorpha aerea*, *Cladophora* spp., *Ulva* spp.) (Fig. 35A). However, barnacles and mussels (*Perna canaliculus* and *Mytilus* sp.) were also dominant in this depth stratum (5–50% cover). *Evechinus chloroticus* was absent from the shallow stratum, but most abundant at 4–6 m, where large brown algae were rare and the substratum was dominated by crustose corallines, coralline turf, red foliose algae and sediment (Fig. 35C). *Ecklonia radiata* was the dominant large brown algae at greater depths (7–9 m and 10–12 m), but was generally sparse, and coralline turf and red foliose algae (e.g. *Euptilota formosissima*, *Rhodymenia* sp., *Plocamium* spp., *Rhodophyllis gunnii* and *Asparagopsis armata*) dominated. *Carpophyllum flexuosum*, *Marginariella urvilliana* (sheltered morphology) and *Sargassum verruculosum* were also present in low densities in the deeper strata. The substratum was dominated by a red foliose algal mat, coralline turf and sediment, with a low percentage cover of sponges and ascidians (Fig. 39C). *Patiriella* spp. was common in the shallow stratum, but rarer at greater depths, where *Stichopus mollis* tended to be more common (Fig. 35B). Herbivorous gastropods were rare.

At sites located at the entrance of Doubtful Sound, the algal communities at all depths were characterised by a mixture of large brown algae, red foliose algae and green algae (Fig. 35A). The algal assemblages in the shallow stratum were similar to those of the outer Bligh Sound sites, with *Xiphophora gladiata* and *Glossophora kunthii* being abundant, along with coralline turf and several short turfing algal species (e.g. *Halopteris* sp. (probably *H. congesta*), *Microzonia velutina*, *Lophurella hookeriana*). *Lessonia variegata* and *Landsburgia quercifolia* were also common in the shallow stratum at some of the outer sound sites. *Lessonia variegata* was most common in the 4–6 m stratum, whereas *Landsburgia quercifolia* and *Carpophyllum flexuosum* were common at all depths excluding the 0–2 m stratum. *Ecklonia radiata* occurred in low numbers at all depths but was most abundant in the deepest stratum. Red foliose algae such as *Euptilota formosissima*, *Plocamium* spp., *Rhodophyllis gunnii*, *Anotrichium crinitum* and *Delisea elegans* were common at all depths, whereas *Caulerpa brownii* was most abundant at 10–12 m. *Evechinus chloroticus* occurred in dense patches in the 4–6 m and 7–9 m depth strata. Mobile macroinvertebrates were rare except for *Patiriella* spp. and *Ophiopsammus maculata* (Fig. 35B). The percentage cover of sponges and bryozoans tended to increase with depth, whereas the cover of coralline turf declined with depth (Fig. 35C).

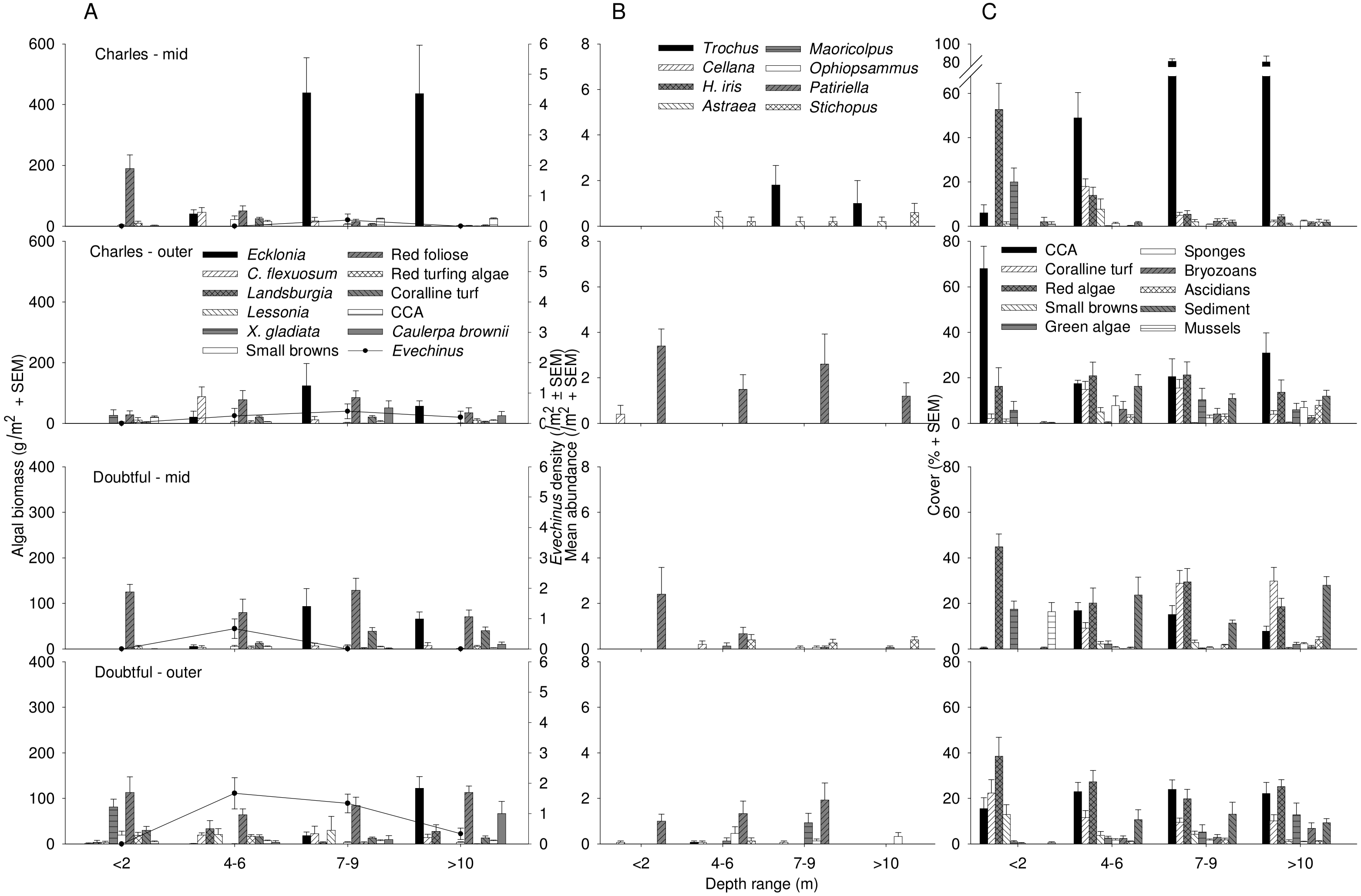


Figure 35. Depth-related patterns in biomass (g AFDW/m^2) of dominant macroalgal groups and density of *Evechinus chloroticus* (A), density of common mobile invertebrates (B) and cover of common encrusting forms (C) for site groups at Charles and Doubtful Sound within the Fiordland bioregion.

Preservation Inlet

Two sites were sampled at Preservation Inlet, one very sheltered site in the inner fiord (Weka Point) and one more exposed site at the fiord entrance (Sandfly Point). Reef communities varied considerably between these two sites (Fig. 36A). Large brown algae (*Xiphophora gladiata*, *C. flexuosum* and *C. retroflexa*) were restricted to the shallow stratum at Weka Point and CCA dominated at greater depths. The biomass and cover of other groups was low at these depths (Fig. 36C). *Evechinus chloroticus* was abundant across all depths sampled and *Cellana stellifera*, *Patiriella* spp., *Maoricolpus roseus* and *Stichopus mollis* were also common (Fig. 36B). The mussel *Mytilus* sp. was also a dominant component in the shallow stratum.

Sandfly Point was more similar to other outer Fiordland sites with *X. gladiata*, red foliose algae and coralline turf dominating the shallow strata (0–2 m and 4–6 m) and *Landsburgia quercifolia* and *Caulerpa brownii* dominating at 7–9 m (Fig. 36A). The deepest stratum (10–12 m) was dominated by *C. brownii* (> 50% cover). *Ecklonia radiata*, *Marginariella* spp., *Lessonia variegata* and *C. platylobium* were notably absent. Bryozoans, ascidians and sediment were an important component in the deeper strata (Fig. 36C). *Evechinus chloroticus* was recorded in relatively high numbers at 4–6 m and 7–9 m where it occurred in large patches. Other mobile macroinvertebrates were rare at all depths (Fig. 36B).

3.4.11 Stewart Island bioregion

The sites sampled in the Stewart Island bioregion spanned a large environmental gradient, from sheltered reefs inside Paterson Inlet to offshore islands and the highly exposed southern coast of the South Island. Based on algal community structure, sites were divided into six groups which broadly corresponded to this gradient (Fig. 37A). The sites from inside Paterson Inlet (excluding Octopus Island) formed one group (termed 'very sheltered') and were separated from the remaining more open coast sites at the 55% similarity level. The remaining sites were divided among five groups that broadly corresponded to differences in wave exposure. The most sheltered of these included sites on the northeastern coast of Stewart Island (termed 'sheltered'), while the most exposed sites sampled at Green Islets formed their own group ('Green Islets'). Three highly exposed sites formed another group and these were characterised by large *Durvillaea willana* forests and have been termed the 'Durvillaea' group. The remaining sites were divided among two groups: one including moderately exposed sites from Titi Islands, Port Adventure, Ruapuke Island and Codfish-Ruggedy (termed 'moderately exposed') and the other group included the more exposed sites from Bluff, Codfish-Ruggedy, Ruapuke and Titi Islands (termed 'highly exposed'). Fetch and Sediment were strongly correlated with PC1 and each explained 20% of the variation among sites (Fig. 37B, Table 4). These two variables were inversely correlated and sediment cover was typically highest at the most sheltered sites. *Macrocystis pyrifera* and *Carpophyllum flexuosum* were positively correlated with PC1 and more common at more sheltered sites, while *Lessonia variegata*, *Landsburgia quercifolia*, red foliose algae and coralline turf were negatively correlated and more abundant at exposed sites (Fig. 37C). Evechinus was positively correlated with PC2 and both *Ecklonia radiata* and *Marginariella* spp. were negatively correlated. Evechinus, Sediment and Fetch were all significantly related to algal community structure and explained 32% of the variation among sites (Table 4).

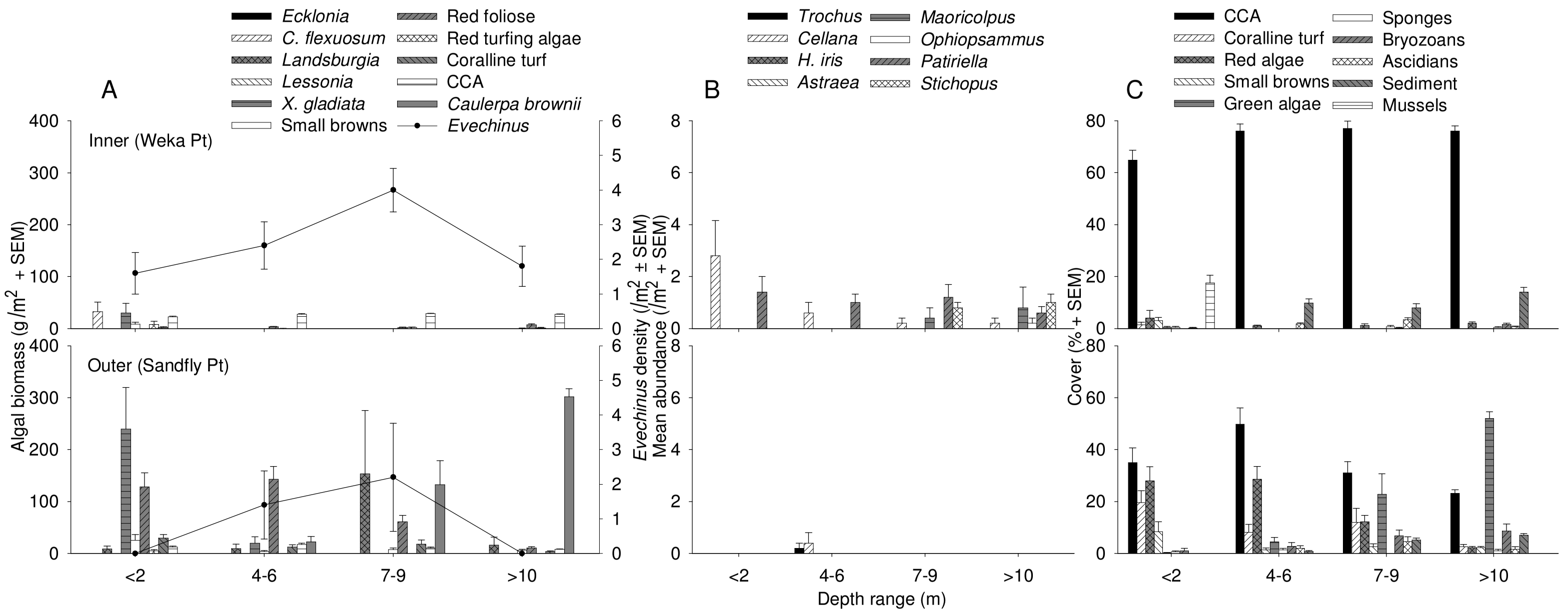
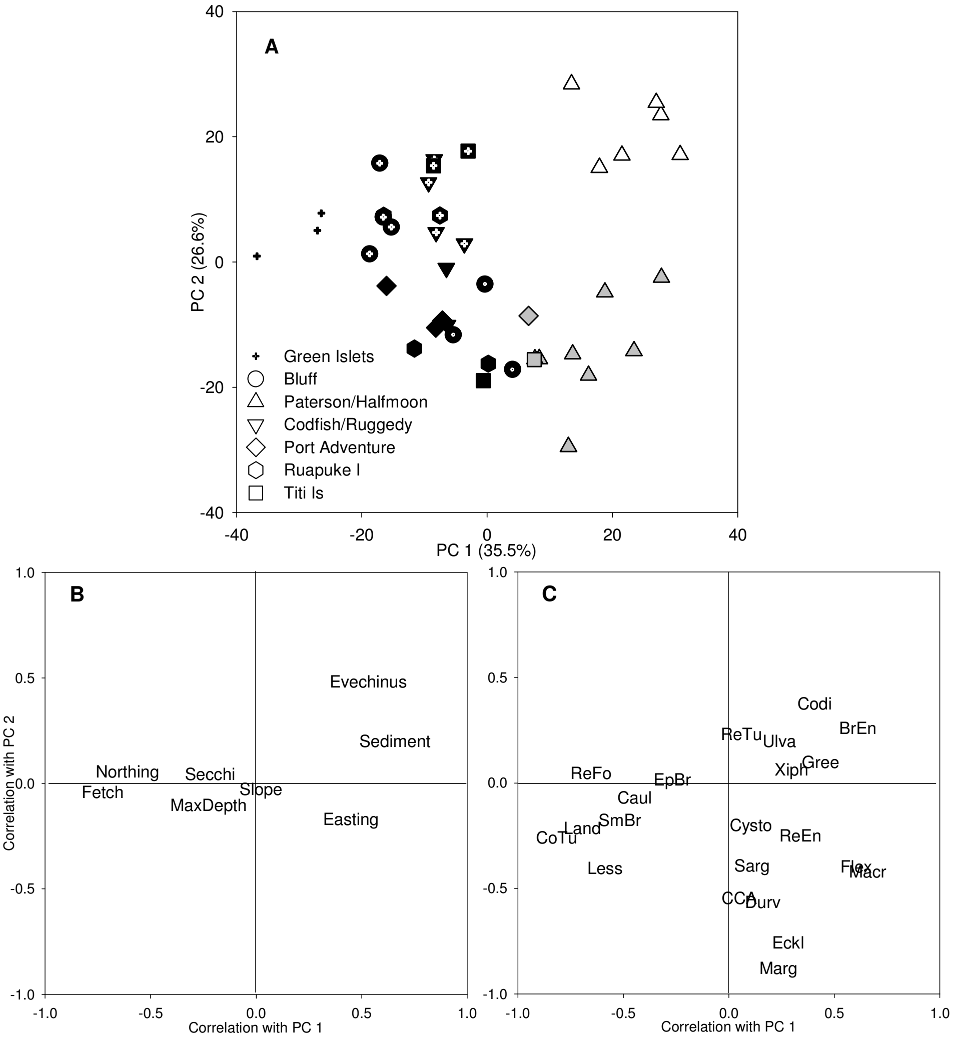


Figure 36. Depth-related patterns in biomass (g AFDW/m^2) of dominant macroalgal groups and density of *Evechinus chloroticus* (A), density of common mobile invertebrates (B) and cover of common encrusting forms (C) for site groups at Preservation Inlet within the Fiordland bioregion.

Figure 37. Principal coordinates analysis of sites sampled in the Stewart Island bioregion, based on fourth-root transformed biomass of 23 macroalgal groups (A). Bi-plots give correlations between principal coordinates axes and environmental variables (B) and original macroalgal species groups (C) (see Table 1 for macroalgal group codes). Sites shaded according to groupings identified at the 70% similarity level. White = very sheltered, grey = sheltered, black = four exposed groups (blank = moderately exposed, dots = *Durvillaea*, cross-hair = highly exposed, and Green Islets sites (+) formed their own group). See section 3.4.11 for explanation of groups.



Very sheltered: Inner Paterson Inlet

All sites inside Paterson Inlet, excluding Octopus Island, were grouped together in the very sheltered group based on algal community structure (Fig. 37). *Evechinus chloroticus* was abundant at these sites across all depths and large brown algae (predominantly *Xiphophora gladiata* and *Carpophyllum flexuosum*) were restricted to a shallow band (< 1 m depth) (Fig. 38A). Several other species including *Cystophora scalaris*, *C. retroflexa*, *Macrocystis pyrifera*, *Marginariella boryana* and the green alga *Codium convolutum* were also common in this stratum. In the deepest stratum an assemblage of red foliose algae often occurred on the sand-reef boundary (e.g. *Dasya collabens*, *Delisea elegans*, *Adamsiella chauvinii*, *Asparagopsis armata*, *Rhodymenia* spp. and *Brongniartella australis*). Mobile macroinvertebrates were abundant, in particular *Cellana stellifera* at 0–2 m and 4–6 m, and *Maoricolpus roseus* at 7–9 m and 10–12 m (Fig. 38B). The starfish *Patiriella* spp., ophiuroid *Ophiopsammus maculata* and holothurians *Stichopus mollis* and *Ocnus* spp. were common at all depths. Low numbers of *Haliotis iris* and *H. australis* were recorded at some sites. The percentage cover of crustose coralline algae declined with depth and sediment increased (Fig. 38C). Coralline turf was rare, and sponges, ascidians and bare rock were common.

Sheltered

The sites in this group were mainly situated on the open northeastern coast of Stewart Island (in the lee of the prevailing southwesterly swell) and included Octopus Island and open coast sites at Paterson Inlet and a site from both Titi Islands (Edwards Island), Port Adventure (Browns Garden) and the Codfish-Ruggedy locations (Lucky Point). These sites were dominated by large brown algae at all depths (Fig. 38A). The shallow stratum was dominated by *Marginariella urvilliana*, *Xiphophora gladiata* and at some sites *Lessonia variegata* (Native North) and *Durvillaea willana* (West Head, Bob's Point, Horseshoe). *Glossophora kunthii*, *Spatoglossum chapmanii*, *Halopteris* sp. and *Codium convolutum* were also common in this zone. The deeper strata were characterised by a mixed assemblage of *Macrocystis pyrifera*, *Ecklonia radiata*, *Carpophyllum flexuosum*, *Marginariella boryana* and *Cystophora platylobium* (Fig. 38A). The biomass of red foliose algae (e.g. *Euptilota formosissima*, *Plocamium* spp., *Delisea plumosa*, *D. elegans*, *Rhodophyllis gunnii* and *Callophyllis* spp.) tended to increase with depth and the small brown algae *Sporochnus stylosus*, *Halopteris* sp., *Carpomitra costata* and *Desmarestia ligulata* were also common. Crustose coralline algae were the dominant substratum cover at all depths, although there was also a high percentage cover of sediment at 10–12 m (Fig. 38C). Percentage cover of coralline turf was highest in the shallowest stratum, whereas the percentage cover of red algae, small browns, ascidians and sponges was greater in deeper strata. *Evechinus* were generally rare, except for the two sites located at the entrance of Paterson Inlet (Native North, Neck North) where they were abundant in the deepest strata (7–9 m and 10–12 m) and macroalgal biomass was reduced. *Ophiopsammus maculata*, *Patiriella* spp., *Stichopus mollis* and *Trochus viridis* were the most common mobile macroinvertebrate species, but overall abundance was considerably lower than at the inner Paterson Inlet sites (Fig. 38B).

Moderately exposed

This group included a selection of moderately exposed sites from Titi Islands (Herekopere), Port Adventure (Tia Island, Lords River Head, Owens Island), Ruapuke Island (North Head, Bird Rock, Caroline Bay) and Codfish Island (Codfish East, Codfish Southeast). At these sites *Xiphophora gladiata*, *Lessonia variegata* and *Marginariella urvilliana* typically dominated the shallow stratum, while *L. variegata* and, to a lesser extent, *Landsburgia quercifolia*, dominated at 4–6 m (Fig. 38A). The deeper strata were characterised by a mixed assemblage of *Ecklonia radiata*, *Carpophyllum flexuosum*, *Lessonia variegata*, *Landsburgia quercifolia*, *Cystophora* spp., *M. boryana*, *Caulerpa brownii* and red foliose algae. The biomass of *E. radiata* was generally lower than at sites in the sheltered group, while the cover of red algae was typically higher and cover of sediment lower (Fig. 38C). Patches of *Evechinus* were common in the deepest strata at most of the sites excluding the Ruapuke Island site where they were rare. Other mobile macroinvertebrate species generally occurred at lower numbers compared to sites in the sheltered group (Fig. 38B).

Durvillaea

This group included three sites at Bluff (Pig Island, Tiwai Point and Stirling Point) where *Durvillaea willana* formed large forests in the shallow subtidal to depths of

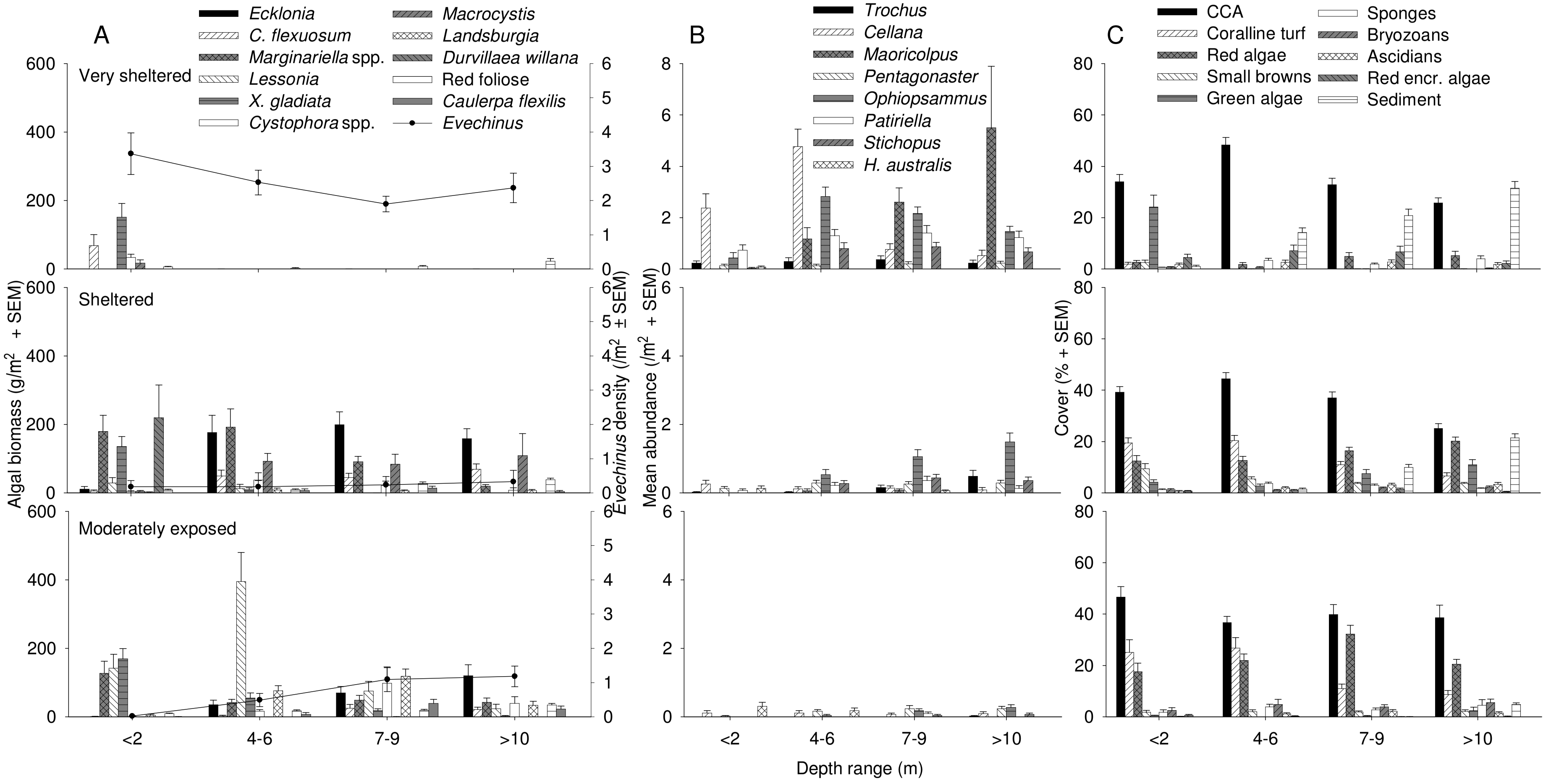


Figure 38. Depth-related patterns in biomass (g AFDW/m^2) of dominant macroalgal groups and density of *Evechinus chloroticus* (A), density of common mobile invertebrates (B) and cover of common encrusting forms (C) for the Very sheltered, Sheltered and Moderately exposed site groups within the Stewart Island bioregion. Sites from each location are grouped according to the groups identified in Fig. 37.

4–5 m (Fig. 39A). These sites also had high biomasses of *Marginariella urvilliana* and/or *Lessonia variegata* at mid-depths, with *Cystophora platylobium* and red foliose algae dominating the deepest stratum. Crustose corallines were the dominant cover at shallow depths beneath the *D. willana* canopy while, in the deeper strata, red foliose algae, sediment and ascidians were also important components (Fig. 39C). *Pyura pachydermatina* was particularly abundant at Pig Island (25.7 ± 6.0/m^2) and Stirling Point (12.2 ± 4.2/m^2). *Evechinus chloroticus* was generally restricted to the deepest stratum where it was recorded in low numbers. Mobile macroinvertebrates were present in low numbers, although *Maoricolpus roseus* was common in the deepest stratum at Stirling Point (Fig. 39B). Paua (*Haliotis iris*) were generally rare but small patches of large individuals (> 150 mm) were observed at Tiwai Point.

Highly exposed

The remaining Bluff sites (Oraka Point, Shag Rock, Barracouta Point, Lookout Point) and the most exposed sites from Codfish-Ruggedy (North Sealers, Ruggedy NE, Ruggedy Passage, Black Rock Point), Ruapuke Island (South Islets) and Titi Islands (Bench North, Bench SE Point) made up this group. The biomass of large brown algae was typically reduced at these sites across all depths (Fig. 39A), with *Xiphophora gladiata* and *Lessonia variegata* dominating the shallow stratum (< 2 m), and *Landsburgia quericfolia*, red foliose algae and *Caulerpa brownii* at greater depths. *Lessonia variegata*, *Marginariella* spp. and *Cystophora platylobium* also occurred at low biomasses. In general, the deeper strata at these sites were dominated by a mix of red foliose algae, *C. brownii*, ascidians, sponges and sediment (Fig. 39C). *Evechinus chloroticus* was recorded at low numbers in the deeper strata, but large patches (> 100 individuals) were observed at depths greater than 10 m at a number of sites (e.g. Shag Rock, Lookout Point). Individual *E. chloroticus* were typically large (up to 190 mm TD), and no individuals smaller than 100 mm were recorded (Appendix 6). Other mobile macroinvertebrates occurred at low numbers, e.g. *Cellana stellifera* and *Haliotis iris* in the shallow stratum and *Ophiopsammus maculata* in the deepest stratum (Fig. 39B).

Green Islets

All of the sites sampled at the Green Islets were highly exposed to the south and southwest and, based on algal community structure, formed their own distinct group (Fig. 37). *Lessonia variegata* was the dominant large brown algae at each site and across all depths (Fig. 39A). *Landsburgia quercifolia* was the only other common large brown algae and typically occurred in the deeper strata. A number of common large brown algal species were notably absent from these sites, e.g. *Xiphophora gladiata*, *Cystophora platylobium*, *Marginariella* spp., *Durvillaea willana*, *Ecklonia radiata* and *Carpophyllum flexuosum*. Coralline turf and red foliose algae were a dominant component of the algal assemblages at all depths. CCA, coralline turf, red foliose algae, bryozoans and sponges were the primary space occupiers (Fig. 39C). *Evechinus chloroticus* was generally absent from depths less than 10 m, but occurred in dense patches in the deepest stratum (10–12 m) at Archway and NW Bay. All individual *E. chloroticus* recorded were > 100 mm TD (Appendix 6). *Haliotis australis*, *Ophiopsammus maculata* and *Patiriella* spp. were the most common mobile macroinvertebrates, but generally occurred in low numbers (Fig. 39B).

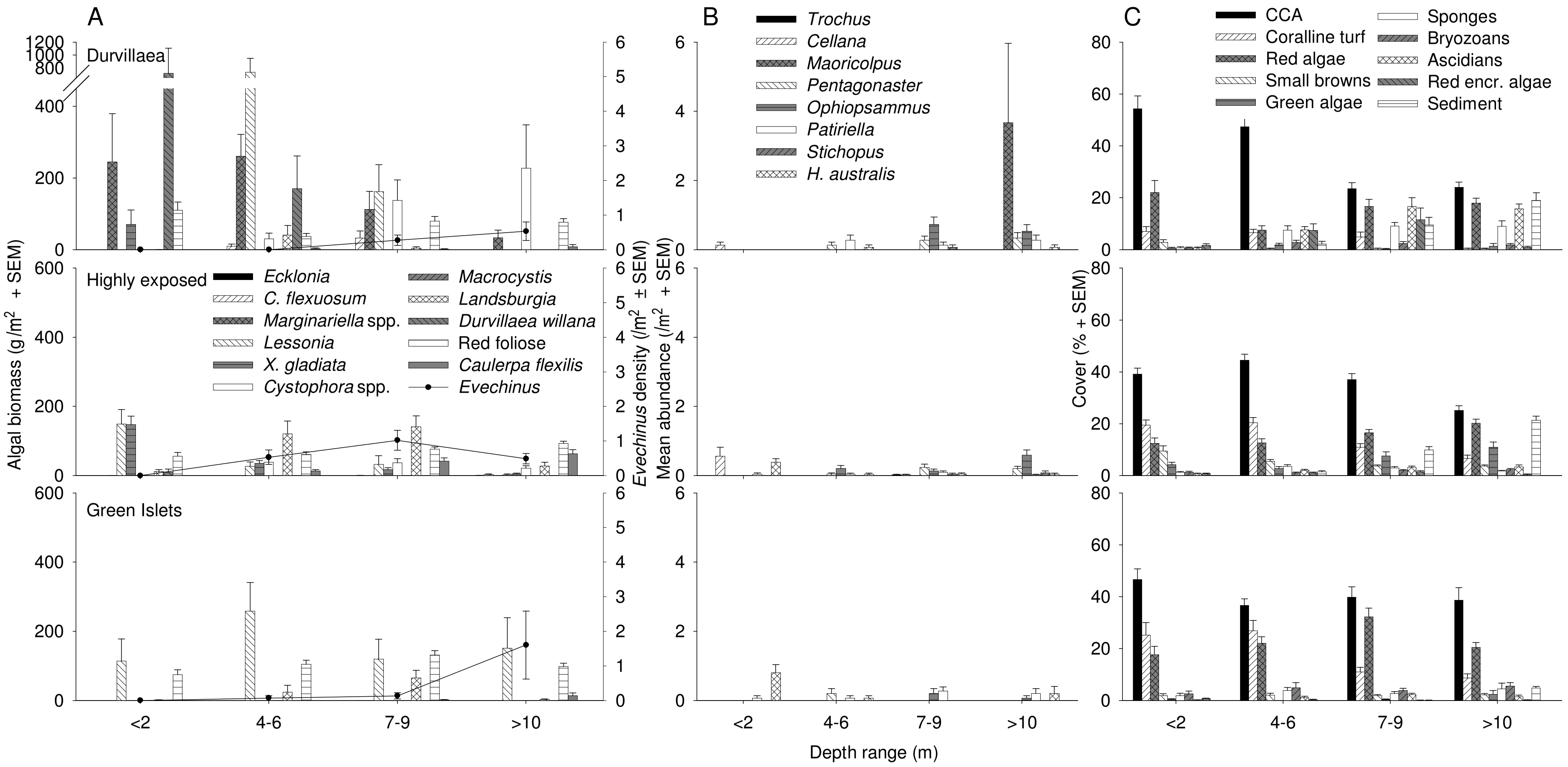


Figure 39. Depth-related patterns in biomass (g AFDW/m^2) of dominant macroalgal groups and density of *Evechinus chloroticus* (A), density of common mobile invertebrates (B) and cover of common encrusting forms (C) for the *Durvillaea*, Highly exposed and Green Islet groups within the Stewart Island bioregion (site groups identified in Fig. 37).

4. Discussion

4.1 BIOGEOGRAPHIC DISTRIBUTION OF KEY SPECIES

This study provides quantitative information on the distribution of a large number of shallow subtidal reef species throughout mainland New Zealand based on a consistent methodology employed across all sites. While we were unable to sample large stretches of coast (e.g. Wairarapa and the northwestern coast) and the one-off sampling procedure may have missed particular species that are present at certain sites and locations, this study provides an unprecedented quantitative description of subtidal reefs across mainland New Zealand that will provide a basis for futher study of New Zealand's reefs.

The biogeographic classification of Shears et al. (in press) based on this national dataset provided a spatial framework within which to describe regional and national scale variation in communities. One of the most prevalent patterns identified by Shears et al. (in press) was a clear division in algal species composition between the Northern and Southern biogeographic provinces. In the present study we found that algal community structure based on the biomass of 23 algal species groups exhibited a similar division between provinces (Fig. 2). In general, several dominant macroalgal species had clear Northern (e.g. *C. maschalocarpum*, *C. plumosum*, *C. angustifolium*, *Osmundaria colensoi*, *Pterocladia lucida* and *Caulerpa flexilis*) or Southern (e.g. *Durvillaea willana*, *Marginariella* spp., *Macrocystis pyrifera*, *Hymenena* spp. and *Caulerpa brownii*) distributions. Few species, however, were solely restricted to either the Northern or Southern Province. For example, *Marginariella boryana* and *Macrocystis pyrifera* had Southern distributions, but both species were found at one site at Long Island (classified in the Northern Province). Similarly, while a shallow band of *Carpophyllum maschalocarpum* was a characteristic feature of locations in the Northern Province, *C. maschalocarpum* was also an important component at some locations in the Southern Province (Wellington, Kaikoura Peninsula and Banks Peninsula North). *Carpophyllum maschalocarpum* was not recorded at any of the locations on the West Coast of the South Island, despite being reported from Open Bay Islands (Neale & Nelson 1998) and Fiordland (Nelson et al. 2002).

Carpophyllum angustifolium and *C. plumosum* were found only at Northeastern locations, although *C. plumosum* occurs at Gisborne (Hogan et al. 1991) and on the Wairarapa Coast (Nelson 1994). *Carpophyllum angustifolium* typically dominated the sublittoral fringe on exposed reefs throughout the Northeastern bioregion, but was not recorded at Cape Karikari or Cape Reinga in this study. Moore (1961) reported the northerly range of this species to about Cape Brett (Moore 1961); however, it has been recorded from North Cape and the Three Kings Islands (Nelson 1994). At highly exposed Northern locations (e.g. Cape Reinga, Gannet Rock) *C. maschalocarpum* exhibits a long slender morphology resembling *C. angustifolium* (NS, pers. obs.). Furthermore, potential hybrids of these species may complicate these distributional patterns and additional work on the taxonomy and ecology of these species is needed to resolve these contrasting patterns.

In contrast to the other *Carpophyllum* species, which characterise the shallow subtidal fringe in Northern locations, *C. flexuosum* typically occurred in deeper water and was found throughout the country. This species formed extensive forests in areas with low wave action (e.g. Long Bay, Long Island and the eastern side of Kapiti Island) or areas with high turbidity (e.g. Banks Peninsula North and Gisborne). Schiel & Hickford (2001) found *C. flexuosum* to be the dominant fucalean alga at several Southern locations, e.g. Banks Peninsula North and Fiordland. However, we found *C. flexuosum* to have a rather patchy distribution in Southern New Zealand, as it was not recorded at Otago Peninsula, Catlins, Kaikoura or several locations on the west coast (e.g. Raglan, New Plymouth, and all Buller and Westland locations except Open Bay Islands).

Ecklonia radiata was the most commonly recorded large brown algal species and made up 25.5% of total algal biomass. *Ecklonia radiata* occurs throughout New Zealand, but was notably absent from some locations including Otago Peninsula, Catlins, Bluff, Green Islets, Abel Tasman, Nelson and numerous west coast locations. The large mono-specific stands of *E. radiata*, typical of the Northeastern bioregion (Choat & Schiel 1982), were not observed in any other areas except Mahia, Kapiti Island and occasional sites in the Fiordland (Charles inner) and Stewart Island (Tia Island, Lucky Point and Edwards Island) bioregions. At other Southern locations (e.g. Wellington, Kaikoura, Paterson Inlet, Codfish-Ruggedy, Ruapuke Island, Titi Islands, Port Adventure and outer-fiord sites), *E. radiata* was found in a mixed assemblage with other large brown algal species, e.g. *Lessonia variegata*, *Landsburgia quercifolia*, *Cystophora* spp. and *Marginariella* spp., which is consistent with Southern sites examined by Choat & Schiel (1982) and Schiel & Hickford (2001). The absence of *E. radiata* from some locations is probably the result of a combination of factors including water temperature, high wave action, turbidity, sandscour and urchin grazing. For example, on the west coast, *E. radiata* was only found at Fiordland locations, Open Bay Islands and Gannet Rock sites, and one offshore site at New Plymouth (Seal East). It is probably absent from most other west coast coastal sites (e.g. Raglan, Karamea South, Cape Foulwind, Jackson Head and Cascades) because of extreme wave action and high levels of sandscour and turbidity. At the west coast offshore islands, *E. radiata* appeared to be restricted to either shallow (e.g. Gannet Rock) or deep (e.g. New Plymouth) water by high densities of *Evechinus chloroticus* at mid-depths. *Ecklonia radiata* does occur at some coastal sites near New Plymouth, but high turbidity limits its distribution in these areas (R. Cole, NIWA, pers. comm. 2006). High abundances of sea urchins may be responsible for the absence of *E. radiata* from some locations, e.g. Abel Tasman and Nelson, as algal assemblages in these locations were dominated by *C. maschalocarpum* and *C. flexuosum*, two species that are considerably more resistant to grazing than *E. radiata* (Cole & Haggitt 2001). Low water temperatures may also play a role in excluding *E. radiata* from some parts of New Zealand. For example, while *E. radiata* has been reported in the Otago Harbour (Batham 1956) and observed on the outer coast at Karitane (J. Fyfe, DOC, pers. comm. 2006), it was not recorded in the Chalmers bioregion in this study. *Ecklonia radiata* does occur further south, at Stewart Island and the Snares Islands, but is absent from other more southern subantarctic islands (Nelson 1994). The close proximity of the Otago coast to the subtropical convergence means that water temperatures in this area are typically colder than those at Stewart Island and the Snares Islands (Heath 1985).

Some species exhibited clear Southern distributions. For example, *Macrocystis pyrifera*, which is associated with cooler water temperatures (Hay 1990), was found only at South Island locations and at one North Island site (Palmer Head, Wellington). Although *M. pyrifera* was not recorded at Otago Peninsula or Catlins sites, extensive forests are present north of Nugget Point where there is some protection from the large southerly swell (Fyfe 1992). *Durvillaea willana* was found only at Southern New Zealand locations, being most abundant at the Catlins, Otago Peninsula and some Paterson Inlet (West Head and Bob's Point) and Bluff (Pig Island and Tiwai Point) sites. Species such as *Lessonia variegata* and *Landsburgia quercifolia* tended to achieve greatest biomasses at Southern locations, but were also common at Cape Reinga and offshore islands in Northeastern. Both *Marginariella* species were important components in the Stewart Island and Cook bioregions and had clear differences in their depth distributions with *M. urvilliana* typically occurring in the shallow depth strata (< 2 m and 4–6 m), while *M. boryana* was more abundant in the deeper strata (7–9 m and 10–12 m).

In addition to biogeographic patterns in the distributions of key algal species, there was a general increase in macroalgal diversity with latitude. This pattern is the opposite of that described for reef fish in New Zealand, where the highest diversity occurs in the north (Francis 1996). Although the mechanism for this pattern in algal diversity is unknown, algal diversity was also strongly correlated with water clarity, where highly turbid sites typically had lower algal diversity. This pattern was clearly evident within some bioregions, e.g. offshore islands in the Northeastern bioregion had low turbidity and a relatively high algal diversity compared to coastal sites.

The dominant mobile macroinvertebrate species recorded in this study also exhibited clear biogeographic patterns between Northern and Southern locations. However, there was no clear bioregional separation of locations, as has been documented for macroalgal species composition (Shears et al. in press). This was largely owing to the lower number of species recorded, and the widespread distributions of most of the dominant species (e.g. *Evechinus chloroticus*, *Trochus viridis*, *Patiriella* spp., *Cellana stellifera*). Herbivorous gastropods, predominantly *T. viridis*, *Cookia sulcata*, *Cantharidus purpureus*, *Cellana stellifera* and *Turbo smaragdus*, were more abundant in the Northern Province, whereas the starfishes *Patiriella* spp., *Pentagonaster pulchellus*, *Diplodontias* spp. and the ophiuroid *Ophiopsammus maculata* were more common in the Southern Province. *Evechinus chloroticus* was found to be the dominant invertebrate grazer on shallow subtidal reefs throughout New Zealand, although it was rare along large stretches of coastline, e.g. the entire east and southeast coast from Gisborne to the Catlins, including the northern shore of Cook Strait. *Haliotis iris* was generally rare but was the most common large grazer at some sites at Cape Foulwind and Banks Peninsula North. Historically *H. iris* may have been more abundant and played a greater role in structuring algal assemblages in other areas prior to the commencement of commercial harvesting (e.g. Stewart Island).

4.2 NATIONAL PATTERNS IN COMMUNITY STRUCTURE

There was a high degree of variability in benthic community structure among bioregions, among sites within bioregions, and among depth ranges within sites. There were, however, some consistent patterns in community structure at the national and bioregional levels. Overall, leathery macrophytes were the dominant component of the shallow subtidal reefs examined in this study (68% of total biomass). The leathery macrophyte group was made up of large brown algal species which were the dominant structural component of reef communities at all locations, except for Buller and West Coast locations where smaller algal groups and encrusting invertebrates dominated (also see Shears 2007). As a result, the Buller and Westland bioregions provide a unique example of temperate reef systems where both large brown algae and macroinvertebrate grazers, such as sea urchins and paua, are rare.

The immediate subtidal (< 2 m depth) in most bioregions (excluding Buller and Westland) was typical of temperate reef systems worldwide in that it was characterised by high densities and biomasses of fucalean algae (Schiel & Foster 1986; Underwood et al. 1991). In Northern locations, this habitat was dominated by *Carpophyllum maschalocarpum* and/or *C. angustifolium*, whereas in most Southern locations it was occupied by varying combinations of *Xiphophora gladiata*, *Durvillaea willana*, *Lessonia variegata*, *Marginariella urvilliana* or *Cystophora* spp. At some sites, the shallow band of large brown algae was absent, e.g. at inner-fiord sites where the shallow subtidal was dominated by mussels and an assemblage of ephemeral green and red algae. This is most likely because of the presence of a low-salinity layer of surface water that may directly inhibit the recruitment of large brown algae, as well as exclude predators and grazers, and therefore allow mussels to dominate (Witman & Grange 1998). The absence of large brown algae from the shallow subtidal in many West Coast locations may be due to extreme wave action. *Durvillaea antarctica* was patchily distributed on the intertidal–subtidal boundary in these areas and potentially acts to exclude other algae from the shallow subtidal through physical abrasion.

We found large variation in the organisation of algal assemblages with depth across most sites. The bimodal depth distribution of macroalgae previously described for northern New Zealand (Choat & Schiel 1982) was recorded at some Northeastern locations and exposed sites at Kapiti Island. In the Northeastern bioregion, this bimodality is thought to be a result of high abundances of *Evechinus chloroticus* reducing algal biomass at mid-depths, whereas fucaleans dominate the shallows and *Ecklonia radiata* forests occur at greater depths (Choat & Schiel 1982). A similar bimodal algal distribution has been recorded in Dusky Sound (Villouta et al. 2001) and was recorded in this study at a few Doubtful Sound sites, where *Evechinus chloroticus* was abundant at 4–6 m. However, at the majority of sites examined algal biomass was found to decline with depth. This may be due to several factors such as high abundances of *E. chloroticus* at greater depths (e.g. Gannet Rock, Abel Tasman and Nelson) or other factors, such as low light levels (high turbidity), high levels of sedimentation, sand abrasion and low levels of propagule supply, which may prevent the establishment of deeper algal stands (Schiel & Foster 1986). For example, high turbidity appears to restrict macroalgal forests to shallow depths at the Banks sites. At these sites *Ecklonia radiata* was rare below 5 m and *C. flexuosum* occurred at low densities. This is in contrast to Schiel & Hickford (2001) who found high densities of *E. radiata* (13–15 plants per m^2) at 9–12 m of depth at Godley Head in the early 1990s. Those authors also described mixed stands of *E. radiata*, *Landsburgia quercifolia*, *Lessonia variegata* and *Marginariella* spp. at c. 8 m depth for another site nearby (Taylors Mistake), which is in stark contrast to the patterns we observed. Schiel & Hickford (2001) commented that underwater visibility tended to be better at Banks Peninsula than at Kaikoura. However, we found the opposite pattern (average Secchi disc depth during the sampling period was c. 2.5 m at Banks Peninsula North compared with c. 6 m at Kaikoura). It is unknown whether these contrasting descriptions of algal assemblages for Banks Peninsula North represent site-level variation or long-term changes. In general, little is known about the temporal variability in subtidal algal assemblages around much of New Zealand, the mechanisms responsible for variation in community structure, and the factors that potentially restrict deeper water algal assemblages in many regions.

4.3 ENVIRONMENTAL CORRELATES AND STRUCTURING PROCESSES

At the national and bioregional levels, both macroalgal and mobile macroinvertebrate communities were most strongly related to turbidity (Secchi depth) and/or wave exposure (fetch). The largest variation in community structure among sites was associated with a gradient from turbid, more coastally influenced locations, to more oceanic locations with clearer water, rather than any clear latitudinal gradient. The importance of the environmental variables also increased with decreasing spatial scale, such that they explained greater variation at the bioregional level for all datasets. However, the variable that explained the greatest variation in community structure differed among bioregions. This was largely associated with the types of gradients sampled within each bioregion and how environmental variables covaried across them. For example, at the Northeastern bioregion locations, water clarity was generally lowest at the sheltered coastal sites and increased with increasing wave exposure. However, at the offshore island locations the water was clear at both sheltered and exposed sites. Furthermore, the reefs at the turbid coastal sites extended to only c. 5 m depth, whereas at the offshore islands the reefs extended beyond 12 m of depth, even at the most sheltered sites. As a result, the maxium depth sampled (MaxDepth) and turbidity (Secchi) explained the greatest variation in algal community structure among Northeastern sites and the wave exposure estimates had less explanatory power. Similar patterns were seen in the Abel bioregion where the 'exposed-offshore' group included both exposed and sheltered sites from Kapiti Island and wave exposure explained only 7% of the variation across all sites. While the relationships between community structure and environmental variables reflect differences in the environmental gradients sampled among sites within each bioregion, they also provide insights into the potentially important physical factors controlling community structure.

Water clarity (Secchi depth) was consistently one of the environmental variables that explained the most variation in each of the datasets examined at all spatial scales. This was particularly apparent for bioregions or locations where sites spanned an onshore–offshore gradient, e.g. many west coast locations. The majority of the inshore sites sampled on the west coast (e.g. Raglan, Buller and Westland) were highly turbid, had shallow (< 10 m) reefs and had a high degree of sediment resuspension and abrasion associated with the high wave action. At these sites, large brown algae were largely restricted to a shallow subtidal fringe and the deeper subtidal communities were dominated by short turfing algae and sessile invertebrates such as mussels, sponges and ascidians. It is hypothesised that large brown algae are restricted to shallow depths at these coastal sites by a combination of high water motion, sandscour and high turbidity. In contrast, offshore sites had clearer water, more expansive subtidal reefs that extend into deeper water (e.g. Open Bay Islands, Gannet Rock, Sugarloaf Island at New Plymouth), less sediment and more extensive macroalgal habitats. However, sea urchins were also more abundant at these sites, compared with inshore sites, and appeared to play a role in excluding macroalgae from deep water in these environments.

In bioregions where the sites were not located across a strong turbidity gradient, wave exposure (fetch) was most strongly related to community structure, e.g. Stewart Island. In these cases, groupings of sites corresponded to broad differences in wave exposure and the relative abundance of different species varied across these gradients. For example, *Carpophyllum flexuosum* was consistently dominant at the most sheltered sites within some bioregions (e.g. Northeastern and Banks), whereas species such as *Ecklonia radiata*, *Macrocystis pyrifera* and/or *Marginariella boryana* were more typical of moderately exposed sites (e.g. those at Banks and Stewart Island), and species such as *Lessonia variegata*, *Landsburgia quercifolia* and/or *Durvillaea willana* were most typical of highly exposed sites (e.g. those at Chalmers, Stewart Island and Cook). There were, however, numerous exceptions to these general patterns; e.g. *C. flexuosum* was abundant at exposed outer-fiord sites, and also on exposed reefs at Gisborne. These findings demonstrate strong couplings between the environmental variables measured and community structure at a variety of scales, but also highlight the complex and co-varying nature of these relationships and the need for research into the mechanisms responsible for the observed patterns.

4.4 THE ROLE OF SEA URCHINS

The urchin barrens habitat is generally considered to be a feature of subtidal reefs in northern parts of New Zealand (Schiel 1990), although several studies suggest urchins have important effects on algal assemblages in southern regions, e.g. Abel Tasman (Davidson & Chadderton 1994), Kaikoura (Dix 1969) and Fiordland (Villouta et al. 2001). In the present study, *Evechinus chloroticus* was abundant in Northeastern locations; however, it was also found to be abundant and to form urchin barrens habitat at numerous other locations throughout New Zealand. These locations included contrasting environments, from relatively wave-protected coastal embayments (e.g. Paterson Inlet, Nelson, Long Island, Abel Tasman and sites in Fiordland) to exposed offshore islands on the west coast (e.g. Open Bay Island, Gannet Rock and the Sugarloaf Islands at New Plymouth). At the national level, Evechinus explained only 4% of the variation in algal community structure, but explained up to 17% (Stewart Island) at the bioregional level. Overall the low variation at these spatial scales is not surprising as the analysis was carried out on depth-averaged algal biomass data and the effects of grazing by *E. chloroticus* are generally restricted to specific depth ranges (Shears & Babcock 2004a).

There was large variation in the relationship between *E. chloroticus* abundance and environmental variables among bioregions. At the national level, *E. chloroticus* was most strongly related to water clarity (Secchi) and was rare at the most turbid locations (e.g. Long Bay, Raglan, Gisborne, Karamea, Cape Foulwind, Banks Peninsula North, Flea Bay and the Catlins), and abundant at locations with high water clarity (e.g. Gannet Rock, Poor Knights Islands, Mokohinau Islands and Tuhua Islands). These patterns were most evident in bioregions where sites were located across an onshore–offshore gradient, e.g. those in Northeastern, Raglan, Buller and Westland bioregions. In all cases, offshore islands with higher water clarity supported greater abundances of urchins. The estimate of water clarity used in this study, however, was based on a one-off field measurement of Secchi depth and it is proposed that better information on national patterns in ambient turbidity (suspended sediment) would explain a higher proportion of the variation in the abundance of *E. chloroticus*. A potential mechanism excluding *E. chloroticus* from turbid areas is the adverse effect of suspended sediments on larval survival (Phillips & Shima 2006), settlement success and the survival of juvenile *E. chloroticus* (Walker 2007). The percentage cover of sediment on the reef, however, was not a good predictor of the abundance of *E. chloroticus* at a national scale and, in some bioregions, *E. chloroticus* was actually positively associated with sediment cover (e.g. Paterson Inlet, Nelson and Long Island).

Evechinus chloroticus exhibited contrasting relationships with wave exposure among bioregions. In the Northeastern bioregion, *E. chloroticus* was generally positively associated with wave exposure, although the species was rare at the most exposed sites at Cape Reinga. However, as mentioned above this wave-exposure gradient also corresponded to a gradient in water clarity from turbid sheltered coastal sites where *E. chloroticus* was rare to exposed and offshore island locations that have clear water and abundant *E. chloroticus* (Grace 1983; Shears & Babcock 2004b). In the Abel and Stewart Island bioregions, however, this pattern in the abundance of *E. chloroticus* was reversed, with the species being abundant at sheltered sites (e.g. Paterson Inlet, Long Island, Nelson and Abel Tasman) and rare at more exposed open coast sites (e.g. Titi Islands, and exposed Kapiti Island and Long Island sites). However, water clarity at these sheltered sites was considerably higher (Secchi depth 5–10 m) than at sheltered Northeastern sites and did not appear to limit the distribution of *E. chloroticus*.

The apparent decline in the abundance of *E. chloroticus* with increasing exposure at sites in the Abel and Stewart Island bioregions is consistent with increasing wave action preventing the species from overgrazing, as has been suggested for the most exposed locations in the Northeastern bioregion (e.g. Cape Reinga; Shears & Babcock 2004b). However, exposed sites at Titi Islands, Kapiti and Long Island had only moderately high wind fetch values. In other parts of New Zealand, *E. chloroticus* is abundant at sites with similar or even higher wave-exposure estimates (e.g. Gannet Rock, New Plymouth and some Northeastern sites). Furthermore, algal assemblages at these sites suggested they are not subjected to extreme wave action. For example, at ‘exposed-offshore’ sites at Long Island, *C. flexuosum* plants were tall (total length > 1 m) and exhibited a sheltered morphology (Cole et al. 2001). Similarly, on the western side of Kapiti Island, *Ecklonia radiata* occurred at high biomasses at shallow depths suggesting these sites were not exposed to large swell waves. These observations suggest that other mechanisms are excluding *Evechinus chloroticus* from these sites. Individual *E. chloroticus* at these sites were also large (> 100 mm TD), present at the bottom of the reef (10–12 m), and juveniles were rare, suggesting low recruitment into these habitats. In Doubtful Sound, Wing et al. (2003) suggest that low settlement of *E. chloroticus* at the entrance of the fiord is due to the loss of larvae to the open ocean. Furthermore, in such situations where kelp dominates, negative feedback effects may further reduce settlement and prevent the species from establishing in these areas (Andrew & Choat 1985; Rowley 1990; Konar & Estes 2003). The high abundances of both adults and juveniles in the relatively sheltered embayment locations (e.g. Paterson Inlet, Long Island, Nelson and Abel Tasman) may result from a high retention of larvae owing to high residence times and stratification of the water column in summer. This has been shown to occur in Doubtful Sound, where the greatest abundance and settlement of *E. chloroticus* occur at mid-fiord sites (Wing et al. 2003). More research into urchin recruitment and larval urchin dispersal is needed to better understand the distribution patterns of urchins and the occurrence of urchin barrens habitat.

4.5 CONSERVATION AND MANAGEMENT IMPLICATIONS

With increased awareness of the potential effects of land-based activities on coastal ecosystems, there is a growing literature in New Zealand on the effects of various components of sedimentation on reef-associated species (e.g. Phillips & Shima 2006; Schiel et al. 2006; Steger & Gardner 2007; Walker 2007). All of these studies show negative effects of sediment on survival, settlement or metabolic rates of different life history stages. High turbidity is generally associated with high levels of sedimentation and we found that turbidity (Secchi) was consistently important in explaining variation in algal community structure among sites at all spatial scales examined. While this suggests that sedimentation may play a fundamental role in structuring New Zealand's reef communities, it is important to note that gradients in water clarity and, potentially sedimentation, may largely be natural (e.g. coastal–offshore), with certain parts of the New Zealand coast naturally having larger sediment inputs (Carter 1975) and higher turbidity, e.g. Portland, Banks and locations on the West Coast. Furthermore, while such areas of high turbidity had distinctive attributes or community structures, we demonstrate complex associations between water clarity and a variety of other physical (wave exposure) and, potentially biological processes (phytoplankton productivity). Identifying the actual mechanisms responsible for these patterns and separating anthropogenic from environmental variation is necessary to inform management and remains the challenge to ecologists.

The effects of fishing are also likely to have influenced the patterns in algal and invertebrate communities described in this study both directly and indirectly. For example, the low numbers of paua recorded throughout the country are likely to be a direct result of overfishing of this species. In contrast, the prevalence of *Evechinus chloroticus* in many areas may be an indirect effect of overfishing of sea urchin predators. Such effects have been shown through comparisons of marine reserves and fished sites in parts of Northeastern (Babcock et al. 1999; Shears & Babcock 2002, 2003), but these trophic cascade effects have not been demonstrated in other parts of the country (Shears & Babcock 2004a). However, the establishment of networks of marine reserves throughout the country, and continued monitoring of existing reserves, will allow broader generalisations about where these effects occur. While trophic cascade effects are likely to occur following the recovery of predator populations in areas where *E. chloroticus* is abundant, in parts of the coastline where urchins are not common more subtle and potentially more complex interactions may occur as a result of the cessation of fishing.

The biogeographic classification for mainland New Zealand based on the dataset analysed here (Shears et al. in press) provides a large-scale spatial framework for further ecological study and systematic conservation planning. The description of 11 major bioregions has important implications for any conservation effort that aims to protect New Zealand's coastal marine biodiversity through the establishment and management of a comprehensive system of adequate and representative marine reserves (Day et al. 2002). The analyses and descriptions in the present report demonstrate how the structure of algal and invertebrate assemblages on shallow reefs vary greatly across environmental gradients within bioregions. It is important that this variation is represented in the design of no-take marine reserve networks within bioregions. Although we were only able to sample large environmental gradients in a few bioregions, similar variation in community structure is expected to occur in all bioregions should such gradients exist.

5. Conclusions

This study provides the first quantitative description of subtidal habitats for many of the areas examined. Both national and regional patterns in community structure, and their associations with environmental variables, were complex and multidimensional largely owing to the highly complex nature of the New Zealand coast and the inter-related nature of the environmental variables examined. However, some general relationships between biological pattern and environmental variables were apparent. Firstly, the proportion of variation explained by a local-scale environmental variable tended to increase with decreasing spatial scale for all biological datasets. The structure of algal and benthic communities was most strongly associated with water clarity, suggesting that community structure varies most strongly across a gradient from coastally influenced sites (e.g. shallow areas or embayments) with high turbidity to more oceanically influenced locations (e.g. offshore islands). The effect of wave exposure did not vary consistently across these gradients and water clarity was a better predictor of community structure and species composition.

The abundance of *Evechinus chloroticus*, the dominant invertebrate grazer, also varied considerably around New Zealand. The environmental variables that were found to be correlated with the abundance of *E. chloroticus* varied among bioregions, and the species was found to be abundant in contrasting environments, demonstrating a complex association with environmental conditions. Water clarity explained the greatest variation in the abundance of *E. chloroticus*, its abundance being low in highly turbid areas (e.g. southeastern coast). While there is much we still need to understand about the processes driving variability at the local and regional level, we can see similarities in the relationships between environmental factors and marine community structure around the entire country.

6. Acknowledgements

This project has been made possible with the support and assistance of a large number of people around the country, in particular numerous DOC conservancy staff who provided their time, resources and local knowledge. Special thanks to Clinton Duffy, Robert Russell, Natalie Managh, Jarrod Walker, Debbie Freeman, Don Neale, David Feary, Phil Ross and Helen Kettles who all provided invaluable diving assistance during the study. Clinton Duffy also provided valuable experience and knowledge of reefs around the country, and organised local area support and the logistics of fieldtrips. Dr Eduardo Villouta provided the initiative for this project, valuable technical advice throughout, and software for calculating wind fetch. Thanks to the staff of the Leigh Marine Lab, particularly Arthur Cozens for providing logistical support, and also Dr Wendy Nelson for assistance with seaweed identification. Franz Smith and Marti Anderson provided valuable statistical support. Eduardo Villouta, Franz Smith and Clinton Duffy also provided valuable advice and comments on earlier versions of this report. This study was funded by Department of Conservation, Science and Research Division, under Science Investigation No. 2481, and additional surveys were supported by the Southland and West Coast Conservancies.

7. References

Adams, N.M. 1994: Seaweeds of New Zealand: an illustrated guide. Canterbury University Press, Christchurch. 360 p.

Airoldi, L.; Virgillio, M. 1998: Response of turf-forming algae to spatial variations in the deposition of sediments. *Marine Ecology Progress Series 165*: 271–282.

Anderson, M.J. 2000: PCOORD: a FORTRAN computer program for principal coordinate analysis. Department of Statistics, University of Auckland, Auckland. 7 p.

Anderson, M.J. 2002: DISTLM v2: a FORTRAN computer program to calculate a distance-based multivariate analysis for a linear model. Department of Statistics, University of Auckland, Auckland. 9 p.

Anderson, M.J.; Ford, R.B.; Feary, D.A.; Honeywill, C. 2004: Quantitative measures of sedimentation in an estuarine system and its relationship with intertidal soft-sediment infauna. *Marine Ecology Progress Series 272*: 33–48.

Andrew, N.L. 1988: Ecological aspects of the common sea urchin, *Evechinus chloroticus*, in northern New Zealand: a review. *New Zealand Journal of Marine & Freshwater Research 22*: 415–426.

Andrew, N.L.; Choat, J.H. 1982: The influence of predation and conspecific adults on the abundance of juvenile *Evechinus chloroticus* (Echinoidea: Echinometridae). *Oecologia 54*: 80–87.

Andrew, N.L.; Choat, J.H. 1985: Habitat related differences in the growth and survivorship of juvenile echinoids. *Marine Ecology Progress Series 27*: 155–161.

Babcock, R.C.; Kelly, S.; Shears, N.T.; Walker, J.W.; Willis, T.J. 1999: Changes in community structure in temperate marine reserves. *Marine Ecology Progress Series 189*: 125–134.

Batham, E.J. 1956: Ecology of southern New Zealand sheltered shores. *Transactions of the Royal Society of New Zealand 84*: 447–465.

Benedetti-Cecchi, L.; Airoldi, L.; Abbiati, M.; Cinelli, F. 1996: Estimating the abundance of benthic invertebrates: a comparison of procedures and variability between observers. *Marine Ecology Progress Series 138*: 93–101.

Broitman, B.R.; Navarrete, S.A.; Smith, F.; Gaines, S.D. 2001: Geographic variation of southeastern Pacific intertidal communities. *Marine Ecology Progress Series 224*: 21–34.

Carter, L. 1975: Sedimentation on the continental terrace around New Zealand: a review. *Marine Geology 19*: 209–237.

Choat, J.H.; Schiel, D.R. 1982: Patterns of distribution and abundance of large brown algae and invertebrate herbivores in subtidal regions of northern New Zealand. *Journal of Experimental Marine Biology & Ecology 60*: 129–162.

Clarke, K.R.; Warwick, R.M. 1994: Change in marine communities: an approach to statistical analysis and interpretation. Natural Environment Research Council, Plymouth, UK. 144 p.

Cole, R.G. 1993: Distributional relationships among subtidal algae, sea urchins and reef fish in northeastern New Zealand. University of Auckland, Auckland. 160 p.

Cole, R.G.; Haggitt, T.R. 2001: Dietary preferences of *Evechinus chloroticus* and the persistence of the fucalean macroalga *Carpophyllum flexuosum* on coralline-dominated areas in northeastern New Zealand. Pp. 425–430 in Barker, M.F. (Ed.): Echinoderms 2000. Swets & Zeitlinger, Lisse.

Cole, R.G.; Babcock, R.C.; Travers, V.; Creese, R.G. 2001: Distributional expansion of *Carpophyllum flexuosum* onto wave-exposed reefs in northeastern New Zealand. *New Zealand Journal of Marine & Freshwater Research 35*: 17–32.

Colwell, R.K.; Coddington, J.K. 1994: Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society (Series B) 345*: 101–118.

Cowen, R.K.; Agegian, C.R.; Foster, M.S. 1982: The maintenance of community structure in a central California giant kelp forest. *Journal of Experimental Marine Biology & Ecology 64*: 189–201.

Davidson, R.J.; Chadderton, W.L. 1994: Marine reserve site selection along the Abel Tasman National Park coast, New Zealand: consideration of subtidal rocky communities. *Aquatic Conservation: Marine & Freshwater Ecosystems 4*: 153–167.

Day, J.; Fernandes, L.; Barnett, B.; Slegers, S.; Kerrigan, B.; Breen, D.; De'ath, G.; Lewis, A.; Innes, J.; Oliver, J. 2002: The representative areas program for protecting the biodiversity of the Great Barrier Reef World Heritage Area. Pp. 687–696 in Moosa, M.K.; Soemodihardjo, S.; Soegiarto, A.; Romimohtarto, K.; Nontji, A.; Suharsono, S. (Eds): Proceedings of the ninth International coral reef symposium, 23–27th October 2000, Bali. Indonesian Institute of Sciences, Jakarta.

Dayton, P.K. 1985: Ecology of kelp communities. *Annual Review of Ecology and Systematics 16*: 215–245.

Dix, T.G. 1969: The biology of the echinoid *Evechinus chloroticus* (Val.) in different habitats. Unpublished PhD thesis, University of Canterbury, Christchurch. 109 p.

Eriksson, B.K.; Johansson, G.; Snoeijs, P. 2002: Long-term changes in the macroalgal vegetation of the inner Gullmar Fjord, Swedish Skagerrak coast. *Journal of Phycology 38*: 284–296.

Fowler-Walker, M.J.; Connell, S.D. 2002: Opposing states of subtidal habitats across temperate Australia: consistency and predictability in kelp-canopy benthic associations. *Marine Ecology Progress Series 240*: 49–56.

Francis, M. 1996: Geographic distribution of marine reef fishes in the New Zealand region. *New Zealand Journal of Marine & Freshwater Research 30*: 35–55.

Fyfe, J. 1992: Four Otago marine reserve options: an overview of biological values. Unpublished report to Department of Conservation, Otago Conservancy. 64 p.

Gorman, R.M.; Bryan, K.R.; Laing, A.K. 2003: Wave hindcast for the New Zealand region: nearshore validation and coastal wave climate. *New Zealand Journal of Marine & Freshwater Research 37*: 567–588.

Gorostiaga, J.M.; Santolaria, A.; Secilla, A.; Diez, I. 1998: Sublittoral benthic vegetation of the eastern Basque coast (N. Spain): structure and environmental factors. *Botanica Marina 41*: 455–465.

Grace, R.V. 1983: Zonation of sublittoral rocky bottom marine life and its changes from the outer to the inner Hauraki Gulf, northeastern New Zealand. *Tane 29*: 97–108.

Harrold, C.; Pearse, J.S. 1987: The ecological role of echinoderms in kelp forests. *Echinoderm Studies 2*: 137–233.

Harrold, C.; Watanabe, J.M.; Lisin, S. 1988: Spatial variation in the structure of kelp forest communities along a wave exposure gradient. *Pubblicazioni della Stazione Zoolgica di Napoli I: Marine Ecology 9*: 131–156.

Hay, C.H. 1990: The distribution of *Macrocystis* (Phaeophyta: Laminariales) as a biological indicator of cool sea surface temperature, with special reference to New Zealand waters. *Journal of the Royal Society of New Zealand 20*: 313–336.

Heath, R.A. 1985: A review of the physical oceanography of the seas around New Zealand—1982. *New Zealand Journal of Marine & Freshwater Research 19*: 79–124.

Hogan, K.; Seymour, T.; Gordon, P. 1991: Kaiora marine reserve proposal: a preliminary intertidal, subtidal and site survey. Department of Conservation, East Coast Conservancy, Gisborne.

Hurd, C.L.; Nelson, W.A.; Falshaw, R.; Neill, K.F. 2004: History, current status and future of marine macroalgal research in New Zealand: taxonomy, ecology, physiology and human uses. *Phycological Research 52*: 80–106.

Irving, A.D.; Connell, S.D. 2002: Sedimentation and light penetration interact to maintain heterogeneity of subtidal habitats: algal versus invertebrate dominated assemblages. *Marine Ecology Progress Series 245*: 83–91.

Jones, G.P.; Andrew, N.L. 1990. Herbivory and patch dynamics on rocky reefs in temperate Australasia: the roles of fish and sea urchins. *Australian Journal of Ecology 15*: 505–520.

Konar, B.; Estes, J.A. 2003. The stability of boundary regions between kelp beds and deforested areas. *Ecology 84*: 174–185.

Larson, G.L.; Buktenica, M.W. 1998: Variability of secchi disk readings in an exceptionally clear and deep caldera lake. *Archiv fur Hydrobiologie 141*: 377–388.

Lawrence, J.M. 1975: On the relationships between marine plants and sea urchins. *Oceanography and Marine Biology Annual Review 13*: 213–286.

Leliaert, F.; Anderson, R.J.; Bolton, J.J.; Coppejans, E. 2000: Subtidal understorey algal community structure in kelp beds around the Cape Peninsula (Western Cape, South Africa). *Botanica Marina 43*: 359–366.

Lourie, S.A.; Vincent, A.C.J. 2004: Using biogeography to help set priorities in marine conservation. *Conservation Biology 18*: 1004–1020.

Lumb, C.M. 1989: Algal depth distribution as an indicator of long-term turbidity change. Pp. 69–74 in McManus, J.; Elliot, M. (Eds): Developments in estuarine and coastal study techniques. Olsen & Olsen, International Symposium Series, Fredensborg, Denmark.

McArdle, B.H.; Anderson, M.J. 2001: Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology 82*: 290–297.

Moore, L.B. 1961: Distribution patterns in New Zealand seaweeds. *Tuatara 9*: 18–23.

Neale, D.; Nelson, W. 1998: Marine algae of the West Coast, South Island, New Zealand. *Tuhinga 10*: 87–118.

Nelson, W. 1994: Distribution of macroalgae in New Zealand—an archipelago in space and time. *Botanica Marina 37*: 221–233.

Nelson, W.A.; Villouta, E.; Neill, K.F.; Williams, G.C.; Adams, N.M.; Slivsgaard, R. 2002: Marine macroalgae of Fiordland, New Zealand. *Tuhinga 13*: 117–152.

O'Loughlin, P.M.; Waters, J.M.; Roy, M.S. 2002: Description of a new species of *Patiriella* from New Zealand, and review of *Patiriella regularis* (Echinodermata, Asteroidea) based on morphological and molecular data. *Journal of the Royal Society of New Zealand 32*: 697–711.

Phillips, N.E.; Shima, J.S. 2006: Differential effects of suspended sediments on larval survival and settlement of New Zealand urchins *Evechinus chloroticus* and abalone *Haliotis iris*. *Marine Ecology Progress Series 314*: 149–158.

Reed, D.C. 1990: The effects of variable settlement and early competition on patterns of kelp recruitment. *Ecology 71*: 776–787.

Rowley, R.J. 1990: Newly settled sea urchins in a kelp bed and urchin barren ground: a comparison of growth and mortality. *Marine Ecology Progress Series 62*: 229–240.

Schiel, D.R. 1990: Macroalgal assemblages in New Zealand: structure, interactions and demography. *Hydrobiologia 192*: 59–76.

Schiel, D.R.; Foster, M.S. 1986: The structure of subtidal algal stands in temperate waters. *Oceanography and Marine Biology Annual Review 24*: 265–307.

Schiel, D.R.; Hickford, M.J.H. 2001: Biological structure of nearshore rocky subtidal habitats in southern New Zealand. *Science for Conservation 182*. Department of Conservation, Wellington, New Zealand. 54 p.

Schiel, D.R.; Wood, S.A.; Dunmore, R.A.; Taylor, D.I. 2006: Sediment on rocky intertidal reefs: effects on early post-settlement stages of habitat-forming seaweeds. *Journal of Experimental Marine Biology & Ecology 331*: 158–172.

Schils, T.; De Clerck, O.; Leliaert, F.; Bolton, J.J.; Coppejans, E. 2001: The change in macroalgal assemblages through the Saldanha Bay/Langebaan Lagoon ecosystem (South Africa). *Botanica Marina 44*: 295–305.

Shears, N.T. 2007: Biogeography, community structure and biological habitat types of subtidal reefs on the South Island West Coast, New Zealand. *Science for Conservation 281*. Department of Conservation, Wellington. 53 p.

Shears, N.T.; Babcock, R.C. 2002: Marine reserves demonstrate top-down control of community structure on temperate reefs. *Oecologia 132*: 131–142.

Shears, N.T.; Babcock, R.C. 2003: Continuing trophic cascade effects after 25 years of no-take marine reserve protection. *Marine Ecology Progress Series 246*: 1–16.

Shears, N.T.; Babcock, R.C. 2004a: Indirect effects of marine reserves on New Zealand's rocky coastal communities. *DOC Science Internal Series No. 192*. Department of Conservation, Wellington, New Zealand. 49 p.

Shears, N.T.; Babcock, R.C. 2004b: Community composition and structure of shallow subtidal reefs in northeastern New Zealand. *Science for Conservation 245*. Department of Conservation, Wellington, New Zealand. 65 p.

Shears, N.T.; Smith, F.; Babcock, R.C.; Duffy, C.A.J.; Villouta, E. in press: Evaluation of biogeographic classification schemes for conservation planning: application to New Zealand's coastal marine environment. *Conservation Biology*.

Steger, K.K.; Gardner, J.P.A. 2007: Laboratory experiments on the effects of variable suspended sediment concentrations on the ecophysiology of the porcelain crab *Petrolisthes elongatus* (Milne Edwards, 1837). *Journal of Experimental Marine Biology & Ecology 344*: 181–192.

Steneck, R.S.; Dethier, M.N. 1994: A functional group approach to the structure of algal-dominated communities. *Oikos 69*: 476–498.

Underwood, A.J.; Kingsford, M.J.; Andrew, N.L. 1991: Patterns in shallow subtidal marine assemblages along the coast of New South Wales Australia. *Australian Journal of Ecology 16*: 231–250.

Underwood, A.J.; Chapman, M.G.; Connell, S.D. 2000: Observations in ecology: you can't make progress on processes without understanding the patterns. *Journal of Experimental Marine Biology & Ecology 250*: 97–115.

Villouta, E.; Chadderton, W.L.; Pugsley, C.W.; Hay, C.H. 2001: Effects of sea urchin (*Evechinus chloroticus*) grazing in Dusky Sound, Fiordland, New Zealand. *New Zealand Journal of Marine & Freshwater Research 35*: 1007–1024.

Walker, J.W. 1999: Subtidal reefs of the Hauraki Gulf. Unpublished MSc thesis, University of Auckland, New Zealand. 79 p.

Walker, J.W. 2007: Effects of fine sediments on settlement and survival of the sea urchin *Evechinus chloroticus* in northeastern New Zealand. *Marine Ecology Progress Series 331*: 109–118.

Wing, S.R.; Gibbs, M.T.; Lamare, M.D. 2003: Reproductive sources and sinks within a sea urchin, *Evechinus chloroticus*, population of a New Zealand fjord. *Marine Ecology Progress Series 248*: 109–123.

Witman, J.D.; Grange, K.R. 1998: Links between rain, salinity, and predation in a rocky subtidal community. *Ecology 79*: 2429–2447.

Appendix 1

DETAILS OF SAMPLING LOCATIONS AND SITES

LOCATION	SITE	EASTING	NORTHING	DATE
Northeastern				
Cape Karikari	Takini South	2549612	6708196	7/10/1999
Cape Karikari	CK4	2552073	6704156	8/10/1999
Cape Karikari	Koware South	2552750	6704345	8/10/1999
Cape Karikari	Whale	2545848	6712376	9/10/1999
Cape Karikari	Whangatupere	2551761	6707401	9/10/1999
Cape Karikari	Omahuri	2548866	6708787	10/10/1999
Cape Karikari	Pihoaka Point	2551727	6708248	10/10/1999
Cape Karikari	Sunburn Point	2548292	6711752	10/10/1999
Cape Reinga	Lighthouse	2481893	6753367	11/10/1999
Cape Reinga	Tapotupotu	2486322	6751851	11/10/1999
Hahei	Cooks Bluff	2757571	6483105	10/05/1999
Hahei	Sandy Cove	2758899	6482610	10/05/1999
Hahei	SE Motueka	2760416	6482908	11/05/1999
Hahei	Twin gauge	2762066	6481777	11/05/1999
Hahei	Mahurangi Pinn	2761755	6481256	12/05/1999
Hahei	Whitecaves	2761731	6479881	12/05/1999
Hahei	Mussell Rock	2756861	6482939	13/05/1999
Hahei	Razor	2760471	6483166	13/05/1999
Hahei	Mahungarape	2755919	6486296	14/05/1999
Hahei	Whitecliffs	2758466	6482784	1/05/2000
Leigh	ABC	2671853	6546767	16/12/1998
Leigh	Nordic	2673093	6543630	15/03/1999
Leigh	Rodney	2674176	6545146	15/3/1999
Leigh	Kemps	2669136	6547458	16/03/1999
Leigh	Onespot	2673503	6545795	16/03/1999
Leigh	Mathesons	2672272	6542562	17/03/1999
Leigh	Ti Point	2672136	6540956	17/03/1999
Leigh	Outpost	2673923	6544131	18/03/1999
Leigh	Schiels	2671943	6546990	23/03/1999
Leigh	Tower	2672527	6546361	24/03/1999
Leigh	Martins rock	2670741	6546565	4/05/1999
Leigh	Okakari Point	2669323	6547541	4/05/1999
Leigh	TeRere	2670114	6546945	4/05/1999
Leigh	Cape Rodney	2674152	6545535	25/05/1999
Leigh	Waterfall	2672183	6546526	25/05/1999
Long Bay	DOC sign	2667199	6499909	13/04/1999
Long Bay	Skull Rock	2667364	6499835	13/04/1999
Long Bay	Wet Rock	2666661	6501912	13/04/1999
Long Bay	Mushrooms	2667662	6498879	14/04/1999
Long Bay	Outer Tor	2667497	6498445	14/04/1999
Long Bay	Hot tub	2668514	6505648	15/04/1999
Long Bay	Matakatia	2668858	6506334	15/04/1999
Long Bay	Ritch Reef	2668964	6506036	15/04/1999
Long Bay	N-sign	2666782	6501120	12/09/1999

Continued on next page

Appendix 1—continued

LOCATION	SITE	EASTING	NORTHING	DATE
Long Bay	Pines	2666811	6502553	12/09/1999
Mokohinau Islands	Lizard	2701371	6585652	1/06/1999
Mokohinau Islands	Dragon	2700547	6585296	2/06/1999
Mokohinau Islands	PinnSth	2699726	6584844	2/06/1999
Mokohinau Islands	Sentinel	2700385	6584921	2/06/1999
Mokohinau Islands	Arches	2700220	6585467	3/06/1999
Mokohinau Islands	Pudding	2700557	6586008	3/06/1999
Mokohinau Islands	SW Bay	2700666	6585531	3/06/1999
Mokohinau Islands	House Bay	2701287	6586216	4/06/1999
Mokohinau Islands	Light Point	2701840	6586156	6/07/1999
Poor Knights Islands	Cleanerfish	2668059	6636866	8/06/1999
Poor Knights Islands	Skull Bay	2668289	6636118	8/06/1999
Poor Knights Islands	Frasers	2669024	6633668	9/06/1999
Poor Knights Islands	Labrid	2668543	6633083	9/06/1999
Poor Knights Islands	Rock Lilly Cove	2668741	6636787	9/06/1999
Poor Knights Islands	Bartels' Bay	2668554	6634747	10/06/1999
Poor Knights Islands	Light Bay	2668637	6637499	10/06/1999
Poor Knights Islands	Matt's Crack	2668846	6634467	10/06/1999
Poor Knights Islands	Nursery	2668452	6634558	11/06/1999
Tawharanui	Takatu	2677683	6535969	19/04/1999
Tawharanui	Twin Peaks	2678018	6535722	19/04/1999
Tawharanui	Pinnacle	2677435	6535904	20/04/1999
Tawharanui	T-Cave	2678192	6535511	20/04/1999
Tawharanui	Karamuroa	2672542	6537667	21/04/1999
Tawharanui	P-Point	2673550	6536649	21/04/1999
Tawharanui	Iguana	2677210	6535671	22/04/1999
Tawharanui	Mid-Point	2676710	6535623	22/04/1999
Tawharanui	Comet	2674920	6535612	3/05/1999
Tawharanui	North Cove	2676045	6535619	3/05/1999
Tuhua Island	Turanganui	2800918	6431404	15/03/2000
Tuhua Island	Awatukoro Point	2796796	6430789	16/03/2000
Tuhua Island	Hurihurihunga	2799367	6431942	16/03/2000
Tuhua Island	Maorichief	2798268	6431898	16/03/2000
Tuhua Island	Bait Pond	2797426	6431457	17/-3/2000
Tuhua Island	Okawa	2800838	6430305	17/03/2000
Tuhua Island	Hot Springs	2800658	6431789	18/03/2000
Tuhua Island	Te Roto	2800658	6429485	18/03/2000
Portland				
Gisborne	Pouawa South	2963647	6274453	16/01/2002
Gisborne	Baldy Reef	2961200	6272250	17/01/2002
Gisborne	Makorori	2958008	6269378	17/01/2002
Gisborne	Pouawa North	2963796	6274642	17/01/2002
Mahia	Black Reef	2928393	6206527	18/06/2002
Mahia	Portland South	2929760	6198616	18/06/2002
Raglan				
Gannet Rock	Gannets leap	2647833	6357898	22/03/2001
Gannet Rock	SE Bay	2647813	6357785	22/03/2001
New Plymouth	Seal East	2596933	6238202	18/12/2000
New Plymouth	Lion W	2598866	6238943	19/12/2000

Continued on next page

Appendix 1—continued

LOCATION	SITE	EASTING	NORTHING	DATE
New Plymouth	Saddleback SW	2597835	6239366	19/12/2000
New Plymouth	Seal West	2596816	6238252	19/12/2000
New Plymouth	Moa Bay	2599112	6239076	20/12/2000
New Plymouth	Shilling Rock	2597679	6237742	20/12/2000
Raglan	Raglan Island	2665705	6372184	23/03/2001
Raglan	Redline Rock	2664760	6369665	23/03/2001
Raglan	Taranaki Point	2666602	6357875	23/03/2001
Cook				
Kaikoura	9Pin	2568050	5866257	7/12/1999
Kaikoura	Homestead	2569415	5865337	8/12/1999
Kaikoura	Seal Reef	2569415	5864996	9/12/1999
Kaikoura	Baxters	2566040	5863924	12/12/1999
Kaikoura	Shark tooth	2567680	5863289	12/12/1999
Kaikoura	Lastone	2567234	5863346	13/12/1999
Wellington	3Peak	2658417	5982512	11/08/1999
Wellington	Durv Rocks	2658148	5982551	11/09/1999
Wellington	Sirens	2657483	5982639	11/09/1999
Wellington	Moa Point	2661443	5982971	11/10/1999
Wellington	Shark fin	2659940	5982726	11/10/1999
Wellington	Palmer	2662396	5983050	11/11/1999
Abel				
Abel Tasman	Foul Point	2515324	6033097	30/11/1999
Abel Tasman	Seal Colony	2515763	6035029	30/11/1999
Abel Tasman	Wharf Rock	2515494	6036413	30/11/1999
Abel Tasman	Isol Rock	2511057	6044518	1/12/1999
Abel Tasman	Nthn Boundary	2513845	6039465	1/12/1999
Abel Tasman	Separation Point	2509748	6047167	1/12/1999
Abel Tasman	Abel Head	2514836	6038883	2/12/1999
Abel Tasman	FG Rock	2515200	6037996	2/12/1999
Abel Tasman	Pinnacle Island	2515568	6030807	2/12/1999
Abel Tasman	Pitt Island	2515648	6028741	3/12/1999
Kapiti Island	Aropawaiti East	2672338	6040876	8/12/2000
Kapiti Island	Onepoto Bay	2671952	6040573	8/12/2000
Kapiti Island	Ulva Rock	2670003	6037336	8/12/2000
Kapiti Island	Tokahaki	2673377	6041217	9/12/2000
Kapiti Island	South West Point	2669541	6033916	10/12/2000
Kapiti Island	Te Rere Stream	2673278	6038374	10/12/2000
Long Island	Nob Rock	2618257	6009413	16/11/1999
Long Island	Thresher Point	2616432	6007500	16/11/1999
Long Island	Bluemine	2614507	6002125	17/11/1999
Long Island	Te Ruatarore	2614687	6008622	17/11/1999
Long Island	Landing	2619057	6010010	18/11/1999
Long Island	Ship Cove	2614745	6012282	18/11/1999
Long Island	South Beach	2616600	6007974	18/11/1999
Long Island	Motuara Island	2617543	6012835	19/11/1999
Long Island	Sleeping Man	2617956	6009865	19/11/1999
Long Island	Twin Cave	2619136	6010290	19/11/1999
Long Island	Cooper Point	2620483	6009053	20/11/1999
Long Island	Kotukutuku	2619512	6008099	20/11/1999

Continued on next page

Appendix 1—continued

LOCATION	SITE	EASTING	NORTHING	DATE
Nelson	NE Beach	2544697	6006050	23/11/1999
Nelson	Pepin Cave	2544497	6007303	23/11/1999
Nelson	Cable NW	2543877	6005684	23/11/1999
Nelson	Goat Rock	2543610	6005362	24/11/1999
Nelson	Hoop	2540206	6002479	25/11/1999
Nelson	Pine/Sign	2540472	6002889	25/11/1999
Nelson	Summit	2541769	6003909	25/11/1999
Nelson	BB House	2539818	6002257	26/11/1999
Nelson	Maheipuku	2544963	6007990	26/11/1999
Banks				
Banks Peninsula North	Godley North	2493891	5736235	18/01/2000
Banks Peninsula North	Lubchenco	2493316	5736088	18/01/2000
Banks Peninsula North	Little Akaloa	2511739	5728539	25/02/2000
Flea Bay	Flea East	2510793	5703958	23/02/2000
Flea Bay	Outer West	2511002	5703426	23/02/2000
Flea Bay	Rockpool Point	2510731	5703669	23/02/2000
Flea Bay	Hectors Wall	2511360	5703579	24/02/2000
Flea Bay	Tern Rock	2511478	5703134	24/02/2000
Chalmers				
Catlins	False Islet	2260635	5409277	12/02/2000
Catlins	Hole Point	2261955	5410586	12/02/2000
Catlins	Tuhawaiki Island	2257416	5406373	12/02/2000
Otago Peninsula	Cape Saunders	2333964	5478632	19/02/2000
Otago Peninsula	Puddingstone	2335078	5479650	19/02/2000
Otago Peninsula	Sandymount	2330190	5476635	20/02/2000
Buller				
Cape Foulwind	Fishing Rod reef	2383024	5941736	24/02/2001
Cape Foulwind	Granite spot	2381671	5938138	24/02/2001
Cape Foulwind	South Seal Rocks	2382840	5940581	24/02/2001
Cape Foulwind	North Granite	2381700	5938290	27/02/2001
Karamea	Falls Creek	2428497	5976797	25/02/2001
Karamea	Kongahu Point	2425899	5973459	25/02/2001
Karamea	Little Wanganui	2430778	5979244	25/02/2001
Westland				
Barn	Barn Island	2134236	5669941	21/02/2001
Barn	Brown Island	2130224	5663309	9/12/2003
Barn	Gorge Island	2125321	5658550	9/12/2003
Big Bay	Penguin Inner	2116300	5642142	8/12/2003
Big Bay	Penguin Rocks	2115697	5642167	8/12/2003
Big Bay	Crayfish Rock	2119708	5646604	12/12/200
Cascades	Cascade Island	2141018	5679231	21/02/2001
Cascades	Cement Face	2143307	5678981	21/02/2001
Cascades	Cascade Point	2138476	5678640	9/12/2003
Jackson Head	Frog Rocks	2155031	5683225	20/02/2001

Continued on next page

Appendix 1—continued

LOCATION	SITE	EASTING	NORTHING	DATE
Jackson Head	Moccasin Gap	2157047	5684270	20/02/2001
Jackson Head	Smoothwater Point	2156495	5684352	20/02/2001
Jackson Head	Jackson Bluff	2158886	5684454	12/12/2003
Jackson Head	Jackson Head	2158984	5685079	12/12/2003
Moeraki	Arnott Point	2204776	5714279	10/12/2003
Moeraki	Moeraki River	2208106	5716501	10/12/2003
Moeraki	Whakapoai	2206988	5715906	11/12/2003
Open Bay Islands	NE Taumaka	2179646	5697156	22/02/2001
Open Bay Islands	SW Popotai	2178539	5696721	22/02/2001
Open Bay Islands	NW Taumaka	2179505	5697478	11/12/2003
Fiordland				
Bligh Sound	Bligh OW	2071295	5589037	25/01/1999
Bligh Sound	Franzinner	2077508	5583660	25/01/2000
Bligh Sound	Chasland Head	2072478	5589151	25/01/2000
Bligh Sound	Turnaround Point	2078109	5586225	25/01/2000
Bligh Sound	Bligh IW	2075802	5583017	26/01/2000
Bligh Sound	Bligh ME	2078872	5586425	26/01/2000
Bligh Sound	Bligh ON	2074630	5591877	26/01/2000
Charles Sound	Charles inner	2048460	5551129	23/01/2000
Charles Sound	Charles outer	2045293	5554418	23/01/2000
Doubtful Sound	Hubs Spur	2029146	5533804	21/01/2000
Doubtful Sound	Hut Bay	2036333	5528325	21/01/2000
Doubtful Sound	Joseph Point	2037307	5525670	21/01/2000
Doubtful Sound	Jamieson	2030626	5528830	22/01/2000
Doubtful Sound	Renown Rock	2037523	5527670	22/01/2000
Doubtful Sound	Sail Rock	2032513	5530768	22/01/2000
Preservation Inlet	Sandfly Point	2017127	5437298	16/03/2005
Preservation Inlet	Weka Point	2020786	5438548	16/03/2005
Stewart Island				
Bluff	Oraka Pt	2114848	5411531	22/03/2005
Bluff	Pig Island	2123913	5410486	22/03/2005
Bluff	Barracouta Point	2147406	5392227	23/03/2005
Bluff	Lookout Point	2152629	5387851	23/03/2005
Bluff	Shag Rock	2144141	5395393	23/03/2005
Bluff	Stirling Point	2154032	5388640	24/03/2005
Bluff	Tiwai Point	2155425	5390468	24/03/2005
Codfish-Ruggedy	Codfish Southeast	2102422	5367193	14/03/2005
Codfish-Ruggedy	Ruggedy Passage	2105692	5376044	14/03/2005
Codfish-Ruggedy	Codfish East	2102363	5368359	17/03/2005
Codfish-Ruggedy	North Sealers	2100414	5370663	17/03/2005
Codfish-Ruggedy	Ruggedy NE	2106226	5376207	17/03/2005
Codfish-Ruggedy	Black Rock Point	2117548	5379304	18/03/2005
Codfish-Ruggedy	Lucky Point	2123254	5377092	18/03/2005
Green Islets	Archway	2033766	5425664	15/03/2005
Green Islets	NW Bay	2031101	5424077	15/03/2005
Green Islets	Prices Point	2041905	5424702	15/03/2005
Paterson Inlet	Octopus	2139273	5353661	31/01/2000
Paterson Inlet	Refuge Island	2138857	5351088	31/01/2000
Paterson Inlet	Neck North	2142802	5353784	1/02/2000

Continued on next page

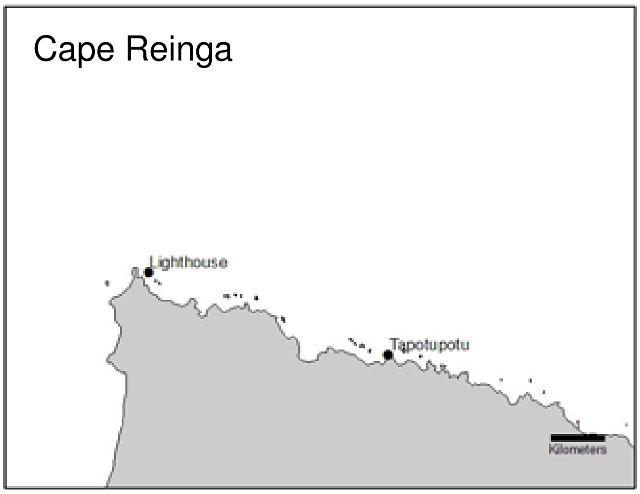
Appendix 1—continued

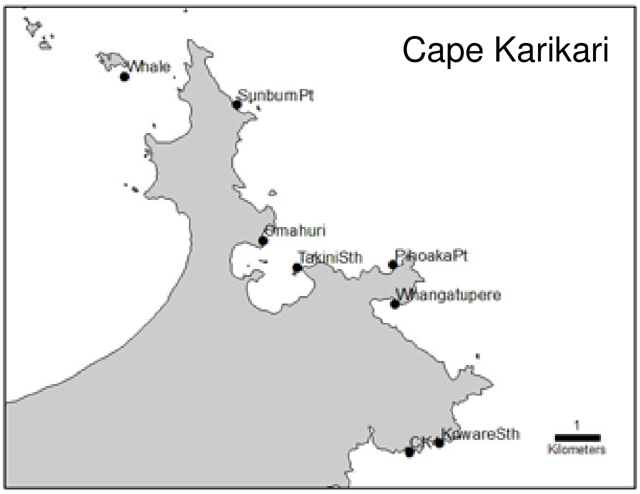
LOCATION	SITE	EASTING	NORTHING	DATE
Paterson Inlet	Balancing Rock	2137416	5353010	1/02/2000
Paterson Inlet	Ulva East	2140838	5352512	1/02/2000
Paterson Inlet	Ackers Point	2140868	5356773	2/02/2000
Paterson Inlet	Native North	2141284	5354940	2/02/2000
Paterson Inlet	Iona South	2138244	5355536	2/02/2000
Paterson Inlet	Horseshoe	2139545	5359778	7/02/2000
Paterson Inlet	Tamihou Island	2137091	5352726	19/03/2005
Paterson Inlet	Ulva East2	2140763	5352545	19/03/2005
Paterson Inlet	Bobs Point	2138192	5361525	21/03/2005
Paterson Inlet	West Head	2135454	5363772	21/03/2005
Port Adventure	Browns Garden	2144760	5338590	12/03/2005
Port Adventure	Lords River Head	2140594	5332620	13/03/2005
Port Adventure	Owens Island	2142866	5331715	13/03/2005
Port Adventure	Tia Island	2146867	5337926	13/03/2005
Ruapuke Island	Bird Rock	2159992	5372755	20/03/2005
Ruapuke Island	Caroline Bay	2165302	5374494	20/03/2005
Ruapuke Island	North Head	2167810	5376729	20/03/2005
Ruapuke Island	South Islets	2166573	5368849	20/03/2005
Titi Islands	Edwards	2144826	5364838	3/02/2000
Titi Islands	Herekopere	2146140	5360395	3/02/2000
Titi Islands	Bench Nth	2147096	5356879	4/02/2000
Titi Islands	Bench SE Point	2147989	5355765	4/02/2000

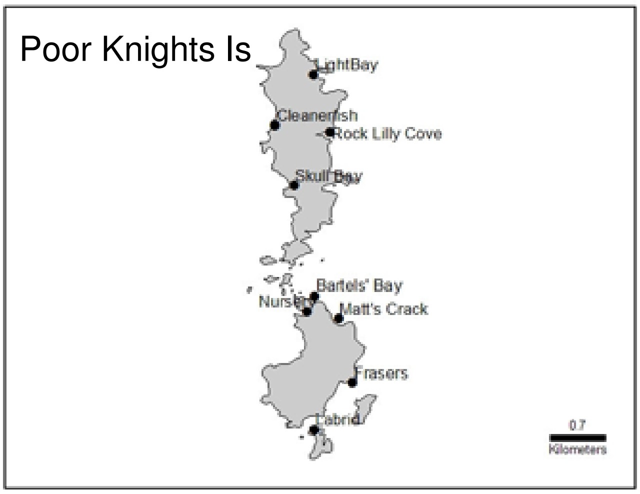
Appendix 2

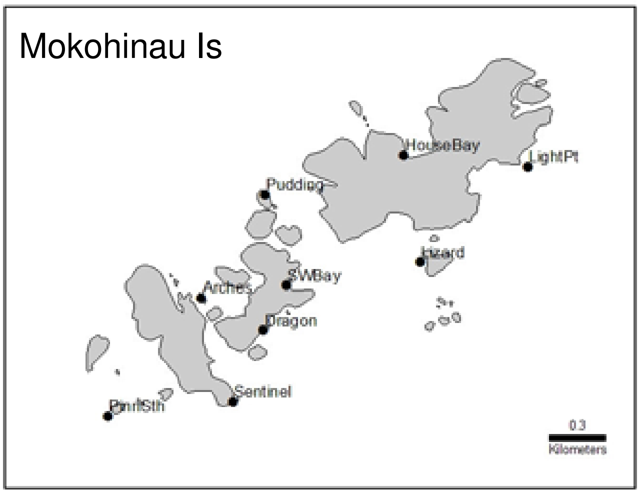
MAPS OF STUDY SITES

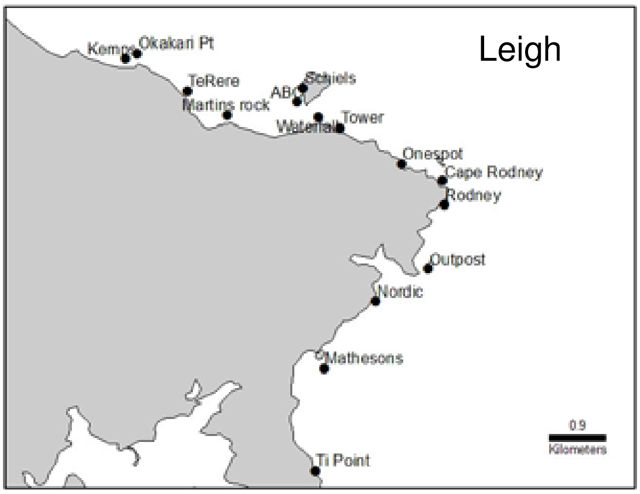
Position of sampling sites shown for each location. See Appendix 1 for site names and co-ordinates.

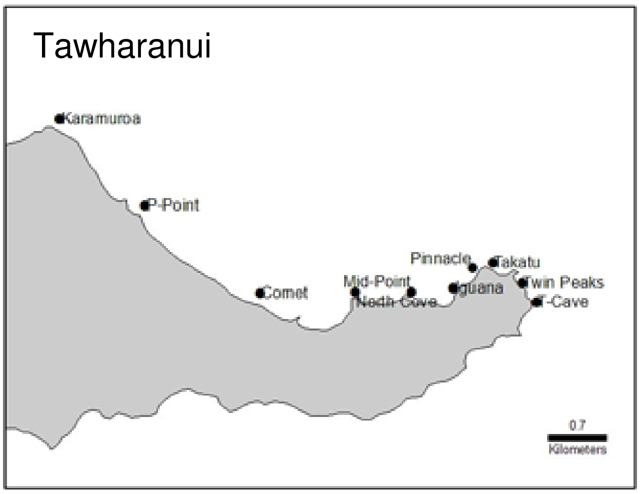




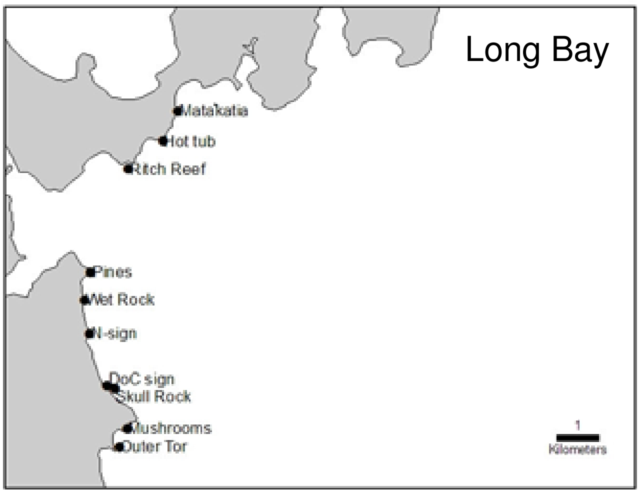


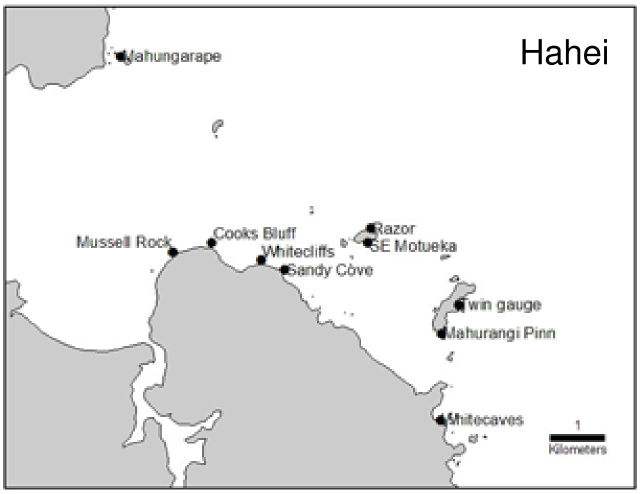


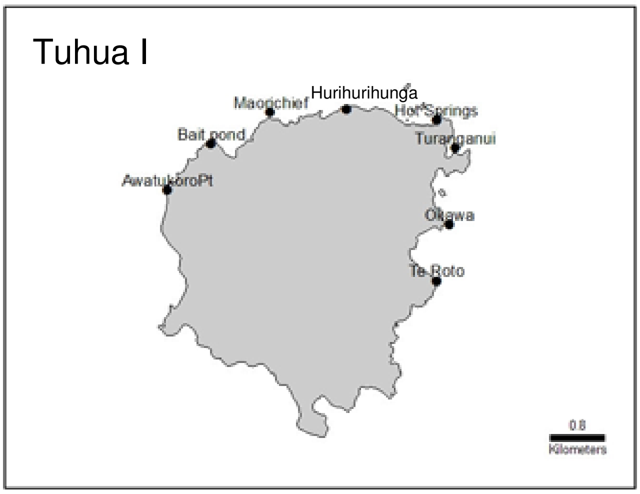


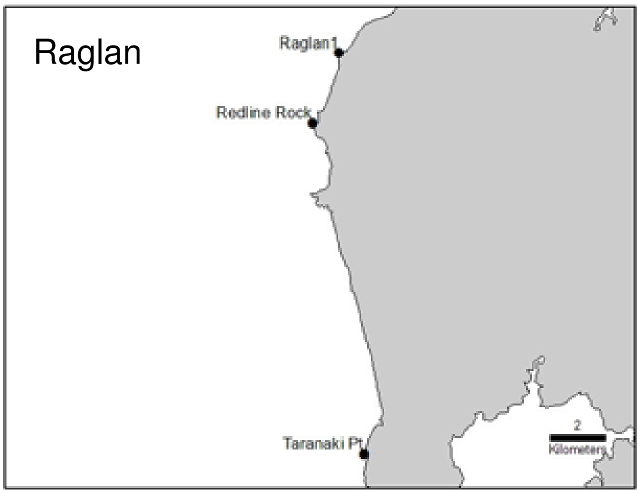


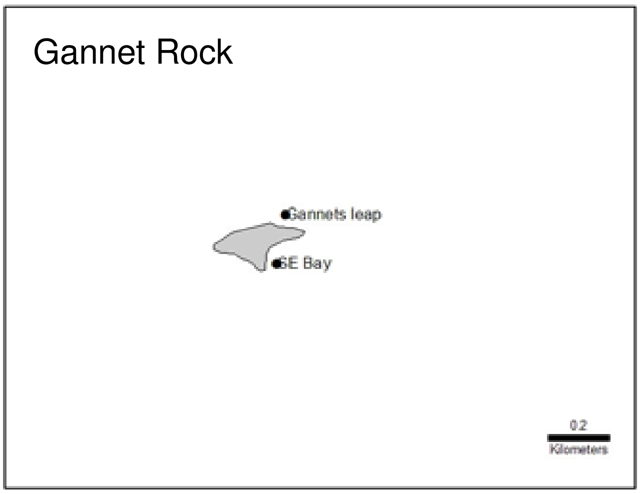
Continued on next page

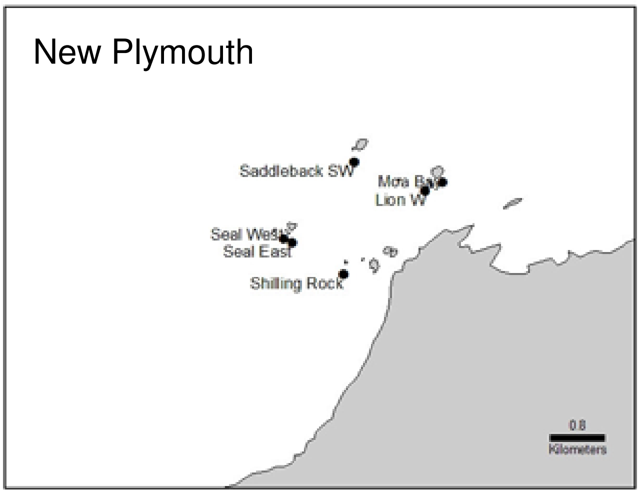




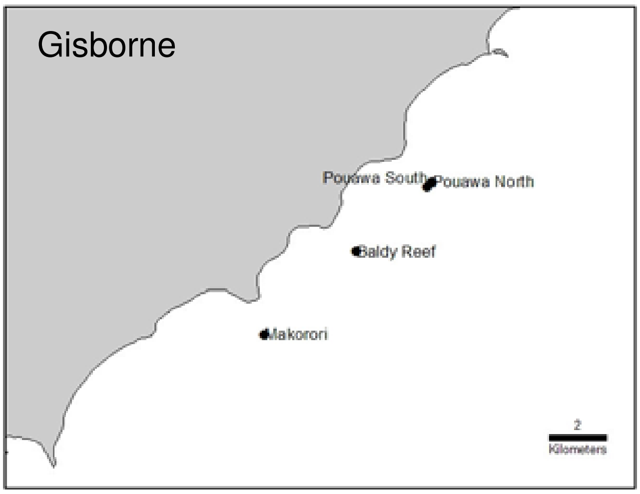


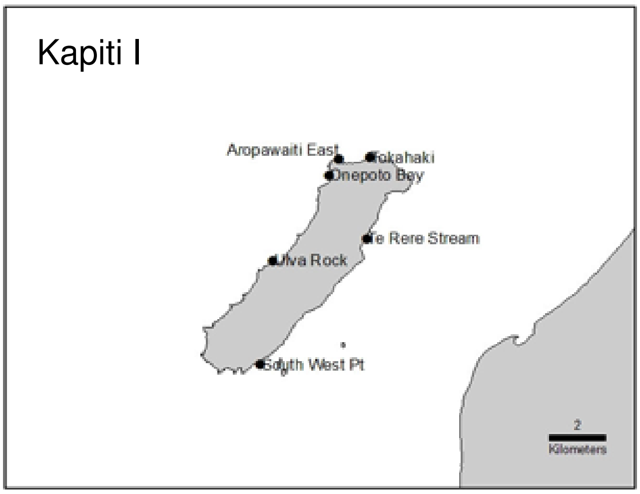


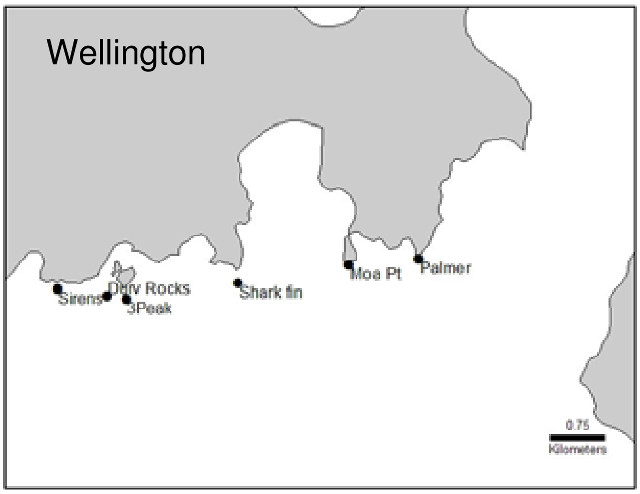


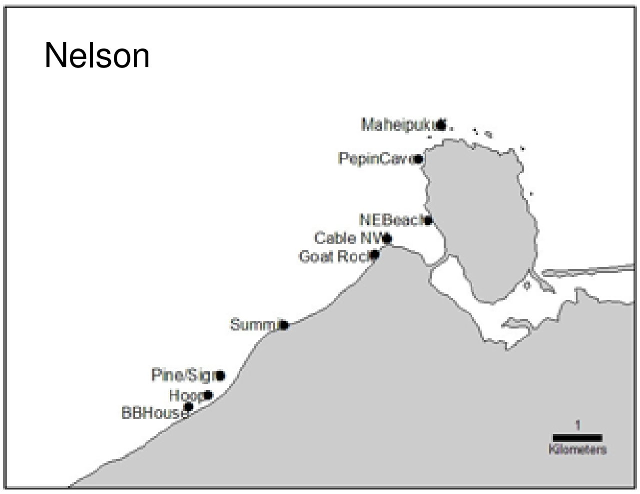


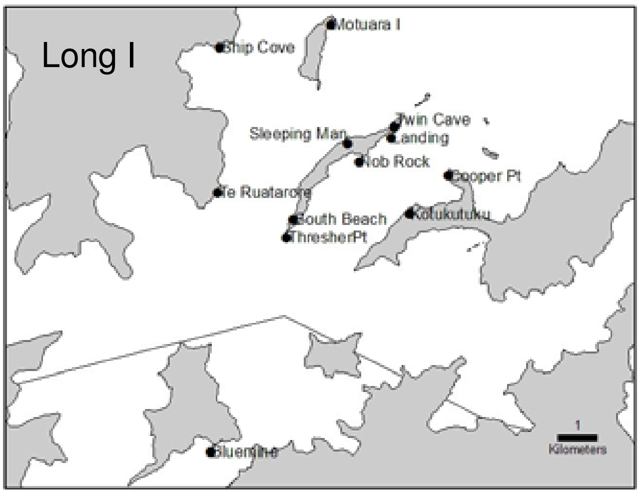
Continued on next page



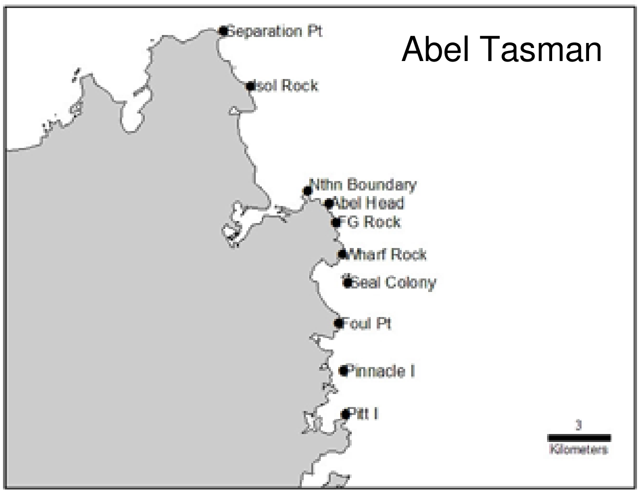


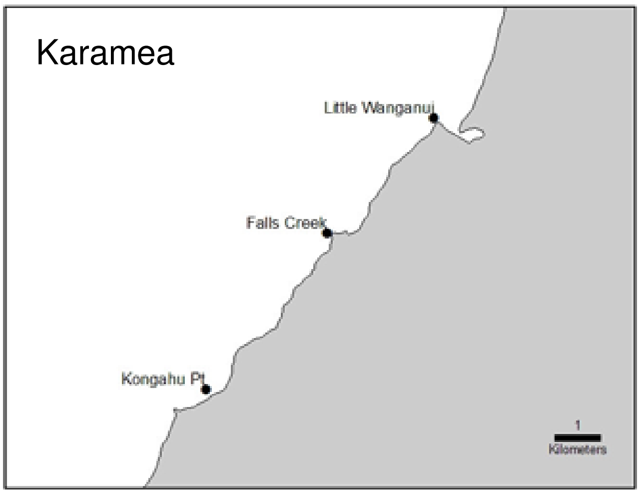


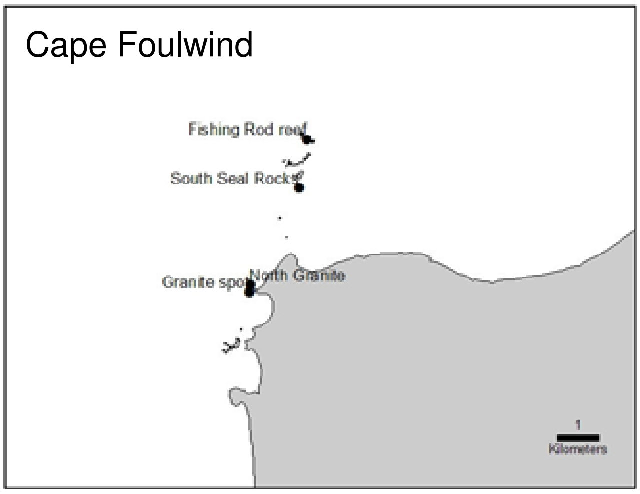


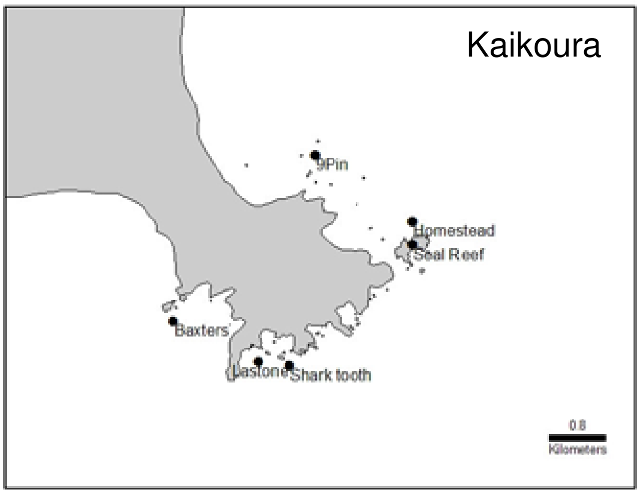


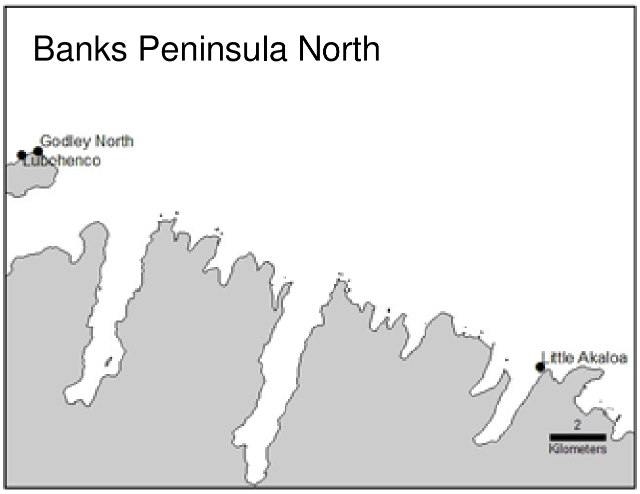
Continued on next page



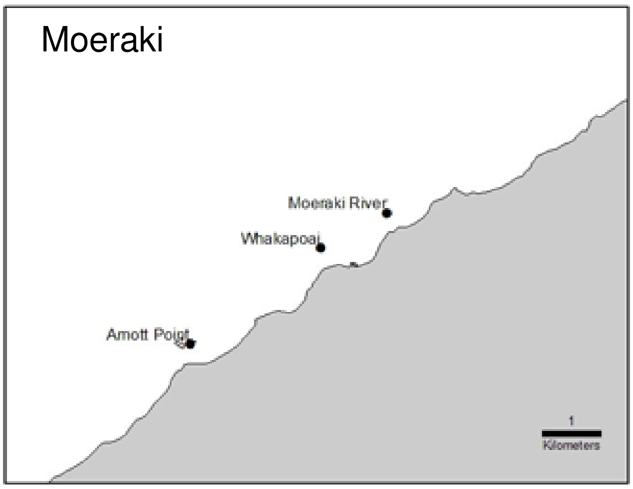


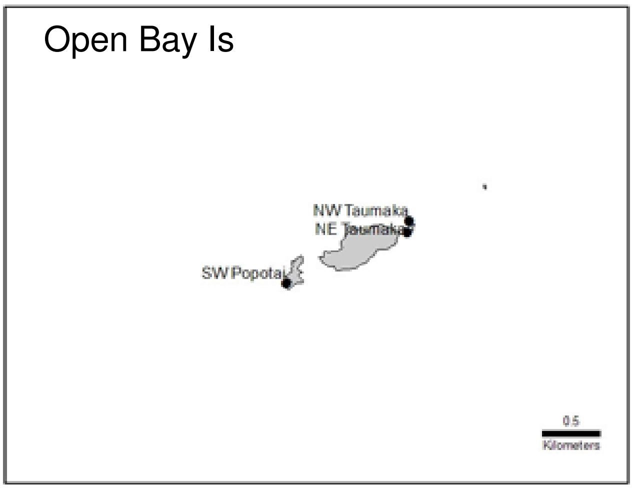


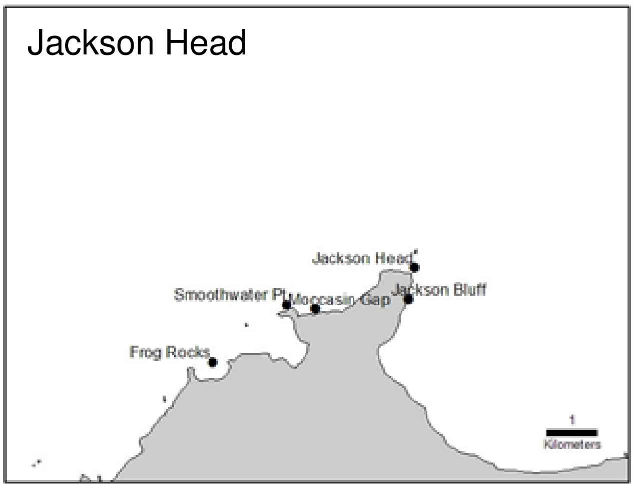


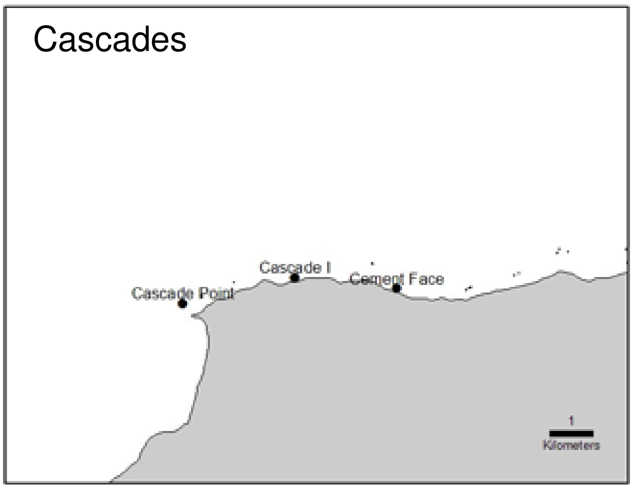


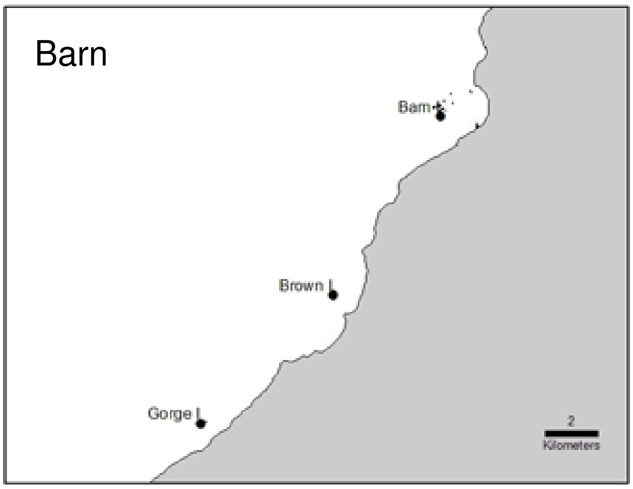
Continued on next page

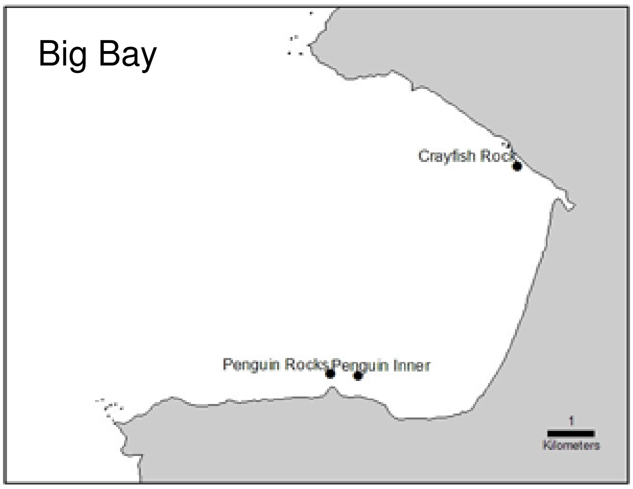




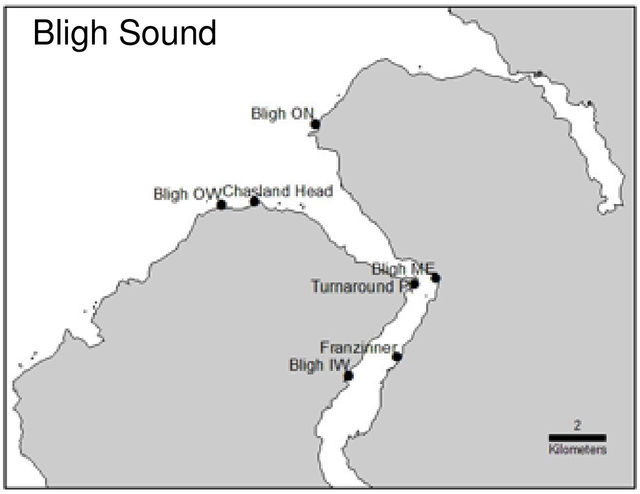


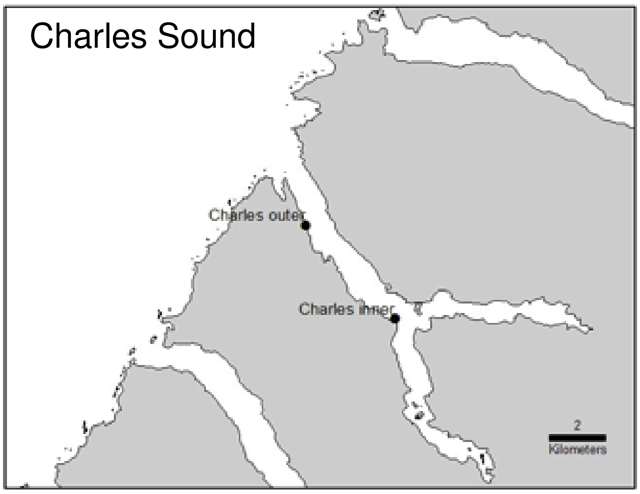


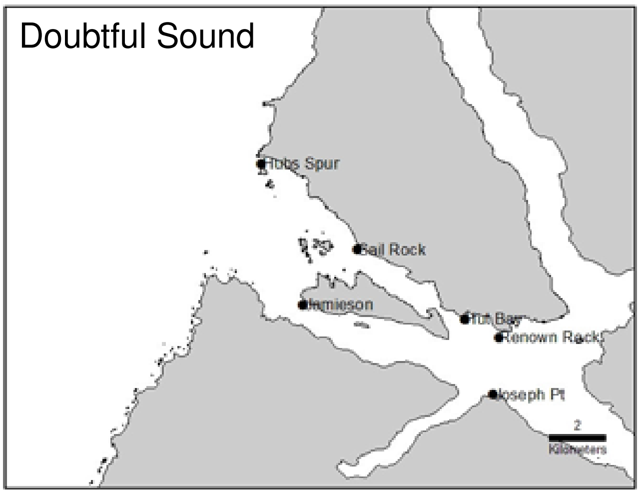


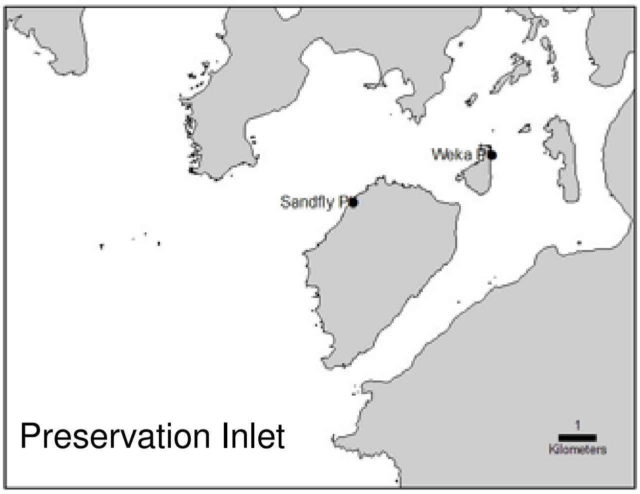


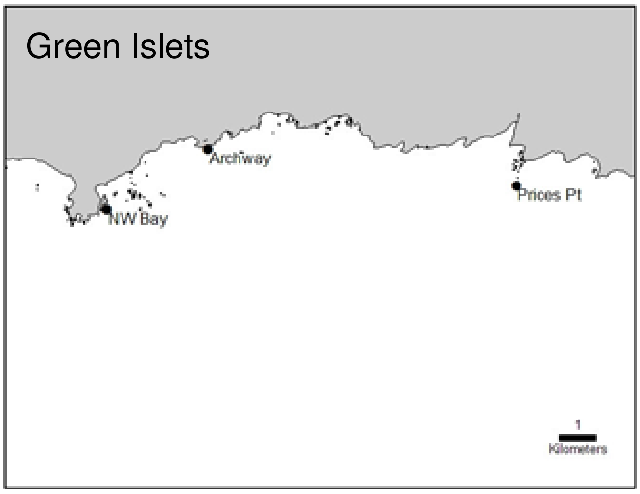
Continued on next page

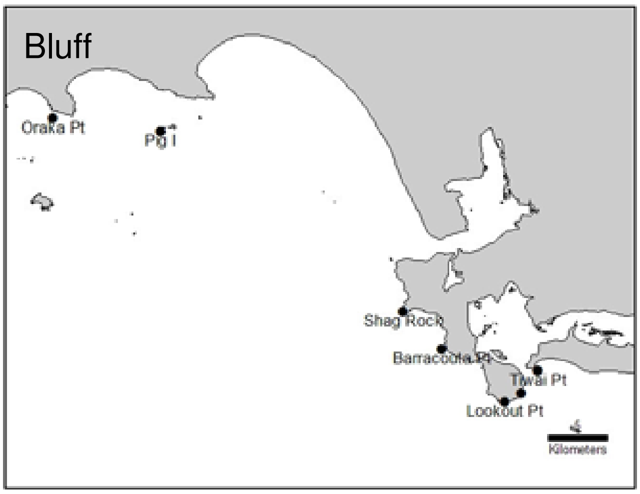




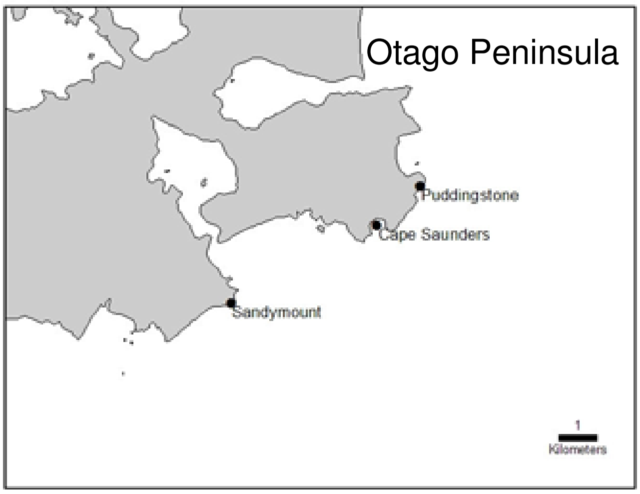


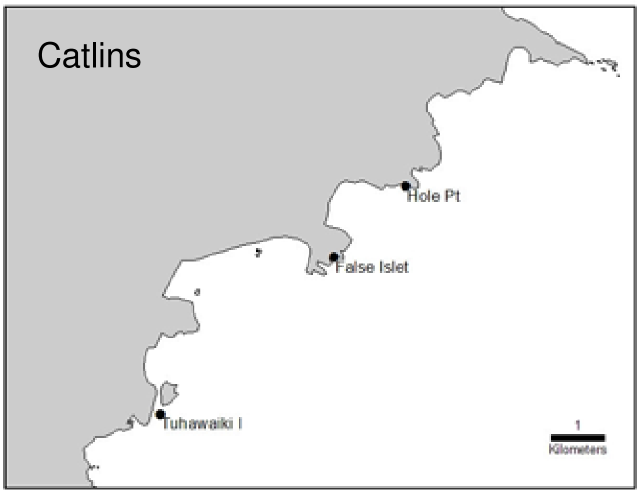


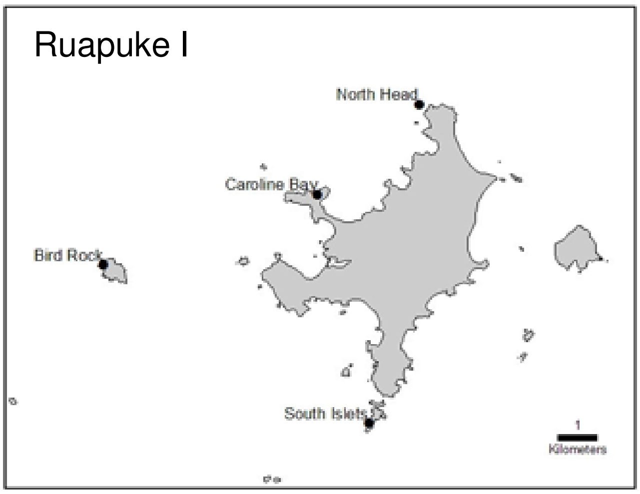


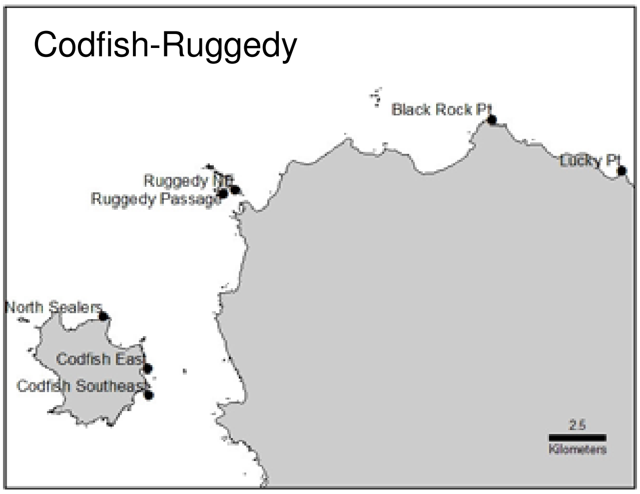


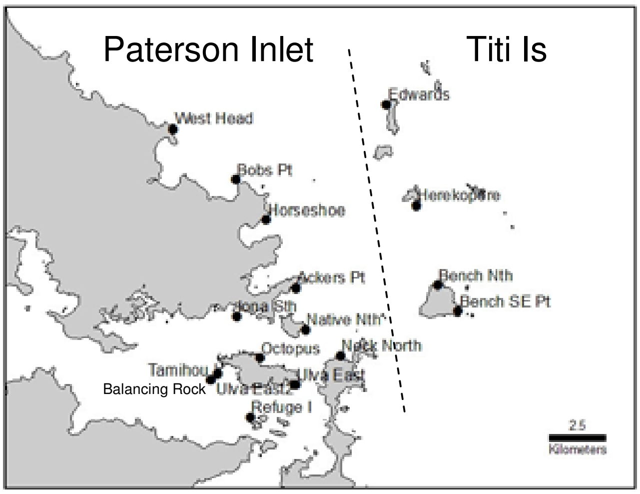
Continued on next page

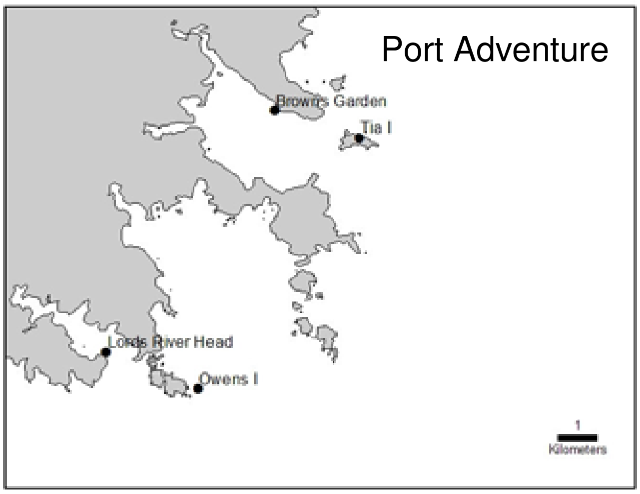

Otago Peninsula
Puddingstone
Cape Saunders
Sandymount
1
Kilometers


Catlins
Hole Pt
False Islet
Tuhawaiki I
1
Kilometers


Ruapuke I
North Head
Caroline Bay
Bird Rock
South Islets
1
Kilometers


Codfish-Ruggedy
Black Rock Pt
Lucky Pt
Ruggedy Nth
Ruggedy Passage
North Sealers
Codfish East
Codfish Southeast
2.5
Kilometers


Paterson Inlet
Titi Is
Edwards
West Head
Bobs Pt
Herekopare
Horseshoe
Ackers Pt
Bench Nth
Bench SE Pt
Iona Sth
Native Nth
Octopus
Neck North
Tamihou
Ulva East
Balancing Rock
Ulva East2
Refuge I
2.5
Kilometers


Port Adventure
Browns Garden
Tia I
Lords River Head
Owens I
1
Kilometers

Appendix 3

MACROALGAL BIOMASS EQUATIONS

Length–weight and/or percentage cover–weight relationships for major algal species and groups. y = dry weight (g), x = total length (cm), SD = stipe diameter (cm), SL = stipe length (cm), LL = laminae length (cm).

GROUP/SPECIES	EQUATION	R^2	n	COLLECTED
Ecklonia radiata	$\ln(y) = 2.625\ln(x) - 7.885$	0.97	21	Cape Reinga
Stipe	$\ln(y) = 1.671\ln(SL) - 3.787$	0.97	46	Leigh
Rest	$\ln(y) = 1.177\ln(SL \times LL) - 3.879$	0.94	55	Leigh
Carpophyllum flexuosum	$\ln(y) = 1.890\ln(x) - 4.823$	0.91	22	Long Bay
	$\ln(y) = 2.049\ln(x) - 5.251$	0.90	52	Tawharanui
	$\ln(y) = 1.792\ln(x) - 4.538$	0.89	59	Mokohinau Islands
	$\ln(y) = 1.282\ln(x) - 2.135$	0.91	31	Nelson
Other *Carpophyllum* spp.				
Carpophyllum angustifolium[a]	$y = 0.068x - 0.27$	0.92	23	Leigh
	$\ln(y) = 1.131\ln(x) - 3.522$	0.89	117	Mokohinau Islands
C. maschalocarpum	$\ln(y) = 2.078\ln(x) - 5.903$	0.88	116	Long Bay
	$\ln(y) = 1.764\ln(x) - 4.311$	0.72	46	Leigh
	$\ln(y) = 1.567\ln(x) - 4.204$	0.96	38	Mokohinau Islands
	$\ln(y) = 1.9624\ln(x) - 4.86$	0.89	41	Nelson
C. plumosum	$\ln(y) = 1.472\ln(x) - 3.850$	0.66	62	Leigh
	$y = 1.638x - 4.413$	0.92	31	Hahei
	$\ln(y) = 1.517\ln(x) - 4.778$	0.69	60	Mokohinau Islands
Cystophora spp.				
C. torulosa	$\ln(y) = 1.551\ln(x) - 2.6282$	0.79	12	Nelson
C. retroflexa	$\ln(y) = 1.560\ln(x) - 3.9486$	0.90	14	Nelson
C. platylobium	$\ln(y) = 2.7464\ln(x) - 7.9721$	0.66	6	Stewart Island
Lessonia variegata	$\ln(y) = 1.677\ln(x) - 5.537$	0.83	9	Mokohinau Islands
Landsburgia quercifolia	$\ln(y) = 1.971\ln(x) - 5.058$	0.83	19	Cape Reinga
	$\ln(y) = 2.5645\ln(x) - 6.741$	0.90	12	Stewart Island
Macrocystis pyrifera	$\ln(y) = 1.7997\ln(x) - 5.672$	0.79	42	Stewart Island
Marginariella spp.				
M. boryana	$\ln(y) = 2.1691\ln(x) - 6.4778$	0.95	21	Kaikoura
M. urvilliana	$\ln(y) = 3.4274\ln(x) - 12.405$	0.77	18	Kaikoura
Sargassum sinclairii	$y = 0.075x + 0.124$	0.58	25	Cape Reinga
	$\ln(y) = 1.3007\ln(x) - 2.6964$	0.79	26	Nelson
Xiphophora spp.				
X. chondrophylla	$y = 1.786x - 4.171$	0.62	18	Hahei
	$\ln(y) = 2.01\ln(x) - 5.377$	0.75	33	Mokohinau Islands
X. gladiata	$\ln(y) = 1.4995\ln(x) - 3.4541$	0.73	27	Bligh
	1% = 58.8 g		5	
Durvillaea willana	$\ln(y) = 2.1216\ln(SD) - 2.7727$	0.95	6	Westport

Continued on next page

Appendix 3—continued

GROUP/SPECIES	EQUATION	R^2	*n*	COLLECTED
Red foliose				
Osmundaria colensoi	$\ln(y) = 1.720 \ln(x) - 3.379$	0.70	14	Mokohinau Islands
	1% = 22.93g		3	
Pterocladia lucida	$\ln(y) = 1.963 \ln(x) - 5.076$	0.73	47	Leigh
	1% = 10 g		3	
Melanthalia abscissa	$\ln(y) = 1.775 \ln(x) - 4.247$	0.64	22	Leigh
Plocamium spp.	$\ln(y) = 2.649 \ln(x) - 8.812$	0.80	34	Mokohinau Islands
Euptilota formosissima	$\ln(y) = 1.616 \ln(x) - 4.971$	0.78	13	Mokohinau Islands
Placentophora colensoi	$\ln(y) = 2.582 \ln(x) - 6.392$	0.87	23	Cape Karikari
Red turfing	1% = 1.74 g		3	Mokohinau Islands
Coralline turf[b]	1% = 1.5 g		3	Mokohinau Islands
Crustose corallines[b]	1% = 0.35 g		3	Leigh
Brown turfing	1% = 1.74 g		3	Mokohinau Islands
Small browns				
Carpomitra costata	$\ln(y) = 1.735\ln(x) - 5.856$	0.43	18	Mokohinau Islands
Zonaria turneriana	$\ln(y) = 2.587\ln(x) - 6.443$	0.83	27	Mokohinau Islands
	1% = 2.48 g		3	
Caulerpa flexilis	1% = 5.81 g		3	Mokohinau Islands
Other greens				
Codium convolutum	1% = 4.68 g		3	Mokohinau Islands
Codium fragile	$\ln(y) = 1.7635\ln(x) - 4.3427$	0.90	13	Doubtful
Ulva spp.	1% = 1.71 g		3	Mokohinau Islands

[a] From Choat & Schiel (1982).

[b] The proportion of $CaCO_3$ in *Corallina officinalis* has been estimated as 45% of the dry weight. The value given is the total dry weight of samples less 45%.

Appendix 4

STRUCTURAL GROUP AFDW CONVERSION FACTORS

Samples collected from Leigh (Lei), Mokohinau Islands (Mok) and Raglan (Rag).

TAXON	STRUCTURAL GROUP	SPECIES	UNIT	AFDW (g)	SE	*n*
Ascidians	Compound ascidians	*Didemnum* sp. (Lei)	1%	1.6	0.2	3
	Solitary ascidians	*Asterocarpa* sp. (Lei)	1%	6.4	0.6	3
	Stalked ascidians	*Pseudodistoma* sp. (Lei)	1%	2.2	0.3	3
Barnacles	Barnacles	*Balanus* sp. (Lei)	1%	1.8	0.2	3
Mollusca	Oysters	*Crassostrea* sp. (Lei)	1%	5.0	1.4	3
	Large mussels	*Perna canaliculus* (Lei)	1%	26.0	5.0	3
	Small mussels	*Xenostrobus pulex* (Lei)	1%	8.9	0.5	3
Brachiopoda	Brachiopods	Unknown brachiopod (Lei)	0.25%	0.4	0.1	3
Bryozoa	Branched bryozoans	*Cribricellina cribraria* (Mok)	1%	3.5	0.8	3
	Encrusting bryozoans	*Membranipora* sp. (Mok)	1%	0.5	0.1	3
Coelenterates	Colonial anemones	*Actinothoe albocincta* (Lei)	1%	2.3	0.4	3
	Large solitary anemones	*Phlyctinactis* sp. (Lei)	1%	4.0	0.6	3
	Cup corals	*Monomyces rubrum* (Lei)	0.25%	0.3	0.1	3
	Soft corals	*Alcyonium* sp. (Mok)	1%	3.1	0.5	3
Hydrozoa	Hydroid turf	Unknown hydroid (Mok)	0.25%	0.4	0.0	3
		Amphisbetia bispinosa (Rag)	1%	8.1	0.4	2
	Hydroid trees	*Solanderia ericopsis* (Mok)	1%	10.0	1.2	3
Porifera	Encrusting sponges	*Cliona celata* (Lei)	1%	11.4	2.2	3
	Finger sponges	*Raspailia topsenti* (Mok)	1%	44.9	7.1	2
	Massive sponges	*Polymastia croceus* (Lei)	1%	22.2	2.0	3
		Ancorina alata (Lei)	1%	64.7	4.4	3

Appendix 5

OCCURRENCE OF MACROALGAL SPECIES

Percentage of quadrats in which each species was recorded (*n* indicates the number of quadrats sampled at each location).

TABLE A5.1. NORTHERN LOCATIONS.

BIOREGION	NORTHEASTERN									PORTLAND		RAGLAN			ABEL			
LOCATION	CAPE REINGA	CAPE KARIKARI	POOR KNIGHTS IS	MOKOHINAU ISLANDS	LEIGH	TAWHARANUI	LONG BAY	HAHEI	TUHUA ISLAND	GISBORNE	MAHIA	RAGLAN	GANNET ROCK	NEW PLYMOUTH	KAPITI ISLAND	LONG ISLAND	NELSON	ABEL TASMAN
n	35	160	180	175	275	180	75	165	160	75	40	26	40	120	115	235	175	200
Large brown algae																		
Carpophyllum angustifolium	-	-	20.0	14.9	6.9	2.2	-	10.3	23.8	-	-	-	-	-	-	-	-	-
Carpophyllum flexuosum	-	31.9	7.8	23.4	12.7	27.8	48.0	37.0	8.1	52.0	2.5	-	-	-	58.3	17.9	25.7	13.5
Carpophyllum maschalocarpum	94.3	41.9	18.3	27.4	50.9	52.8	80.0	49.7	49.4	49.3	72.5	26.9	27.5	43.3	51.3	22.1	29.1	24.5
Carpophyllum plumosum	20.0	15.6	8.9	9.1	14.2	8.9	20.0	28.5	18.1	-	-	-	-	-	-	-	-	-
Cystophora retroflexa	-	-	-	0.6	-	-	24.0	-	17.5	-	-	-	-	-	25.2	0.4	5.7	-
Cystophora torulosa	-	0.6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3.4	3.0
Durvillaea antarctica	-	-	-	-	-	-	-	-	-	-	7.5	-	-	-	-	-	-	-
Ecklonia radiata	57.1	55.0	66.7	45.1	76.0	73.9	60.0	80.6	44.4	74.7	65.0	-	10.0	6.7	91.3	20.0	-	-
Landsburgia quercifolia	45.7	7.5	5.6	-	1.1	-	-	3.0	-	-	-	-	12.5	-	14.8	1.3	-	-
Lessonia variegata	25.7	7.5	20.0	12.6	-	-	-	7.9	-	-	-	-	-	-	-	-	-	-
Macrocystis pyrifera	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4.7	-	-
Marginariella boryana	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3.4	-	-
Sargassum sinclairii	28.6	36.3	16.7	10.3	5.5	7.2	33.3	25.5	19.4	17.3	10.0	-	7.5	2.5	36.5	6.0	20.0	1.0
Xiphophora chondrophylla	-	27.5	23.9	16.6	5.5	1.7	-	30.3	26.9	-	-	-	-	-	-	-	-	-
Small brown algae																		
Carpomitra costata	5.7	13.1	4.4	9.7	-	-	-	5.5	17.5	33.3	15.0	-	-	1.7	33.0	14.0	1.7	11.5
Distromium scottsbergii	-	3.8	7.8	1.7	4.4	-	-	0.6	11.9	8.0	-	-	-	0.8	-	-	-	-
Halopteris spp.	5.7	0.6	3.9	3.4	0.7	-	-	1.2	8.1	1.3	47.5	-	-	17.5	22.6	11.1	3.4	-
Perithalia capillaris	-	1.9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sporochnus sp.	8.6	3.8	-	-	-	-	-	-	-	-	-	-	-	1.7	2.6	0.9	-	1.5
Zonaria spp.	57.1	20.6	21.7	38.3	7.3	11.7	62.7	39.4	69.4	81.3	47.5	7.7	2.5	4.2	81.7	8.9	-	-

Continued on next page

Table A5.1—continued

BIOREGION	NORTHEASTERN									PORTLAND		RAGLAN			ABEL			
LOCATION	CAPE REINGA	CAPE KARIKARI	POOR KNIGHTS IS	MOKOHINAU IS	LEIGH	TAWHARANUI	LONG BAY	HAHEI	TUHUA ISLAND	GISBORNE	MAHIA	RAGLAN	GANNET ROCK	NEW PLYMOUTH	KAPITI ISLAND	LONG ISLAND	NELSON	ABEL TASMAN
Ephemeral brown algae																		
Brown turf (< 5 cm)	-	-	0.6	1.1	-	-	-	-	8.8	-	-	-	-	0.8	-	-	-	-
Colpomenia sinuosa	-	2.5	1.7	4.6	7.3	8.9	1.3	-	8.8	-	5.0	-	5.0	9.2	-	14.9	2.3	8.0
Cutleria multifida	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.9	-	-	-
Desmarestia ligulata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6.0	1.7	-
Dictyota spp.	-	3.8	-	-	6.2	1.7	-	-	-	-	-	-	-	30.0	7.8	-	-	3.0
Endarachne binghamiae	-	-	-	-	-	-	-	-	-	-	-	7.7	2.5	-	-	-	-	-
Glossophora kunthii	5.7	3.1	-	2.9	0.7	0.6	-	1.8	10.0	10.7	10.0	3.8	17.5	9.2	15.7	5.1	18.3	8.0
Spatoglossum chapmanii	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.4	-	-
Brown encrusting																		
Ralfsia spp.	17.1	16.3	8.9	21.1	13.1	35.0	26.7	22.4	21.9	17.3	10.0	11.5	22.5	15.0	15.7	49.4	43.4	22.5
Green algae																		
Bryopsis spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	0.8	-	-	-	-
Caulerpa articulata	-	1.9	-	-	-	-	-	-	-	22.7	-	-	-	-	-	-	-	-
Caulerpa brownii	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3.0	-	-
Caulerpa fastigiata	-	0.6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Caulerpa flexilis	-	3.1	7.2	1.1	-	-	-	-	10.6	-	-	-	-	-	-	-	-	-
Caulerpa geminata	-	1.9	7.2	5.7	0.4	0.6	-	-	3.8	6.7	17.5	-	-	0.8	5.2	0.9	0.6	-
Codium convolutum	14.3	30.6	42.8	41.1	7.6	2.8	-	6.1	10.0	-	-	-	-	7.5	-	5.5	-	-
Codium cranwelliae	5.7	5.0	8.9	1.7	0.4	-	-	21.8	1.3	-	-	-	-	-	-	-	-	-
Cladophora spp.	-	0.6	-	-	-	-	-	-	-	-	-	15.4	7.5	34.2	13.0	2.1	8	7.0
Cladophoropsis herpestica	-	-	-	-	-	-	4.0	-	-	-	-	-	-	-	-	-	-	-
Codium fragile	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.1	-	-
Halicystis sp.	-	-	-	-	-	-	-	-	-	1.3	2.5	-	-	-	-	0.4	-	1.5
Pedobesia clavaeformis	-	3.1	1.1	8.0	-	-	-	-	1.9	-	-	-	-	-	-	-	-	-
Ulva spp.	5.7	2.5	58.9	53.1	-	-	-	-	36.3	-	-	-	-	0.8	27.8	5.5	18.3	-

Continued on next page

Table A5.1—continued

BIOREGION	NORTHEASTERN									PORTLAND		RAGLAN			ABEL			
LOCATION	CAPE REINGA	CAPE KARIKARI	POOR KNIGHTS IS	MOKOHINAU IS	LEIGH	TAWHARANUI	LONG BAY	HAHEI	TUHUA ISLAND	GISBORNE	MAHIA	RAGLAN	GANNET ROCK	NEW PLYMOUTH	KAPITI ISLAND	LONG ISLAND	NELSON	ABEL TASMAN
Encrusting and coralline algae																		
Crustose coralline algae	100	100	99.4	98.9	100	98.3	100	98.8	100	100	100	100	100	99.2	98.3	99.6	100	100
Coralline turf species	68.6	57.5	79.4	77.7	65.8	52.8	10.7	27.3	73.1	8.0	77.5	23.1	2.5	25.0	22.6	20.0	15.4	5.5
Hildenbrandia spp.	85.7	50.0	46.7	36.6	5.5	11.1	14.7	46.7	53.8	53.3	25.0	61.5	10.0	25.0	39.1	9.4	10.9	21.0
Red turfing algae (< 5 cm)																		
Champia novae-zelandiae	2.9	12.5	3.3	13.7	5.5	5.6	-	4.8	1.9	-	-	-	-	-	0.9	0.4	-	-
Curdiea codioides	11.4	14.4	7.2	3.4	13.1	-	-	7.3	-	-	-	-	-	-	-	-	-	-
Laurencia distichophylla	5.7	1.9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Liagora harveyana	-	-	-	-	-	-	-	-	-	-	-	-	-	3.3	-	-	-	-
Red turf (species complex)	62.9	39.4	90.0	56.0	14.2	11.7	-	27.9	56.3	9.3	45.0	53.8	17.5	35.8	40.9	11.1	24.0	4.0
Red foliose algae																		
Anotrichium crinitum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6.1	1.7	6.3	0.5
Aphanocladia delicatula	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.9	-	-	-
Asparagopsis armata	-	1.3	-	-	-	-	-	-	-	-	-	-	-	0.8	10.4	8.5	3.4	7.5
Ballia callitrichia	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.6	-	-	-
Callophyllis sp.	-	7.5	2.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Chondria sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5.1	2.9	1.0
Cladhymenia oblongifolia	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.9	-	-	-
Curdiea coriacea	5.7	1.9	21.1	1.7	-	7.2	-	5.5	1.3	-	-	-	-	-	-	-	-	-
Delisea compressa	-	-	8.3	0.6	-	-	-	-	10.0	-	-	-	-	-	-	-	-	-
Euptilota formosissima	-	-	21.7	6.3	-	-	-	-	3.1	-	-	-	-	-	1.7	1.7	-	-
Gigartina macrocarpa	-	-	10.0	-	-	-	-	-	6.9	-	-	-	-	-	-	-	-	-
Grateloupia sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.4	-	-
Gymnogongrus humilis	-	-	-	-	-	-	-	-	-	-	-	15.4	-	-	-	-	-	-
Humbrella hydra	-	-	-	-	0.4	0.6	-	-	-	-	-	-	-	-	-	-	-	-
Hymenena sp. (Red dots)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.9	-	-	-

Continued on next page

Table A5.1—continued

BIOREGION	NORTHEASTERN									PORTLAND		RAGLAN			ABEL			
LOCATION	CAPE REINGA	CAPE KARIKARI	POOR KNIGHTS IS	MOKOHINAU IS	LEIGH	TAWHARANUI	LONG BAY	HAHEI	TUHUA ISLAND	GISBORNE	MAHIA	RAGLAN	GANNET ROCK	NEW PLYMOUTH	KAPITI ISLAND	LONG ISLAND	NELSON	ABEL TASMAN
Hymenena variolosa	2.9	16.9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Kallymenia berggenii	2.9	1.9	1.7	-	-	-	-	1.8	-	-	-	-	-	-	-	1.7	-	-
Laurencia thyrsifera	31.4	16.9	-	-	-	-	-	-	-	8.0	-	-	-	-	-	-	-	-
Lophurella hookeriana	-	-	-	-	-	-	-	-	-	-	-	7.7	-	-	-	-	-	-
Melanthalia abscissa	40.0	5.6	15.0	8.6	7.3	10.6	-	13.9	15.6	17.3	2.5	38.5	15.0	-	2.6	-	-	-
Nesophila hoggardii	-	-	40.0	-	-	-	-	-	0.6	-	-	-	-	-	-	-	-	-
Osmundaria colensoi	42.9	9.4	32.8	17.1	4.7	1.7	-	6.7	53.8	33.3	80.0	57.7	12.5	-	-	-	-	-
Pachymenia crassa	-	3.1	16.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Phacelocarpus labillardieri	-	-	2.8	-	-	-	-	-	1.9	18.7	12.5	-	-	-	-	-	-	-
Placentophora colensoi	17.1	0.6	10.6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Plocamium cirrhosum	8.6	0.6	1.1	2.3	-	-	-	1.2	0.6	-	5.0	-	-	1.7	2.6	3.4	-	8.5
Plocamium microcladioides	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.9	-	1.7	2.5
Plocamium spp. (all species)	14.3	3.1	25.0	14.9	0.4	-	-	10.9	5.0	16.0	47.5	3.8	-	3.3	24.3	-	3.4	3.5
Polysiphonia muelleriana	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.9	5.1	-
Pterocladiella capillacea	2.9	-	-	-	-	0.6	-	-	11.9	-	-	3.8	7.5	-	1.7	-	-	-
Pterocladia lucida	71.4	23.8	26.1	24.6	19.3	21.7	-	33.9	26.3	30.7	67.5	53.8	12.5	28.3	23.5	0.4	0.6	-
Ptilonia spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.7	-	-	-
Rhodophyllis gunnii	-	-	-	-	-	-	-	-	-	2.7	5.0	-	-	-	17.4	5.5	-	-
Rhodymenia sp. (Manawatawhi/Three Kings Islands)	-	-	13.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rhodymenia spp.	-	-	-	-	-	-	-	-	1.3	-	-	11.5	-	-	1.7	3.8	2.9	-
Scinaia australis	-	0.6	-	-	-	-	-	-	-	-	-	-	-	-	0.9	-	-	-
Stenogramme interrupta	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3.5	-	-	-
Taylorophycus filiformis	-	-	1.7	-	-	-	-	-	0.6	-	-	-	-	-	-	-	-	-

TABLE A5.2. SOUTHERN LOCATIONS.

BIOREGION	COOK		BANKS		BULLER		WESTLAND						FIORDLAND				STEWART ISLAND							CHALMERS	
LOCATION	WELLINGTON	KAIKOURA	BANKS PENINSULA NORTH	FLEA BAY	KARAMEA	CAPE FOULWIND	MOERAKI	OPEN BAY ISLANDS	JACKSON HEAD	CASCADES	BARN	BIG BAY	BLIGH SOUND	CHARLES SOUND	DOUBTFUL SOUND	PRESERVATION INLET	GREEN ISLETS	BLUFF	CODFISH-RUGGEDY	RUAPUKE ISLAND	TITI ISLANDS	PATERSON INLET	PORT ADVENTURE	OTAGO PENINSULA	CATLINS
n	120	117	55	100	45	75	58	99	160	120	60	60	140	39	120	40	60	135	119	80	79	272	78	59	60
Large brown algae																									
Carpophyllum flexuosum	11.7	-	21.8	21.0	-	-	-	37.9	-	-	-	-	22.1	33.3	22.5	5.1	-	4.4	21.0	27.5	5.0	58.4	10.4	-	-
C. maschalocarpum	66.7	25.6	23.6	28.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cystophora platylobium	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	34.1	2.5	47.5	18.8	8.0	0.7	-	1.7
Cystophora retroflexa	0.8	-	-	-	-	-	-	-	-	-	-	-	2.9	-	-	-	-	5.2	16.8	45.0	15.0	1.5	7.4	-	-
Cystophora scalaris	-	-	-	-	-	-	1.0	3.4	-	3.3	-	3.3	-	-	-	3.8	-	-	5.9	7.5	7.5	16.8	1.5	-	-
Cystophora torulosa	-	-	1.8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.7	-	-	-	2.2	-	-	-
Durvillaea antarctica	1.7	5.1	1.8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.5	-	10.0	3.8	5.1	-	-	-
Durvillaea willana	-	2.6	1.8	9.0	-	2.7	-	-	-	1.7	-	-	2.1	7.7	0.8	1.3	-	7.4	-	-	-	5.8	-	23.7	23.3
Ecklonia radiata	75.8	58.1	14.5	22.0	-	-	-	60.3	1.7	-	-	-	57.9	66.7	49.2	-	-	-	8.4	55.0	36.3	48.2	25.9	-	-
Landsburgia quercifolia	75.0	44.4	-	-	-	2.7	12.0	43.1	5.0	8.3	24.1	10.0	27.9	-	14.2	15.4	33.3	31.1	74.8	130.0	12.5	24.8	35.6	-	1.7
Lessonia variegata	54.2	46.2	-	13.0	-	-	-	1.7	-	-	-	-	5.0	-	5.0	-	50.0	29.6	27.7	57.5	8.8	3.6	9.6	61.0	33.3
Macrocystis pyrifera	0.8	7.7	34.5	14.0	-	-	-	-	-	-	-	-	2.1	2.6	-	-	-	-	-	-	21.3	62.8	-	-	-
Marginariella boryana	24.2	59.8	-	1.0	-	-	-	-	-	-	-	-	0.7	-	4.2	-	-	6.7	-	62.5	32.5	53.3	5.2	-	-
Marginariella urvilliana	-	20.5	-	14.0	-	-	-	-	-	-	-	-	-	12.8	-	-	-	23.0	13.4	67.5	15.0	23.4	13.3	-	-
Sargassum sinclairii	7.5	6.0	-	-	-	10.7	10.0	43.1	-	6.7	1.3	11.7	14.3	2.6	13.3	5.1	-	2.2	17.6	25.0	7.5	21.2	1.5	-	-
Sargassum verruculosum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4.2	-	-	-	-	-	-	-	-	-	-
Xiphophora gladiata	3.3	-	3.6	11.0	-	-	-	-	-	-	1.3	-	17.9	5.1	12.5	11.5	-	11.9	31.1	70.0	67.5	41.6	34.1	-	1.7
Small brown algae																									
Carpomitra costata	21.7	29.9	-	-	-	-	9.0	25.9	18.3	10.0	13.9	-	22.1	38.5	21.7	6.4	18.3	3.7	26.9	5.0	8.8	16.1	3.0	-	-
Halopteris spp.	51.7	33.3	45.5	18.0	17.8	14.7	28.0	25.9	128.3	51.7	58.2	25.0	48.6	53.8	29.2	24.4	50.0	41.5	68.9	157.5	75.0	50.4	34.1	-	8.3

Continued on next page

Table A5.2—continued

BIOREGION	COOK		BANKS		BULLER		WESTLAND						FIORDLAND				STEWART ISLAND							CHALMERS	
LOCATION	WELLINGTON	KAIKOURA	BANKS PENINSULA NORTH	FLEA BAY	KARAMEA	CAPE FOULWIND	MOERAKI	OPEN BAY ISLANDS	JACKSON HEAD	CASCADES	BARN	BIG BAY	BLIGH SOUND	CHARLES SOUND	DOUBTFUL SOUND	PRESERVATION INLET	GREEN ISLETS	BLUFF	CODFISH-RUGGEDY	RUAPUKE ISLAND	TITI ISLANDS	PATERSON INLET	PORT ADVENTURE	OTAGO PENINSULA	CATLINS
Hormosira banksii	-	-	-	-	-	-	-	-	-	-	-	-	6.4	-	-	-	-	-	-	-	-	-	-	-	-
Microzonia velutina	25.0	49.6	14.5	35.0	11.1	20.0	28.0	22.4	68.3	63.3	54.4	10.0	17.9	5.1	9.2	2.6	8.3	16.3	-	-	10.0	10.2	-	13.6	1.0
Sporochnus sp.	-	-	-	-	-	-	-	-	-	-	-	1.7	-	2.6	6.7	-	-	-	-	-	-	8.8	-	-	-
Zonaria spp.	55.0	-	-	-	-	-	8.0	13.8	13.3	-	10.1	8.3	23.6	43.6	17.5	1.3	1.7	-	19.3	22.5	36.3	20.4	7.4	-	-
Ephemeral brown algae																									
Asperococcus bullosus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.2	-	-	-
Brown turf	-	-	1.8	-	-	-	-	-	-	-	-	-	-	-	0.8	-	-	-	-	-	1.3	0.7	-	-	-
Colpomenia sinuosa	-	-	-	-	-	-	2.0	13.8	6.7	5.0	1.3	-	4.3	-	3.3	1.3	-	-	-	2.5	6.3	26.3	-	-	-
Cutleria multifida	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	12.4	-	-	-
Desmarestia ligulata	20.8	23.1	7.3	3.0	-	-	1.0	1.7	-	-	-	-	-	-	-	-	21.7	20.7	28.6	60.0	45.0	17.5	7.4	50.8	11.7
Dictyota spp.	13.3	5.1	1.8	-	-	-	21.0	15.5	26.7	1.7	19.0	31.7	28.6	7.7	11.7	-	1.7	-	5.9	-	-	-	0.7	-	-
Endarachne binghamiae	-	-	-	-	8.9	9.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Glossophora kunthii	40.0	11.1	12.7	1.0	11.1	14.7	21.0	22.4	25.0	18.3	16.5	13.3	33.6	-	14.2	6.4	8.3	5.9	33.6	95.0	48.8	29.2	11.1	-	1.7
Spatoglossum chapmanii	1.7	2.6	-	-	-	-	2.0	19.0	1.7	-	5.1	1.7	-	2.6	5.8	2.6	10.0	-	9.2	2.5	42.5	16.8	2.2	-	-
Undaria pinnatifida	3.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Brown encrusting																									
Ralfsia spp.	5.0	3.4	27.3	9.0	2.2	4.0	-	1.7	-	1.7	2.5	-	22.1	7.7	15.8	3.8	-	5.9	0.8	12.5	18.8	87.6	1.5	5.1	8.3
Green algae																									
Bryopsis spp.	-	-	-	-	-	-	1.0	-	-	-	-	1.7	-	-	-	-	-	-	-	-	-	5.1	-	-	-
Caulerpa articulata	8.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Caulerpa brownii	26.7	29.1	-	-	-	-	-	-	-	-	2.5	25.0	10.7	23.1	15.8	16.7	11.7	26.7	19.3	37.5	21.3	4.4	16.3	-	1.7
Caulerpa flexilis	5.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Caulerpa geminata	14.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Chaetomorpha aerea	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.7	-	-	-	-	-	-	-	-	-	-

Continued on next page

Table A5.2—continued

BIOREGION	COOK		BANKS		BULLER		WESTLAND						FIORDLAND				STEWART ISLAND							CHALMERS	
LOCATION	WELLINGTON	KAIKOURA	BANKS PENINSULA NORTH	FLEA BAY	KARAMEA	CAPE FOULWIND	MOERAKI	OPEN BAY ISLANDS	JACKSON HEAD	CASCADES	BARN	BIG BAY	BLIGH SOUND	CHARLES SOUND	DOUBTFUL SOUND	PRESERVATION INLET	GREEN ISLETS	BLUFF	CODFISH-RUGGEDY	RUAPUKE ISLAND	TITI ISLANDS	PATERSON INLET	PORT ADVENTURE	OTAGO PENINSULA	CATLINS
Chaetomorpha coliformis	0.8	0.9	-	-	-	-	-	-	-	-	-	-	2.1	-	0.8	-	-	-	-	-	-	-	-	1.7	10.0
Cladophora sericea	-	-	-	-	-	-	-	-	-	-	-	-	-	12.8	1.7	-	-	-	-	-	-	-	-	-	-
Cladophora spp.	20.0	6.0	-	-	-	-	-	-	-	-	-	-	0.7	-	5.8	-	-	-	-	-	-	7.3	-	3.4	6.7
Cladophoropsis herpesticata	-	-	3.6	-	-	1.3	1.0	3.4	-	-	2.5	-	-	2.6	1.7	-	-	5.2	3.4	5.0	3.8	5.8	-	15.3	1.7
Codium convolutum	4.2	-	-	6.0	-	6.7	1.0	3.4	1.7	8.3	2.5	-	22.9	7.7	14.2	6.4	15.0	19.3	34.5	82.5	22.5	61.3	7.4	45.8	5.0
Codium fragile	0.8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.7	-	-	0.7	-	-	-
Codium gracile	-	-	-	-	-	-	-	-	-	-	-	-	30.7	20.5	18.3	-	-	-	-	-	-	-	-	-	-
Halicystis sp.	-	-	-	-	-	-	-	-	-	-	-	-	0.7	-	1.7	-	-	-	-	-	-	-	-	-	-
Ulva spp.	7.5	3.4	-	-	2.2	-	-	-	1.7	1.7	-	-	1.4	23.1	29.2	2.6	1.7	-	13.4	10.0	12.5	15.3	1.5	3.4	3.3
Encrusting and coralline algae																									
Crustose coralline algae	100.0	94.0	83.6	100.0	77.8	85.3	53.0	98.3	135.0	95.0	75.9	78.3	95.0	97.4	82.5	51.3	100.0	100.0	100.0	200.0	98.8	198.5	57.8	96.6	95.0
Coralline turf species	86.7	55.6	30.9	59.0	20.0	17.3	33.0	70.7	98.3	86.7	74.7	40.0	95.7	76.9	80.0	29.5	98.3	78.5	91.6	197.5	87.5	66.4	45.9	59.3	75.0
Hildenbrandia spp.	63.3	35.9	36.4	63.0	8.9	44.0	4.0	13.8	10.0	11.7	27.8	31.7	25.0	59.0	25.0	11.5	11.7	39.3	21.8	105.0	57.5	90.5	12.6	47.5	41.7
Red turfing algae																									
(Multi-species complex)	65.8	35.9	27.3	1.0	31.1	50.7	50.0	94.8	123.3	86.7	60.8	76.7	32.9	28.2	40.0	15.4	16.7	20.0	16.0	15.0	3.8	33.6	17.8	22.0	55.0
Red foliose algae																									
Adamsiella chauvinii	1.7	16.2	-	-	-	-	-	-	-	-	-	-	0.7	-	11.7	-	-	0.7	4.2	-	-	8.8	-	-	-
Adamsiella angustifolia	-	-	-	-	-	-	-	-	-	-	-	-	3.6	-	-	-	-	-	-	-	-	-	-	-	-
Anotrichium crinitum	0.8	12.8	9.1	-	-	-	30.0	63.8	61.7	20.0	16.5	6.7	2.9	12.8	20.8	-	6.7	19.3	14.3	5.0	6.3	13.9	2.2	13.6	5.0
Aphanocladia delicatula	2.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Asparagopsis armata	-	0.9	-	-	-	-	20.0	46.6	65.0	31.7	12.7	25.0	37.9	51.3	61.7	2.6	-	-	12.6	7.5	11.3	15.3	2.2	-	-
Ballia callitrichia	5.8	12.8	-	5.0	2.2	4.0	-	-	6.7	10.0	3.8	5.0	5.7	12.8	11.7	1.3	18.3	32.6	3.4	10.0	1.3	2.9	2.2	27.1	26.7
Brongniartella australis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6.7	5.0	7.5	-	8.0	-	-	-

Continued on next page

Table A5.2—continued

BIOREGION	COOK		BANKS		BULLER		WESTLAND						FIORDLAND				STEWART ISLAND							CHALMERS	
LOCATION	WELLINGTON	KAIKOURA	BANKS PENINSULA NORTH	FLEA BAY	KARAMEA	CAPE FOULWIND	MOERAKI	OPEN BAY ISLANDS	JACKSON HEAD	CASCADES	BARN	BIG BAY	BLIGH SOUND	CHARLES SOUND	DOUBTFUL SOUND	PRESERVATION INLET	GREEN ISLETS	BLUFF	CODFISH-RUGGEDY	RUAPUKE ISLAND	TITI ISLANDS	PATERSON INLET	PORT ADVENTURE	OTAGO PENINSULA	CATLINS
Callophyllis atrosanguinea	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5.0	1.5	-	-	-
Callophyllis callibrepharoides	-	-	-	-	2.2	-	-	-	-	-	-	-	-	-	-	-	13.3	15.6	1.7	-	-	2.2	-	8.5	5.0
Callophyllis hombroniana	12.5	3.4	-	6.0	-	-	-	-	-	-	-	-	-	-	-	-	-	5.9	-	2.5	2.5	2.9	-	52.5	21.7
Callophyllis ornata	-	-	-	1.0	-	-	-	-	-	-	-	-	-	-	-	-	11.7	10.4	7.6	12.5	11.3	14.6	0.7	22.0	3.3
Callophyllis variegata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	20.0	9.6	6.7	10.0	2.5	13.9	0.7	-	-
Carmontagnea hirsuta	-	-	-	-	2.2	1.3	-	-	-	-	-	-	-	5.1	-	-	-	1.5	0.8	-	1.3	2.2	0.7	1.7	1.7
Carmontagnea scoparia	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.3	-	0.7	-	-	-	1.5	-	-	-
Ceramium spp.	-	-	-	-	-	-	-	-	8.3	1.7	-	-	0.7	2.6	-	-	-	2.2	3.4	-	-	0.7	-	-	-
Champia chathamensis	-	0.9	-	-	-	-	-	-	-	-	-	-	0.7	2.6	-	-	-	3.0	9.2	-	1.3	5.1	-	1.7	1.7
Chondria sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6.7	17.0	2.5	-	-	-	-	-	-
Cladhymenia oblongifolia	4.2	16.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	25.0	26.7	28.6	5.0	3.8	4.4	-	8.5	13.3
Craspedocarpus erosus	10.8	41.0	1.8	-	-	-	-	-	-	-	-	-	-	-	-	-	15.0	32.6	10.9	67.5	40.0	22.6	4.4	-	15.0
Curdiea flabellata	0.8	1.7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3.0	-	-	-	-	-	3.4	15.0
Dasya collabens	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.5	0.8	-	1.3	10.9	-	-	-
Delesseria sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6.7	3.7	1.7	-	-	-	-	8.5	8.3
Delisea elegans	-	-	-	-	-	-	-	-	-	-	-	-	-	7.7	25.0	7.7	-	3.0	-	-	-	10.2	3.0	-	-
Delisea plumosa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	16.8	-	-	-
Echinothamnion spp.	-	9.4	-	-	24.4	2.7	13.0	3.4	70.0	35.0	17.7	5.0	0.7	-	2.5	14.1	8.3	25.2	19.3	5.0	3.8	0.7	2.2	5.1	-
Euptilota formosissima	46.7	72.6	-	1.0	-	-	34.0	20.7	50.0	11.7	11.4	1.7	0.7	33.3	29.2	2.6	26.7	31.1	8.4	12.5	45.0	38.7	15.6	6.8	31.7
*"Gelidium" ceramoides**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8.9	5.0	-	-	0.7	-	-	-
Gigartina sp. (large round circle)	-	0.9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3.3
Gigartina circumcincta	-	-	-	-	22.2	-	-	-	-	-	-	-	-	2.6	0.8	-	-	0.7	1.7	-	3.8	-	-	-	15.0
Gigartina decipiens	-	-	-	-	15.6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Gigartina lanceata	-	-	-	-	6.7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Continued on next page

Table A5.2—continued

BIOREGION	COOK		BANKS		BULLER		WESTLAND						FIORDLAND				STEWART ISLAND							CHALMERS	
LOCATION	WELLINGTON	KAIKOURA	BANKS PENINSULA NORTH	FLEA BAY	KARAMEA	CAPE FOULWIND	MOERAKI	OPEN BAY ISLANDS	JACKSON HEAD	CASCADES	BARN	BIG BAY	BLIGH SOUND	CHARLES SOUND	DOUBTFUL SOUND	PRESERVATION INLET	GREEN ISLETS	BLUFF	CODFISH-RUGGEDY	RUAPUKE ISLAND	TITI ISLANDS	PATERSON INLET	PORT ADVENTURE	OTAGO PENINSULA	CATLINS
Gigartina livida	-	-	-	-	-	-	-	-	-	-	-	-	-	12.8	9.2	-	-	-	-	-	1.3	3.6	-	-	-
Gracilaria chilensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5.8	-	-	-	-	-	-	-	-	-	-
Gracilaria truncata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4.2	-	-	-	-	-	-	-	-	-	-
Griffithsia antarctica	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.3	1.5	-	-	-
Griffithsia crassiuscula	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	20.0	0.8	7.5	-	8.8	0.7	-	-
Griffithsia traversii	0.8	0.9	-	-	-	-	58.0	101.7	166.7	100.0	75.9	100.0	-	-	-	-	-	-	-	-	-	0.7	-	3.4	-
Gymnogongrus humilis	-	-	-	-	6.7	13.3	7.0	-	-	11.7	-	15.0	-	2.6	-	-	-	1.5	0.8	-	-	-	-	13.6	10.0
Halymenia sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.7	2.2	2.5	2.5	1.3	0.7	-	-	-
Heterosiphonia concinna	-	0.9	-	-	-	-	5.0	-	6.7	1.7	1.3	-	-	2.6	1.7	-	11.7	17.0	26.9	-	1.3	0.7	-	28.8	36.7
Hymenena durvillaei	-	1.7	-	-	2.2	-	7.0	-	1.7	6.7	1.3	-	-	-	2.5	2.6	35.0	34.8	25.2	10.0	20.0	2.2	12.6	52.5	60.0
Hymenena palmata	4.2	54.7	-	1.0	-	-	-	-	-	-	-	-	-	-	18.3	17.9	60.0	43.7	47.9	35.0	28.8	6.6	8.1	18.6	33.3
Hymenena sp. (Red dots)	4.2	12.8	7.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.7	-	-	-	-	-	-	-
Hymenocladia sanguinea	-	35.9	-	3.0	-	-	-	-	-	-	-	-	-	-	-	-	-	10.4	5.0	2.5	1.3	0.7	-	5.1	30.0
Iridaea sp.	-	4.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5.0	-	-	10.2	3.3
Kallymenia spp.	5.0	-	-	-	-	-	-	-	-	-	-	-	-	2.6	0.8	-	1.7	5.2	4.2	-	-	-	2.2	-	-
Laingia hookeri	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3.3	9.6	7.6	-	3.8	5.8	3.0	3.4	21.7
Lophurella hookeriana	-	6.0	1.8	-	22.2	5.3	20.0	10.3	75.0	41.7	11.4	33.3	3.6	2.6	6.7	15.4	16.7	13.3	36.1	-	2.5	2.9	0.7	-	10.0
Melanthalia abscissa	3.3	1.7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Microcladia pinnata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.5	-	-	-	-	-	-
Medeiothamnion lyalli	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.7	-	-	-	-	-	0.7	-	-
Schizymenia sp.**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	16.7	0.7	9.2	22.5	12.5	-	3.0	-	-
Phacelocarpus labillardieri	0.8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3.3
Phitymophora linearis	-	-	-	-	-	-	-	-	-	-	-	1.7	-	-	-	-	26.7	4.4	2.5	15.0	-	1.5	-	-	-
Phycodrys quercifolia	-	12.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Platythamnion lindaueri	-	6.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.7	-	-	1.3	-	-	5.1	8.3

Continued on next page

Table A5.2—continued

BIOREGION	COOK		BANKS		BULLER		WESTLAND						FIORDLAND				STEWART ISLAND							CHALMERS	
LOCATION	WELLINGTON	KAIKOURA	BANKS PENINSULA NORTH	FLEA BAY	KARAMEA	CAPE FOULWIND	MOERAKI	OPEN BAY ISLANDS	JACKSON HEAD	CASCADES	BARN	BIG BAY	BLIGH SOUND	CHARLES SOUND	DOUBTFUL SOUND	PRESERVATION INLET	GREEN ISLETS	BLUFF	CODFISH-RUGGEDY	RUAPUKE ISLAND	TITI ISLANDS	PATERSON INLET	PORT ADVENTURE	OTAGO PENINSULA	CATLINS
Phycodrys quercifolia	-	12.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Platythamnion lindaueri	-	6.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.7	-	-	1.3	-	-	5.1	8.3
Plocamium cirrhosum	15.0	1.7	1.8	-	2.2	1.3	-	8.6	-	-	-	-	12.9	7.7	6.7	3.8	20.0	17.0	5.0	5.0	2.5	5.1	-	10.2	11.7
Plocamium microcladioides	0.8	0.9	7.3	-	-	-	-	-	-	-	-	-	0.7	-	0.8	-	1.7	1.5	0.8	-	2.5	4.4	-	-	1.7
Plocamium spp. (all species)	20.8	73.5	23.6	-	8.9	14.7	48.0	55.2	143.3	68.3	50.6	50.0	37.1	33.3	46.7	26.9	80.0	79.3	46.2	30.0	40.0	21.2	6.7	27.1	65.0
Polysiphonia spp.	-	-	-	-	-	-	-	-	-	-	-	-	0.7	7.7	8.3	-	-	5.2	-	-	-	16.8	-	-	-
Pterocladiella capillacea	-	-	-	-	-	-	-	8.6	5.0	1.7	-	-	13.6	2.6	-	-	-	-	-	-	-	-	-	-	-
Pterocladia lucida	23.3	31.6	-	-	8.9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ptilonia spp.	5.8	-	-	-	-	-	3.0	15.5	-	-	2.5	-	-	-	2.5	-	-	-	-	-	1.3	-	-	-	5.0
Rhodophyllis acanthocarpa	-	10.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.5	-	-	-	-	1.7
Rhodophyllis gunnii	23.3	46.2	5.5	1.0	-	-	8.0	13.8	11.7	-	8.9	18.3	21.4	23.1	54.2	25.6	8.3	25.9	4.2	20.0	13.8	8.8	11.9	-	-
Rhodymenia obtusa	7.5	36.8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	21.7	14.8	0.8	-	-	1.5	-	11.9	45.0
Rhodymenia spp.	-	42.7	-	-	-	-	-	-	-	-	-	-	1.4	5.1	12.5	-	-	0.7	-	-	-	0.7	-	5.1	3.3
Sarcodia flabellata	0.8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Schizoseris spp.	-	22.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	51.7	27.4	21.0	12.5	11.3	0.7	1.5	20.3	58.3
Schizymenia novae-zelandiae	-	-	-	-	4.4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Scinia australis	1.7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.7	-	-	-	3.8	-	-	1.7	1.7
Stenogramme interrupta	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6.7	2.5	-	-	-	-	-	1.7
Streblocladia glomerulata	-	19.7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6.7	10.4	34.5	-	17.5	0.7	5.2	13.6	18.3

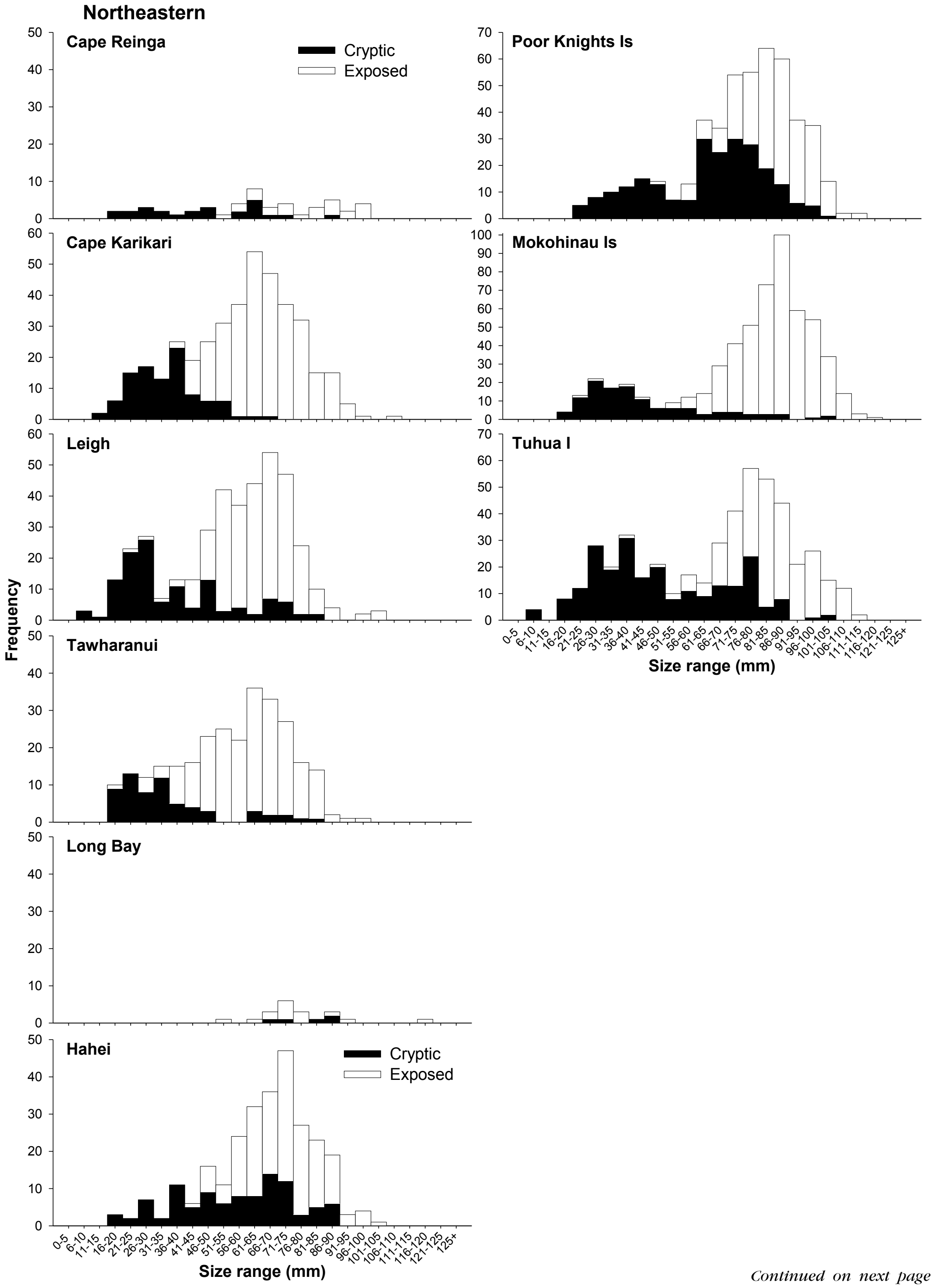
* Genus (also family and order) unknown for this species; restricted to southern New Zealand. Also Wendy Nelson, NIWA, pers. comm. 2006.

** Sensu *Nemastoma lacinata* (Adams 1994).

Appendix 6

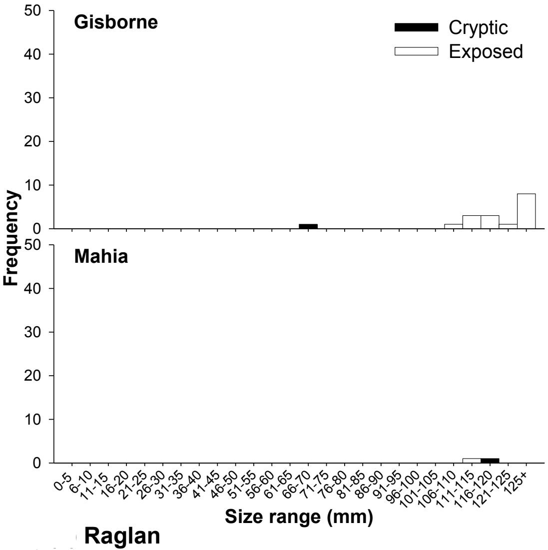
SIZE-FREQUENCY DISTRIBUTIONS OF *Evechinus chloroticus*

All locations within each bioregion. Note that the number of sites and depths sampled vary among locations.

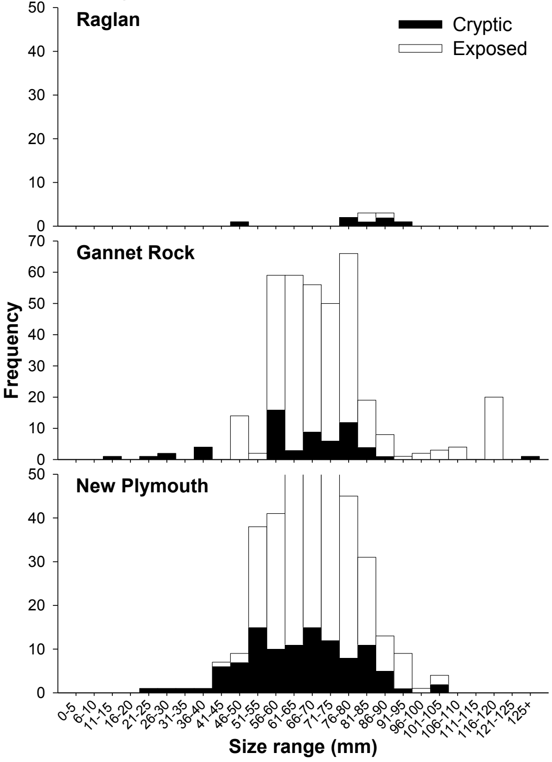


Continued on next page

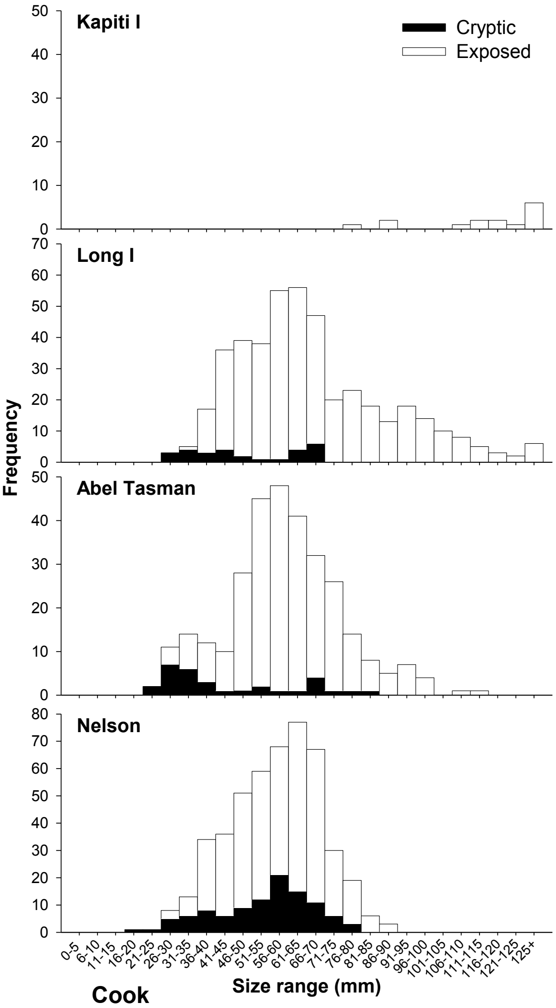
Portland



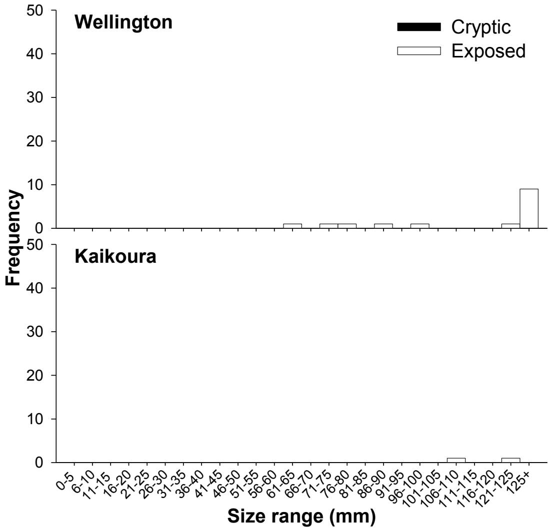
Raglan



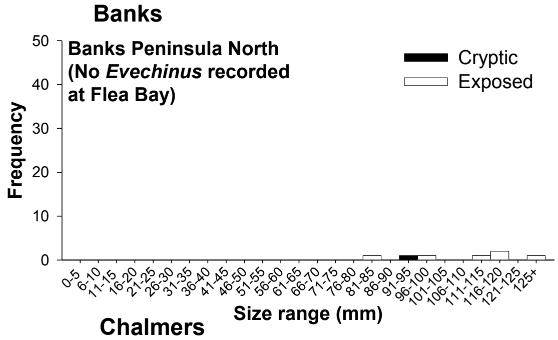
Abel

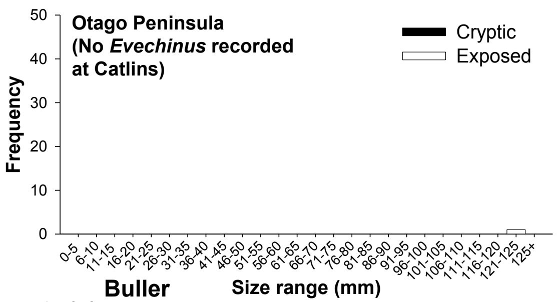


Cook

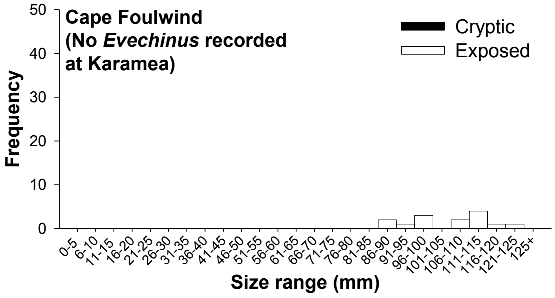


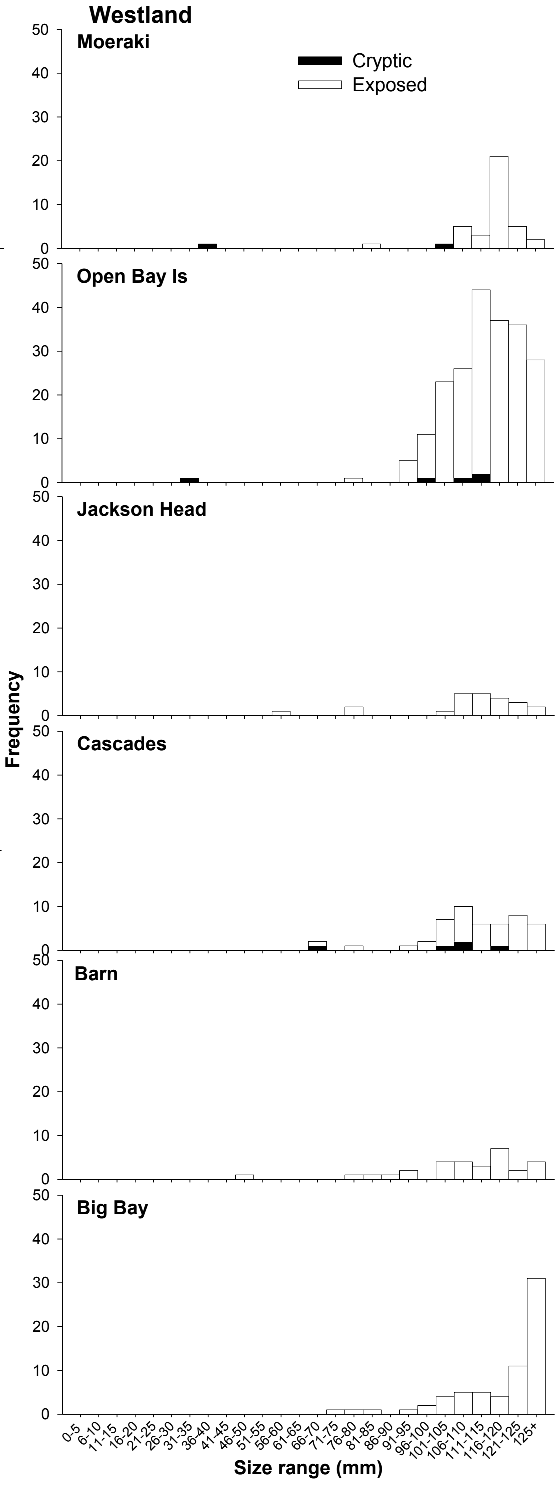
Continued on next page


Banks

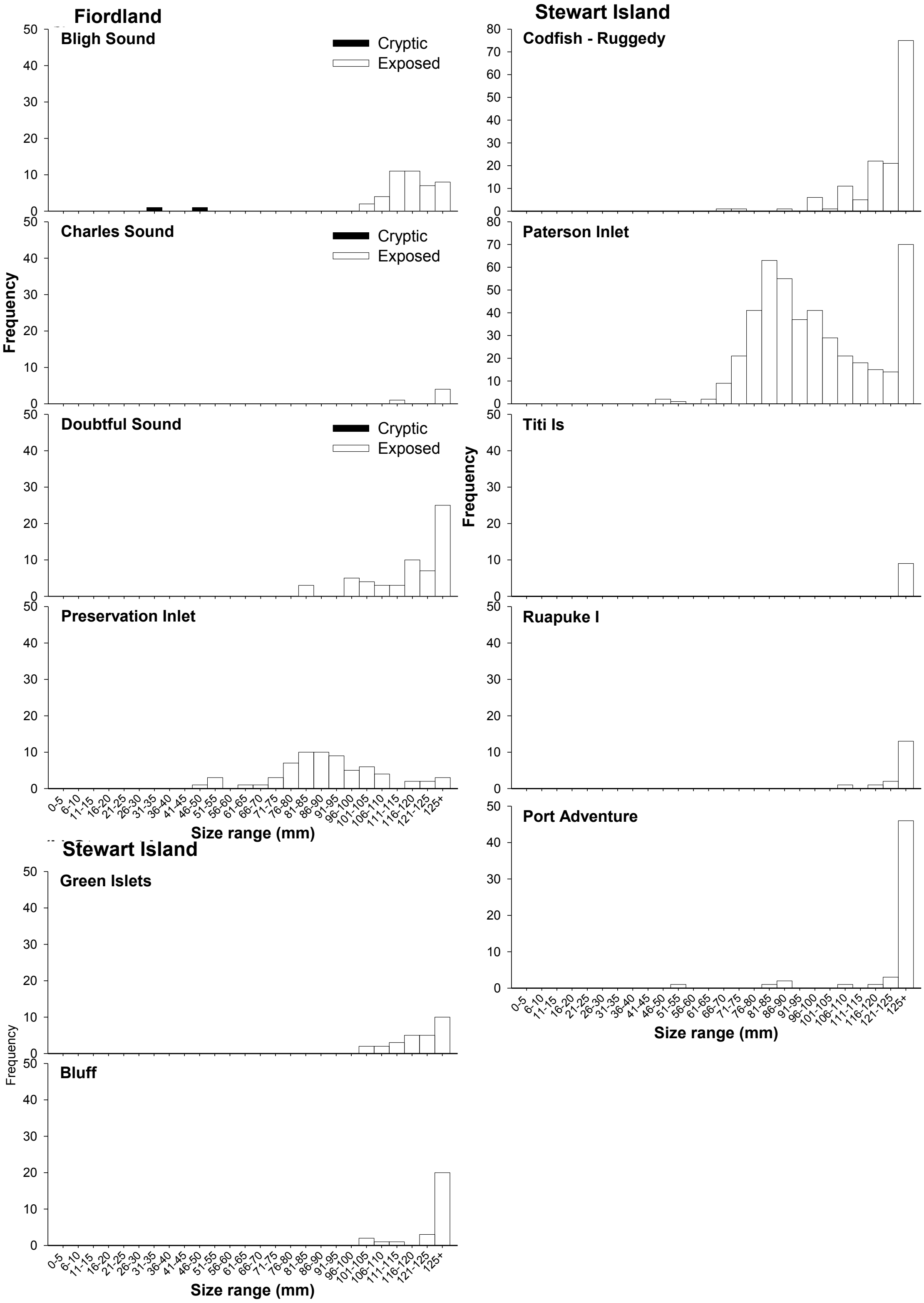

Chalmers

Buller




Westland

Continued on next page


Fiordland
Bligh Sound
Charles Sound
Doubtful Sound
Preservation Inlet
Cryptic
Exposed
Frequency
Size range (mm)
0-5
6-10
11-15
16-20
21-25
26-30
31-35
36-40
41-45
46-50
51-55
56-60
61-65
66-70
71-75
76-80
81-85
86-90
91-95
96-100
101-105
106-110
111-115
116-120
121-125
125+
Stewart Island
Green Islets
Bluff
Stewart Island
Codfish - Ruggedy
Paterson Inlet
Titi Is
Ruapuke I
Port Adventure

Quantifying New Zealand's shallow subtidal reef communities

Shallow subtidal reef communities are some of the most productive habitats in temperate marine ecosystems and are of enormous commercial, recreational and cultural value to society. In general, much of the New Zealand coastline is undescribed and our understanding of the factors controlling coastal reef ecology is poor. This report presents the results of the first nationwide study of mainland New Zealand's subtidal benthic reef communities. The national overview of reef communities, and descriptions of reef assemblages within bioregions and how these vary, will provide a resource for ecologists and conservation workers.

Shears, N.T.; Babcock, R.C. 2007: Quantitative description of mainland New Zealand's shallow subtidal reef communities. *Science for Conservation 280.* 126 p.

New Zealand Government