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# SOME ASPECTS OF THE BIOLOGY OF THREE NORTHWESTERN ATLANTIC CHITONS: TONICELLA RUBRA, TONICELLA MARMOREA, AND ISCHNOCHITON ALBUS (MOLLUSCA: POLYPLACOPHORA)

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UNIVERSITY OF NEW HAMPSHIRE, PH.D., 1978

# SOME ASPECTS OF THE BIOLOGY OF THREE NORTHWESTERN ATLANTIC CHITONS: TONICELLA RUBRA, TONICELLA MARMOREA, AND ISCHNOCHITON ALBUS (MOLLUSCA: POLYPLACOPHORA)

by

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A THESIS

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This thesis has been examined and approved.

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February 16, 1978

Date

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# ABSTRACT

The subtidal ecology of three species of coexisting chitons of the Western Atlantic, Tonicella rubra, T. marmorea, and Ischnochiton albus, is described. The species are compared between two sites having significantly different density and habitat composition. The natural history, population structure, behavior, predators, feeding, and reproductive biology are examined; and particular attention is devoted to the questions of how these species coexist in densities exceeding 1000 individuals/$m^2$ and the role of predators in determining size and structure of the chiton population.

The chiton density at the study site in northeastern Maine was greatest at a depth of six meters; the density decreased with increasing or decreasing depth. Density variations appear to reflect seasonal abundance of food and increased mortality following annual spawning. A significantly lower chiton density in southern Maine is postulated to result from the key predatory fish Tautogolabrus adspersus. This fish was conspicuously absent from the northern site. Unlike the two major predators, winter flounder and Leptasterias littoralis, at the northern site, T. adspersus did not show a prey size selectivity or a seasonally limited feeding pattern.

The bathymetric pattern of species distribution consisted of Tonicella rubra as the dominant in shallow water, T. marmorea as the dominant in deeper water, and Ischnochiton albus as the most prevalent at six meters. This pattern appears to be the result of (1) selective survival of the chiton species having different annual breeding and larval settling periods, (2) selection of microhabitats by young chitons that were inaccessible to adult predators, (3) rates of growth to different adult sizes, and (4) distribution patterns of the major predators.

The three species of chitons demonstrate a similar size distribution pattern characterized by decreasing size with increasing depth. This is attributed to a combination of factors. These include (1) distribution of the major predators and their prey size selectivity, (2) specific chiton growth rates to the markedly different adult sizes, and (3) gradation of cobble size affording selective protection from predation.

The chiton diets differed primarily in the proportions of the three major prey: diatoms, poriferans, and protozoans. The diets reflected variations in seasonal abundance of prey but were not influenced by differences in habitat composition. The component species comprising the differences in diets coupled with the encrusted flora and fauna on the shell plates of the chitons revealed the separate feeding niches.

# GENERAL INTRODUCTION

The subtidal community of northern New England has a complex faunal makeup comprised principally of boreal species and contains several of the more tolerant arctic forms. Among the large diversity of molluscs, only three species of chitons, Tonicella rubra (Linnaeus, 1767), T. marmorea (Fabricius, 1780), and Ischnochiton albus (Linnaeus, 1767), are commonly found in the shallow subtidal zone. These three chitons coexist on the same rock substrates in densities which may exceed $1000/m^2$. They may be the dominant subtidal, benthic, epifaunal mollusc in selected habitats in northern New England (personal observations).

Studies of chiton biology are essentially limited to Christiansen (1954), Boyle (1970), Glynn (1970), and Barnes (1972). Most ecologically oriented reports have dealt with intertidal species. Aside from taxonomic, anatomical, and distributional literature, publications dealing with the biology of T. rubra, T. marmorea, and I. albus consist of scattered notes and a few summarizing paragraphs on their subtidal nature by Yakovleva (1952) and Fischer-Piette and Franc (1960).

This subtidal study is devoted to a description and examination of select elements of the ecology, feeding biology, and reproductive biology of the three chitons found along the coast of Maine. Through the use of two distinctly separate study sites, the data collected presents a foundation for analysis and comparison of (1) the inter- and intraspecific relationships among these chitons, (2) the role of boreal chitons in subtidal community structure, (3) the way that physical and biological differences between the habitats alter the former parameters, and (4) particular emphasis on the manner of niche separation in order to provide an understanding of how these species are able to coexist in very high densities.

In the interest of clarification, the taxonomic position of T. rubra assumed its presently recognized generic status in 1902 with the publication List of British Marine Mollusca by the Conchological Society of Great Britain and Ireland (Balch, 1906). This position was supported by Thiele (1929), Taki (1938), Leloup (1945), Yakovleva (1952), and others. This recognition has been extended to the North American form of T. rubra by Abbott (1974).

The taxonomic position of T. marmorea has remained unchanged since its disposition in the genus Tonicella by Carpenter (1874). I. albus was relegated to the long established genus Ischnochiton (Gray) by Thiele (1929).

# ECOLOGY AND HABITAT DESCRIPTION

## Introduction

Population structure, predation, morphological variation, encrusting and associated organisms, and aspects of behavior were elements of chiton ecology investigated in this study. Additionally, chiton habitats were described carefully and serve as an important aspect for physical and biological factors that are continually affecting chiton biology. Collectively, these data will help to determine how these chitons utilize their environment, how they influence it, and how other members of the community influence their biology.

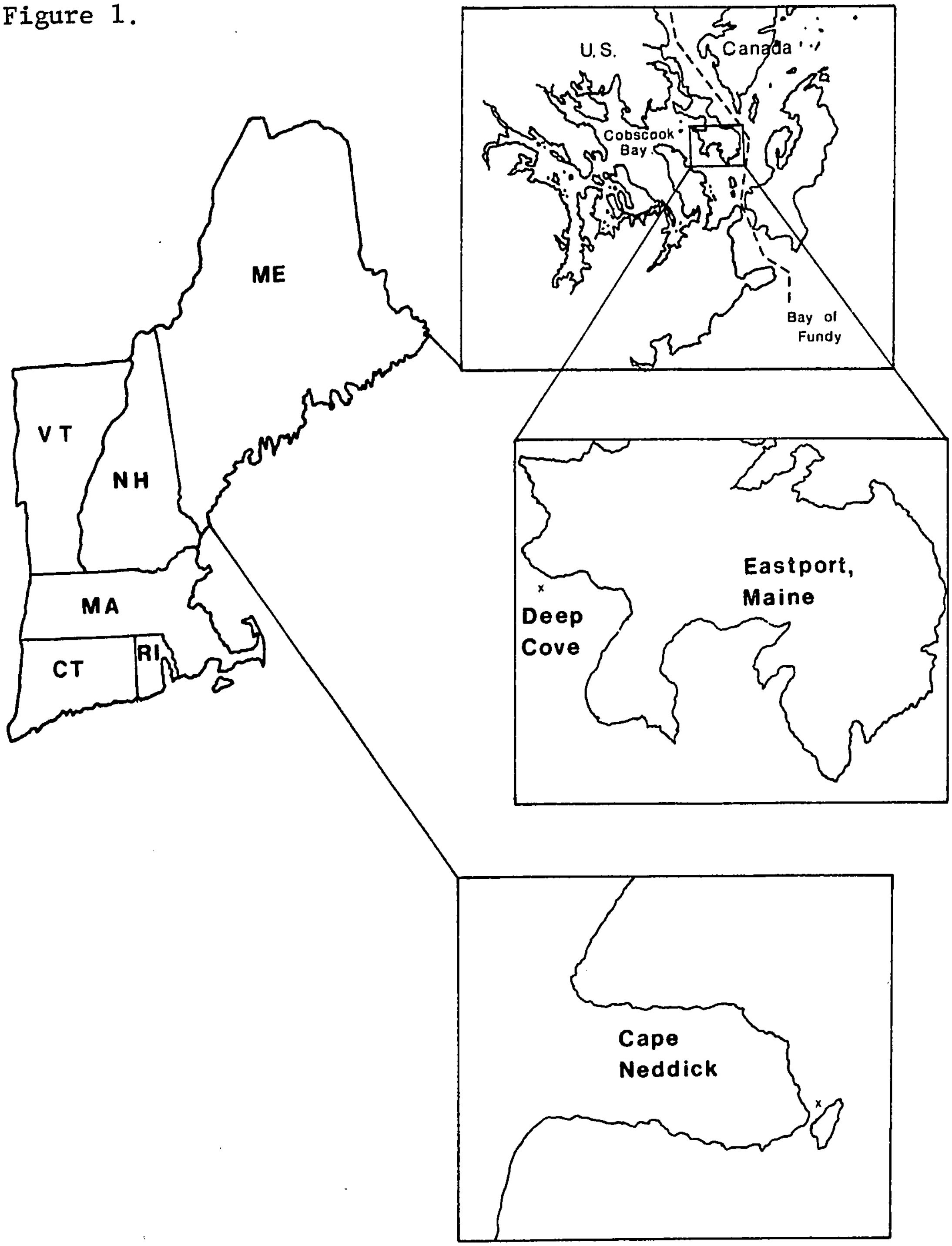
## Materials and Methods

Two locations in northern New England were chosen for this study based on their latitudinal separation, inherent ecological differences and similarities, and their accessibility throughout the year.

The principal site, Deep Cove, has all three species of chitons and is located in northeastern Maine (Fig. 1). The second site, Cape Neddick, situated in southern Maine, is populated by only two species of chitons, *T. rubra* and *T. marmorea*.

Figure 1. Map of New England with study areas at Cape Neddick Nubble and Deep Cove.

Figure 1.


U.S.
Canada
Cobscook Bay
Bay of Fundy
ME
VT
NH
MA
CT
RI
Eastport, Maine
Deep Cove
x
Cape Neddick
x

## Deep Cove

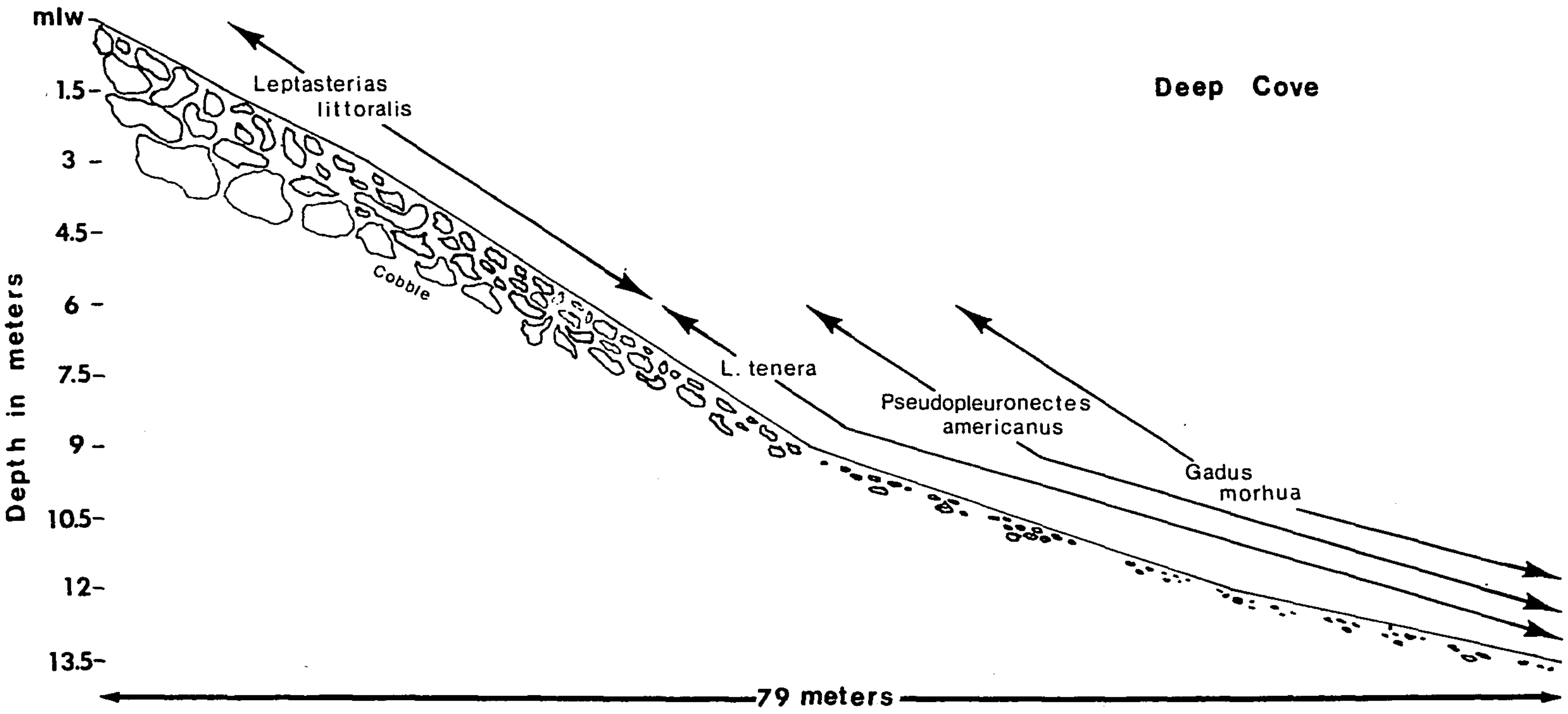
Between September 1971 and September 1973, three species of chitons were sampled at Deep Cove in Maine. SCUBA made possible permanent reference stations at 1.5 meter intervals established along a subtidal transect from mean low water to 13.5 meters (Fig. 2). Sampling was temporarily discontinued at the 12 and 13.5 meter stations during February and March because of low temperatures. Collecting at depths below 13.5 meters was impractical because the substratum leveled and became a soft, silty mud uninhabited by chitons.

A sample size of 1/16 $m^2$ was used at Deep Cove for quantitative and distributional studies. One sample per month per depth interval was sufficient to determine densities when compared with earlier replicate samples. In addition, a monthly sample of 1/4 $m^2$ was taken at 6 meters. The larger sized sample further verified the validity of using 1/16 $m^2$ quadrats for determining density.

Hard and soft substrate were removed from 1/16 $m^2$ area to the level of the underlying marine clay base (@ 6 cm). This technique removed all utilizable substrate and thereby eliminated the problem of immigration and its influence on the surrounding chiton population. It allowed also for more accurate sampling of all individuals, particularly small ones. Samples were deposited in marked, fine mesh bags. The monthly 1/4 $m^2$ sample was used for refer-

Figure 2. Diagram of transect at Deep Cove showing major predator distributions and cobble size in relation to depth.

Figure 2.


mlw
1.5
3
4.5
6
7.5
9
10.5
12
13.5
Depth in meters
Leptasterias littoralis
Deep Cove
Cobble
L. tenera
Pseudopleuronectes americanus
Gadus morhua
79 meters

ence and supplemental data.

All samples were sorted within a few hours after collecting. The associated organisms were separated from the chitons, and samples were fixed in 10% buffered formalin containing 1% gallic acid, a color preservative. This preservative was changed twice, once during species separation and again following isolation of digestive tracts.

Physical and biological data collected monthly included temperature, salinity, turbidity (transparency), current direction, and associated fauna and flora.

## Cape Neddick

At Cape Neddick, a larger quadrat size and replicate sampling compensated for the appreciably lower density of chitons. Replicate samples of 1/4 $m^2$ were taken each month at depths of 4.5 and 6 meters. Due to the substrate conformation, sampling was restricted to the two-depth intervals only. The large rock size at Cape Neddick prevented use of the substrate removal method. Therefore, the procedure employed at Cape Neddick consisted of removing individual animals with forceps and placing these in marked vials. This procedure was not effective for sampling the smallest individuals and was particularly difficult during winter and stormy periods when there was strong surge. Sorting, fixation, and preservation took place as described for the Deep Cove samples.

In the laboratory each chiton was weighed (wet); the length was measured; the shell plates were inspected for plate number; type and location of encrusting organisms was determined; and external morphological aberrations were noted. Shell plates were removed, and gonads were extracted and weighed (wet). Sex and condition of gamete development were determined from microscopic examination of gonad smears. The digestive tract was removed and isolated for diet analysis.

Identification of chiton predators was based on field observations and gut analyses of potential predators. These observations were substantiated with laboratory observations where feasible.

Behavioral studies involved repeated seasonal observations at a number of separate sites. Observations of nocturnal behavior were conducted at Deep Cove. These were made at 1.5 hour intervals from before sunset to after sunrise. Technical difficulties with marking subtidal chitons hampered homing behavior studies.

# Results

## Habitat Description and Natural History

Deep Cove (lat. 44°54'28"N, long. 67°01'23"W).

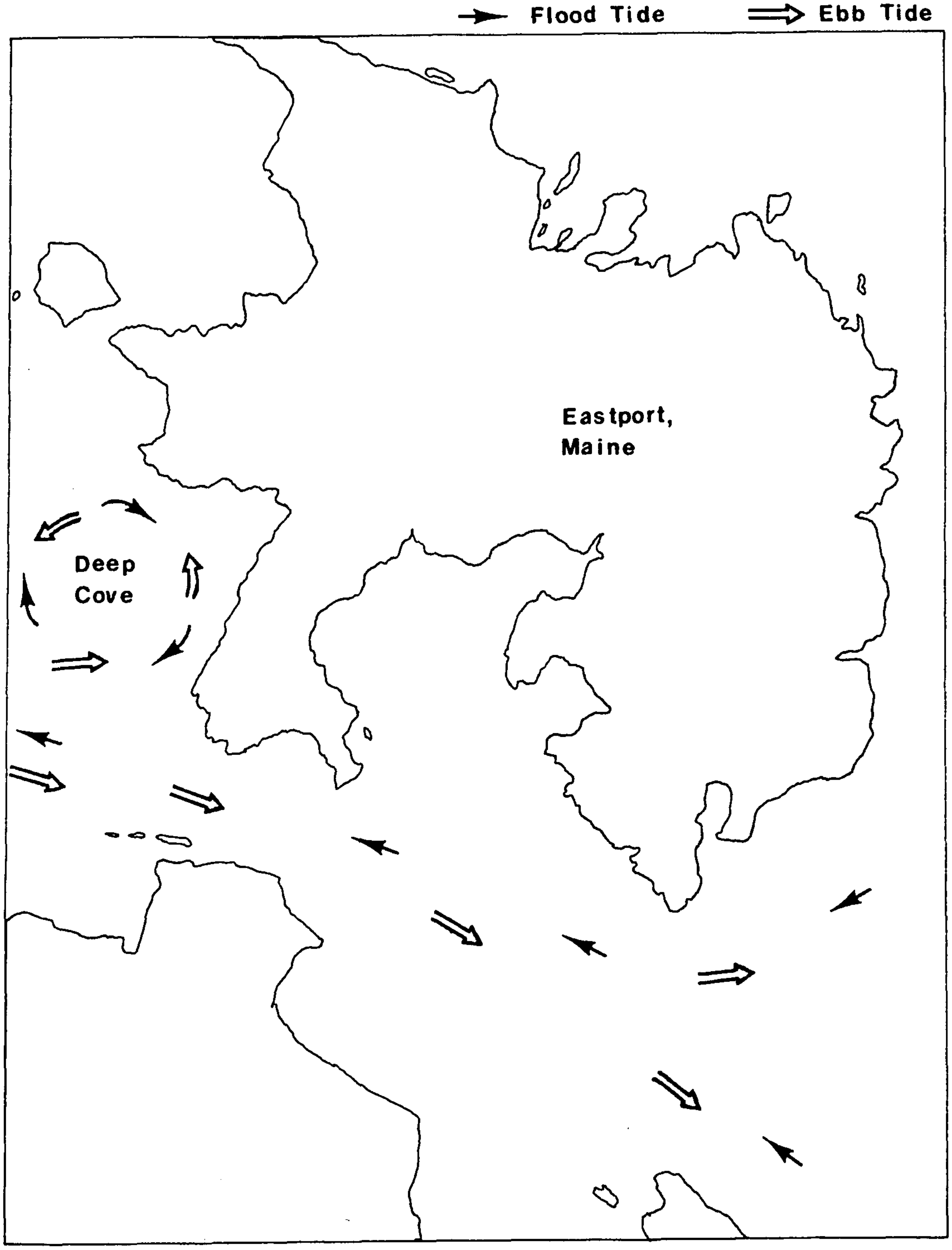
Physical Characteristics. Deep Cove is situated at the mouth of Cobscook Bay, which empties into the Bay of Fundy (Fig. 1). Due to the protection afforded by the bay configuration, wave action is negligible. However, as a result of a mean tidal range of 5.6 meters, the cove is subjected to strong tidal currents (three knots) and large tidal volume, both of which influence turbidity, temperature, and salinity patterns.

On the incoming tide, surface currents within the cove flow in a clockwise eddy (Fig. 3). A reversed pattern of eddy flow exists on the outgoing tide. However, when descending along the transect, subtidal currents demonstrate changes in both vector and intensity. In general, for every five-meter increase in depth, current direction changes 180 degrees (personal observation). As a result, each particular depth interval is subjected to a variety of current velocities and directions during a complete tidal cycle.

The three-knot tidal currents are responsible for a heavy suspension of particulate matter in the water column and a partial renewal of nutrients, e.g., diatoms, with every tidal cycle. Seasonally turbid conditions re-

Figure 3. Patterns of tidal flow in Deep Cove.

Figure 3.



sulted in a mean visibility of between 2.3 meters and 3.8 meters (Table 1). In spite of the strong currents there were no significant changes in substrate composition due to either deposition or erosion during the course of this study. In regions of tidal rapids where no rock substrate exists, the underlying marine clays are resistant to erosion (personal observation).

Water temperature and salinity data are presented in Fig. 4 and Table 1. The maximum water temperature of 12.5° C was recorded during September, and the lowest of 0° C during February and March. Because of the large tidal volume and proximity to the Gulf of Maine, the annual extremes in salinity differed by 3 $^{o}/oo$. However, the second year of this study was characterized by an abnormally cool, wet summer and fall and a warm winter. The result was a further reduction in the seasonal range of temperature and salinity fluctuations.

The substrate at Deep Cove is composed of cobble and silty mud overlaying a base of marine clay. In the vicinity of the transect, the source of the cobble is an intertidal igneous intrusion. The size and frequency of the cobble decreases with increasing depth and distance from the intertidal source (Fig. 2). As a result, the quantity of hard substrate preferred by chitons also decreases with depth.

Table 1a. Physical and chemical data from Deep Cove, Maine (10.5 m).

| Season* | Number of Samples | Mean Temperature (°C) | Mean Salinity (°/oo) | Mean Visibility / Turbidity (m) |
|---|---|---|---|---|
| Winter | 6 | 1.0 ± 0.9 | 30.8 ± 0.4 | 2.3 ± 0.7 |
| Spring | 6 | 4.3 ± 1.9 | 30.1 ± 0.3 | 3.8 ± 0.8 |
| Summer | 10 | 10.9 ± 1.4 | 31.9 ± 0.9 | 3.4 ± 1.2 |
| Fall | 6 | 6.2 ± 2.1 | 31.3 ± 0.7 | 2.4 ± 0.8 |

Table 1b. Physical and chemical data from Cape Neddick, Maine (7.5 m).

| Season* | Number of Samples | Mean Temperature (°C) | Mean Salinity (°/oo) | Mean Visibility / Turbidity (m) |
|---|---|---|---|---|
| Winter | 10 | 0.6 ± 2.2 | 31.1 ± 1.8 | 2.3 ± 1.6 |
| Spring | 10 | 5.4 ± 2.0 | 29.9 ± 1.0 | 4.2 ± 1.8 |
| Summer | 12 | 10.2 ± 1.9 | 31.8 ± 0.6 | 4.6 ± 1.4 |
| Fall | 12 | 7.2 ± 3.1 | 31.6 ± 0.2 | 3.2 ± 1.4 |

*Winter = January, February & March; Spring = April, May & June;

Summer = July, August & September; Fall = October, November & December

Figure 4a. Water temperature contours for Deep Cove and Cape Neddick.

Figure 4a.

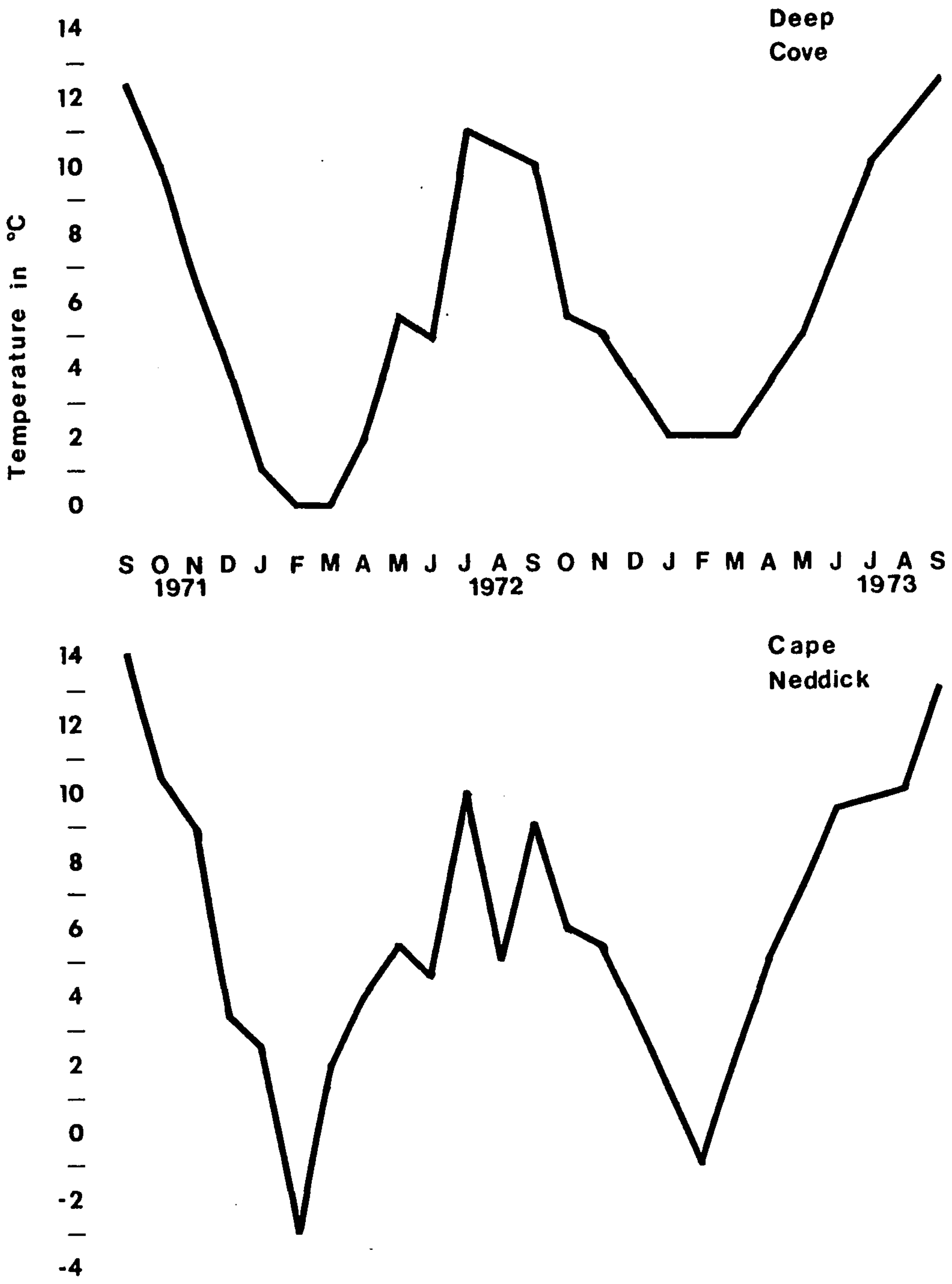
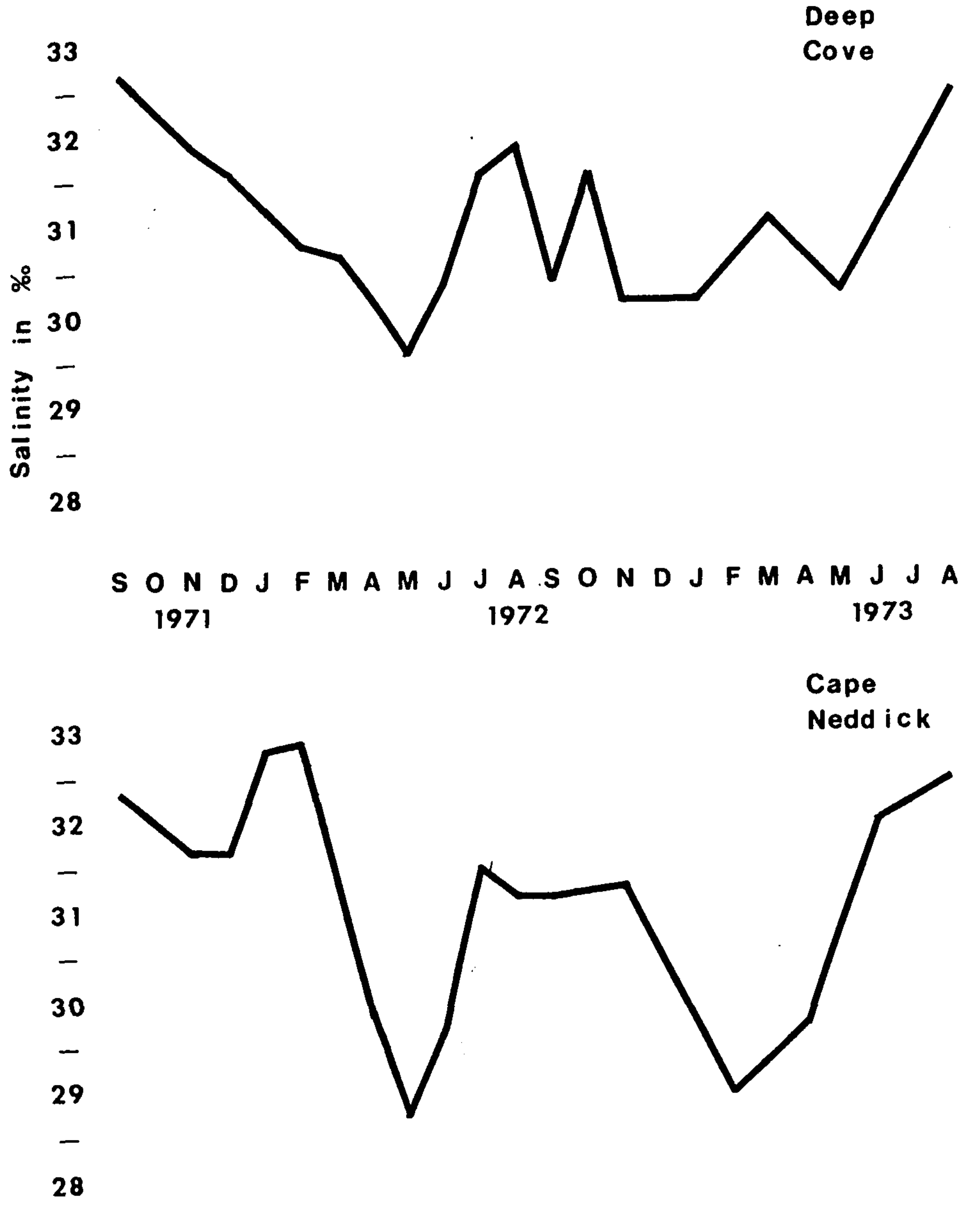

Deep Cove
Temperature in °C
14
12
10
8
6
4
2
0
S O N D J F M A M J J A S O N D J F M A M J J A S
1971
1972
1973
Cape Neddick
14
12
10
8
6
4
2
0
-2
-4

Figure 4b. Salinity contours for Deep Cove and Cape Neddick.

Figure 4b.


Deep Cove
Salinity in ‰
33
32
31
30
29
28
S O N D J F M A M J J A S O N D J F M A M J J A
1971
1972
1973
Cape Neddick
33
32
31
30
29
28

Biological Characteristics. The subtidal faunal composition in Deep Cove was diverse. A list of the associated fauna found along the subtidal transect is presented in Table 2. By contrast, the subtidal algal composition was limited to a few dominant forms.

While the lower intertidal zone has a profuse and diverse covering of fleshy, macroscopic algae, the subtidal is dominated by calcareous and crustose Rhodophyceae. Below three meters, virtually all exposed rock surfaces are covered by the calcareous genera Clathromorphum, Lithothamnium and by the crustose Peyssonelia rosenvingii (Schmitz). Above three meters the occurrence of algae is infrequent and, when present, consists of Clathromorphum sp. and a seasonally occurring colonial diatom.

The three species of chitons, Tonicella rubra, T. marmorea, and Ischnochiton albus, are found most abundantly on the subtidal calcareous algal-covered rock. Occasionally, T. rubra occurred subtidally on rocks associated with algal holdfasts in Maine and New Hampshire. Following a severe storm in New Hampshire, T. rubra was found on rocks attached to Laminaria holdfasts that were deposited in the supralittoral zone. Only one other kelp-chiton association was observed in which I. albus was situated on the stipe of Agarum cribosum.

Cryptic coloration was observed for the two species of Tonicella frequenting calcareous algae at Deep Cove and Cape Neddick. No cryptic coloration was found

Table 2. The associated fauna from Deep Cove, Maine.

Phylum Porifera

Class Calcispongiae

*Clathrina coriacea*
*Leucosolenia botryoides*
*Scypha ciliata*

Class Demospongiae

*Cliona celata*
*C. vastifica*
*Halichondria panicea*
*Haliclona oculata*
*Halisarca* sp.
*Isodictya deichmannae*
*I. palmata*
*Microciona prolifera*
*Mycalecarmia ovulum*
*Myxilla incrustans*
*Pellina sitiens*
*Polymastia robusta*
*Tedania suctoria*

Phylum Cnidaria

Class Hydrozoa

*Calycella syringa*
*Campanularia* sp.
*Corymorpha pendula*
*Eudendrium* sp.
*Hydractinia echinata*
*Obelia commissuralis*
*O. geniculata*
*Podocoryne carnea*
*Sarsia* sp.
*Sertularella rugosa*
*S. tricuspidata*
*Sertularia pumila*
*Thuiaria argentea*
*T. similis*
*Tubularia larynx*
*T. spectabilis*

Class Scyphozoa

*Aurelia aurita**
*Cyanea capillata**
*Haliclystus salpinx*
*Lucernaria quadricornis*

Class Anthozoa

*Bunodactis stella*
*Cerianthus borealis*
*Gersemia rubiformis*
*Gonactinia* sp.
*Metridium senile*
*Stomphia coccinea*
*Tealia crassicornis*
Unidentified sp.

Phylum Ctenophora

*Bolinopsis infundibulum**
*Pleurobrachia pileus**

Phylum Platyhelminthes

*Notoplana atomata*
*Procerodes littoralis*

Table 2 (continued).

Phylum Rhynchocoela

*Amphiporus* sp.
*Cerebratulus lacteus*
*Lineus ruber*
*Tetrastemma* sp.

Phylum Rotifera

*Lepadella* sp.

Phylum Kinorhyncha

*Echinoderes* sp.

Phylum Annelida

Class Polychaeta

Ampharetidae sp.
*Ammotrypane aulogaster*
*Amphitrite affinis*
*A. cirrata*
*A. johnstoni*
*Brada granosa*
*Eulalia viridis*
*Filograna implexa*
*Harmothoe imbricata*
*Lepidonotus squamatus*
*Lumbrinereis fragilis*
*Myxicola infundibulum*
*Nainereis quadricuspidata*
*Nephtys ciliata*
*Nereis pelagica*
*Pectinaria granulata*
*Phyllodoce groenlandica*
*Potamilla reniformis*
*Sabella crassicornis*
*Spirorbis borealis*
*S. spirillum*
*S. violaceus*
*Syllis cornuta*
*Thelepus cincinnatus*
*Tharyx acutus*

Phylum Mollusca

Class Bivalvia

*Anomia aculaeta*
*A. simplex*
*Astarte borealis*
*A. castanea*
*A. elliptica*
*A. subaequilatera*
*A. undata*
*Cardita borealis*
*Cerastoderma pinnulatum*
*Clinocardium ciliatum*
*Crenella glandula*
*Hiatella arctica*
*H. striata*
*Lyonsia hyalina*
*Macoma balthica*
*Modiolus modiolus*
*Musculus discors*
*M. niger*
*Mya arenaria*
*M. truncata*
*Mytilus edulis*
*Nucula proxima*
*Placopecten magellanicus*
*Thyasira* sp.

Table 2 (continued).

Class Gastropoda

*Acmaea testudinalis*
*Acanthodoris pilosa*
*Aeolidia papillosa*
*Alvania arenaria*
*A. areolata*
*A. castanea*
*Aporrhais occidentale*
*Boreotrophon truncatus*
*Buccinum undatum*
*Cadlina laevis*
*Calliostoma occidentale*
*Catriona aurantia*
*Clione limacina**
*Colus pygmaeus*
*C. stimpsoni*
*Coryphella stimpsoni*
*C. verrucosa rufibranchialis*
*Crucibulum striatum*
*Dendronotus frondosus*
*Epitoneum groenlandicum*
*Hydrobia totteni*
*Lacuna vincta*
*Littorina littorea*
*L. obtusata*
*L. saxatilis*
*Lora pleurotomaria*
*L. turricula*
*Margarites costalis*
*M. groenlandica*
*M. helicina*
*Moellaria costulata*
*Natica clausa*
*Neptunea decemcostata*
*Onchidoris aspera*
*O. fusca*
*Onoba aculeus*
*Polinices immaculata* (?)
*P. triseriata*
*Puncturella noachina*
*Skeneopsis planorbis*
*Thais lapillus*
*Trichotropis borealis*
*Turbonilla bushiana*
*Turitellopsis acicula*
*Velutina laevigata*
*V. undata*

Class Polyplacophora

*Ischnochiton albus*
*Tonicella marmorea*
*T. rubra*

Phylum Ectoprocta

*Bugula simplex*
*Caberea ellisii*
*Callopora craticula*
*Cribulina annulata*
*Dendrobeania murrayana*
*Electra pilosa*
*Hippothoa hyalina*
*Lichenopora hispida*
*L. verrucaria*
*Microporella ciliata*
*Porella* sp.
*Turbicellepora canaliculata*
*Tubulipora liliacea*
*Cauloramphus cymbaeformis*

Phylum Brachiopoda

*Terebratulina septentrionalis*

Table 2 (continued).

Phylum Arthropoda

Class Pycnogonida

*Phoxichilidium femoratum*
*Pycnogonum littorale*

Class Crustacea

*Balanus balanoides*
*B. balanus*
*Cancer borealis*
*Caprella septentrionalis*
*Coremapus versiculatus*
*Corophium* sp.
*Crangon septemspinosa*
*Idotea balthica*
*Jaera marina*
*Homarus americanus*
*Hyas coarctacus*
*Lebeus polaris*
*L. groenlandicus*
*Leptocheirus pingius*
*Limnoria lignorum*
*Loxoconcha* sp.
*Pagurus acadianus*
*P. arcuatus*
*P. pubescens*
*Sclerocrangon boreas*

Phylum Echinodermata

Class Echinoidea

*Strongylocentrotus droebachiensis*

Class Holothuroidea

*Chiridotea laevis*
*Cucumaria frondosus*
*Psolus fabricii*

Class Ophiuroidea

*Axiognathus squamatus*
*Gorgonocephalus arcticus*
*Ophiopholis aculeata*
*Ophiura robusta*

Class Asteroidea

*Asterias rubens*
*Crossaster papposus*
*Henricia sanguinolenta*
*Hippasteria phryngiana*
*Leptasterias littoralis*
*L. tenera*
*Pteraster militaris*
*P. pulvillus*
*Solaster endeca*
*Stephanasterias albula*

Phylum Chordata

Subphylum Urochordata

*Amaroucium* sp.
*Ascidia prunum*
*Boltenia echinata*
*B. ovifera*
*Botryllus schlosseri*
*Didemnum albidum*
*Dendrodoa carnea*
*Halocynthia pyriformis*
*Molgula* sp.

Table 2 (continued).

Subphylum Vertebrata

*Clupea harengus**
*Cyclopterus lumpus*
*Gadus morhua*
*Hemitripterus americanus*
*Macrozoarces americanus*
*Myxocephalus scorpius*
*Liparis atlanticus*
*Pholis gunnellus*
*Pseudopleuronectes americanus*

* Indicates pelagic forms.

for *Ischnochiton albus*. The only white-colored substrate of any significance was formed by the ascidian *Didemnum albidum*, but *I. albus* was never found to frequent this substrate during my study.

On occasion, *T. rubra*, *T. marmorea*, and *I. albus* utilized crevices or galleries in the thickened calcareous algae. This behavior was most frequently observed at the Cape Neddick site, where the algae were significantly thicker.

Despite the fact that the three species of chitons were found associated with calcareous algal-covered rocks, the majority of animals spend the diurnal period on the undersides of rocks devoid of this algae. Chiton populations occurred also on other habitats free of calcareous algae. These included (1) isolated hard substrates (shells and bottles) in muddy environments, (2) rock substrates free of calcareous algae, and (3) glass succession slides suspended from floats. Chitons were found in areas having high silt content. However, buried chitons were always found in contact with rock substrates.

The subtidal algal composition at Deep Cove is influenced by the grazing sea urchin *Strongylocentrotus droebachiensis*. This sea urchin is most dense just below mean low water, where the lush intertidal algal growth terminates. This animal moves into the lower intertidal zone to feed on *Enteromorpha* and *Ulva* with the flood tide and returns to the subtidal zone with the ebb tide. In the subtidal zone this urchin traps and feeds on pieces of Ascophyllum nodosum and Fucus vesiculosus that have broken free of their intertidal habitat. During an investigation of the influence of sea urchins and chitons on the subtidal algal composition, the algal community was found to be influenced by water transparency.

At a depth of six meters, three identical cages (5 mm mesh external and 1 mm mesh internal) were each partially filled with two types of rock. Some of the rocks were covered with calcareous and crustose Rhodophyceae, while the remaining were free of encrusting algae. Sea urchins were added to the first cage, chitons to the second, and the third, lacking chitons and sea urchins, acted as a control. The experiment was terminated after one year because of cage deterioration resulting from the boring isopod Limnoria lignorum. The results were as follows: (1) the predator-free (i.e., chitons and sea urchins) cage did not develop fleshy algal growth as anticipated, but the algal composition (calcareous and crustose Rhodophyceae) was similar to that of the substrate surrounding the cages at the six-meter depth; (2) the cage containing the chitons had an algal and faunal composition similar to that of the control cage; (3) in the third case, the sea urchins had consumed part of the cage as well as much of the calcareous algae covering the rocks. The upper few meters of the rope and float marking the location of the cages were covered with heavy growths of brown, red, and green algae to a depth of approximately 2.5 m. Similar vertical distributions of algae were found on floats and ropes anchored at the 4.5 and 9 meter levels. Thus, these chitons had no noticeable influence on the macroscopic, subtidal algal composition. This is substantiated in the Feeding Biology section.

Physical and biological factors determined, in part, the subtidal macroscopic algal composition at Deep Cove. It was evident that turbidity had reduced light penetration and probably limited the growth of many algal species. In addition, the high density of sea urchins is likely to remove most fleshy, macroscopic algae before they can become established in the subtidal of Deep Cove. On occasion, kelps are found on large, isolated boulders and on vertical rock faces. Positions of these algal growths are always near the water surface and relatively inaccessible to the ubiquitous sea urchins. Occurrence of these isolated growths and of the profuse growth on the rope and float markers indicates the presence of algal spores capable of populating the benthic substrate. One unidentified fleshy, macroscopic species of Rhodophyceae occasionally occurred in the subtidal zone of Deep Cove but was never observed to be fed upon by sea urchins or chitons.

Cape Neddick (lat. 43°09'57"N, long. 70°35'32"W).

Physical Characteristics. The second site of study is located off an exposed rocky cape within the town of York in southern Maine (Fig. 1). Only *T. rubra* and *T. marmorea* are common at this site. The site is subjected to severe wave action from northeast winds, which has an abrasive, detrimental influence on many subtidal organisms. The mean tidal range of 2.6 meters does not produce any noticeable currents.

Turbid conditions prevail during periods of wave action and during spring runoff from coastal rivers. The seasonally variable visibility is generally less than five meters but may exceed this during calm periods (Table 1).

Water temperature and salinity data are presented in Fig. 4 and Table 1. The peak water temperature of 14° C was recorded during September, and the minimum of -3° C occurred during February. The latter temperature was recorded during an extended period of cold weather. The maximum salinity recorded was 32.9 °/oo during later fall. The salinity dropped to a low of 28.8 °/oo during the spring runoff.

The subtidal substrate at Cape Neddick was quite variable. Near-shore rock walls and boulders rapidly graded into large cobble. The large cobble terminated abruptly and was replaced by coarse sand. This study was restricted to the large cobble area to facilitate sampling and for making direct comparisons with Deep Cove.

The site at Cape Neddick was subjected to a greater range of temperature, salinity, and wave action than the site at Deep Cove. Habitats occupied by the chitons at Cape Neddick and Deep Cove were similar with respect to rock substrate, encrusting fauna, and calcareous algae.

Biological Characteristics. The faunal and algal compositions at Cape Neddick were quite diverse. Because of many overlapping habitats, no comprehensive algal or faunal lists were compiled. The pertinent species of fauna found are similar to those described for Deep Cove, and these species are mentioned in subsequent sections.

Unlike Deep Cove, the subtidal substrate had a profuse growth of red, green, and brown algae. The specific members of interest were Clathromorphum sp., Lithophyllum sp., Lithothamnium sp., and Chondrus crispus.

The associated flora and fauna showed seasonal variations in occurrence, composition, and density at both sites. For example, a prolific colonial diatom was evident in the shallow subtidal of Deep Cove only during late spring and summer. In general many of the smaller algae were either reduced or absent during winter and early spring. Larval recruitment was observed for algae and animals. Many sessile animals showed seasons of recruitment and growth (e.g., late spring and summer), whereas in winter and early spring they were absent or dormant. These observations were supported by monthly succession slide studies.

## Predation

Several species of vertebrate and invertebrate animals have been identified as predators on the chitons. A list of the relative densities of chiton predators is presented for Deep Cove and Cape Neddick in Table 3. Although no statistical data is presented on predator feeding rates, spatial and temporal differences in predation are considered in the discussion and under the role of predation in determining the population structure in the final discussion.

On multiple occasions at Cape Neddick, the wrasse _Tautogolabrus adspersus_ was observed to readily feed on exposed chitons when rocks were overturned. Since young individuals of this wrasse are in high density and have a relatively high frequency of occurrence, it is possible that this fish is a major chiton predator at Cape Neddick. Other predatory fish, including the winter flounder and hake, occur in low densities and have limited seasonal or infrequent occurrences at Cape Neddick.

The second most important group of chiton predators at Cape Neddick appears to be arthropods. _Cancer irroratus_ and _Homarus americanus_, which are common, were observed to feed on chitons both in the field and laboratory. The remaining species of arthropods and echinoderms are considered less important chiton predators at Cape

Table 3. Chiton predators and their observed relative abundance.

| Predator List | Observed Predation Field | Lab | Reported Predation | Predator Abundance* Deep Cove | Cape Neddick |
|---|---|---|---|---|---|
| Chordata | | | | | |
| *Tautogolabrus adspersus* | + | NA** | - | - | 1 |
| *Pseudopleuronectes americanus* | + | NA | + | 2 | 3 |
| *Melanogrammus aeglefinus* | - | NA | + | - | - |
| *Gadus morhua* | - | NA | + | 4 | - |
| *Urophycis chuss* | - | NA | + | - | 4 |
| Arthropoda | | | | | |
| *Cancer borealis* | + | + | - | 4 | 2 |
| *C. irroratus* | + | + | - | 4 | 3 |
| *Carcinus maenas* | - | + | - | - | 3 |
| *Homarus americanus* | + | + | - | 4 | 1 |
| *Pagurus acadianus* | - | + | - | 3 | 3 |
| *P. arcuatus* | - | + | - | 3 | - |
| *P. pubescens* | - | + | - | 3 | - |
| Echinodermata | | | | | |
| *Asterias rubens* | - | + | - | 1 | 2 |
| *Leptasterias littoralis**** | + | NA | + | 2 | - |
| *L. tenera* | + | NA | - | 1 | - |

* = Abundance Scale: High 1-2-3-4 Low
** = Not attempted under laboratory conditions
*** = Density: 30-100/ m$^2$

Neddick because of their low frequency of occurrence, low density, and/or alternative food sources.

Unlike those at Cape Neddick, chiton predators at Deep Cove have a distinct pattern of distribution along the subtidal transect (Fig. 2). The major fish predators frequent the deeper portions of the transect, whereas the dominant echinoderm predator frequents the shallow subtidal.

The conspicuous predatory fish at Deep Cove, the winter flounder Pseudopleuronectes americanus, occurs primarily during the summer. Based on gut analyses of at least one hundred winter flounders taken over hard substrates, I found that 45-60% of its diet consisted of large chitons. By contrast, winter flounders occurring at Cape Neddick rarely consume chitons but choose alternative food sources, including amphipods and algae.

Arthropod predators at Deep Cove are uncommon; but two species of asteroids occur commonly, and both were observed to feed on chitons. Leptasterias littoralis frequents the low intertidal down to approximately 4.5-6 meters. It is very abundant in the shallow portion of its zone and decreases in frequency with increasing depth. Below 4.5-6 meters, a second but less common seastar, L. tenera, is found. Due to the relatively small adult size of the two species of Leptasterias at Deep Cove, these asteroids are physically limited to feeding on smaller chitons. These asteroids were not found at Cape Neddick.

*Asterias rubens* is found abundantly at Deep Cove and Cape Neddick. After numerous field and laboratory observations, only one aberrant form was observed to feed on a chiton, and therefore it is not considered a significant chiton predator.

## Population Structure

*Population Distribution-Pattern of Species Occurrence.* The percent composition of each chiton species at Deep Cove is presented in Table 4. The numerical relationship of *T. rubra* to that of *T. marmorea* and *I. albus* is 4 : 2 : 1. A numerical dominance of *T. rubra* over *T. marmorea* was also recorded for Cape Neddick, 3 : 1.

The numerical relationships (*T. rubra* > *T. marmorea* > *I. albus*) are presented as percents of the total population by depth interval (Fig. 5). At Deep Cove the percent composition of *T. rubra* decreases with increasing depth; it is the dominant species to a depth of 7.5 meters. By contrast, the percent composition of *T. marmorea* rises with increasing depth, and it becomes the dominant species below 7.5 meters. The largest contribution to the total population of chitons made by *I. albus* occurs at 7.5 meters. The percent composition of *I. albus* in the chiton population decreases both above and below 7.5 meters. The changes in population distribution patterns occurring at mean low water are not significant due to low abundance of chitons at that level.

Table 4. Percent composition of the total chiton population by species.

**Deep Cove**

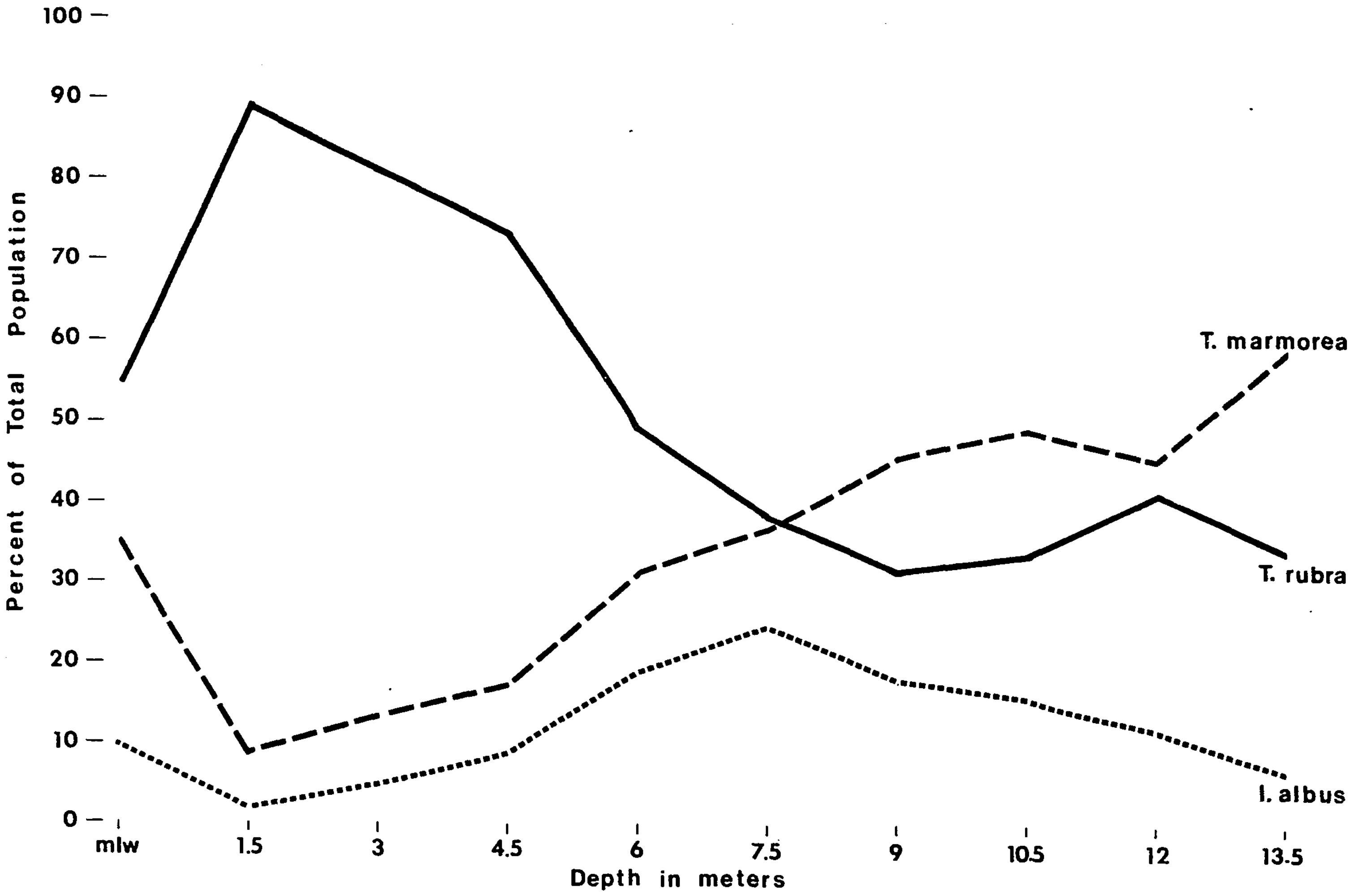
| | *T. rubra* | | *T. marmorea* | | *I. albus* | Sample Size |
|---|---|---|---|---|---|---|
| Percent of Total Population | 55.5 % | | 29.5 % | | 15.0 % | 7156 |
| Species Ratio | 4 | : | 2 | : | 1 | |

**Cape Neddick**

| | *T. rubra* | | *T. marmorea* | *I. albus* | Sample Size |
|---|---|---|---|---|---|
| Percent of Total Population | 72.6 % | | 27.4 % | - | 1779 |
| Species Ratio | 3 | : | 1 | - | |

Figure 5. Bathymetric distribution of chitons at Deep Cove. Percentage of each species comprising the total population by depth interval.

Figure 5.


100
90
80
70
60
50
40
30
20
10
0
Percent of Total Population
mlw
1.5
3
4.5
6
7.5
9
10.5
12
13.5
Depth in meters
T. marmorea
T. rubra
I. albus

At Cape Neddick, the numbers of _T_. _rubra_ declined slightly, whereas those of _T_. _marmorea_ showed a slight rise with increasing depth. These patterns were similar to the chiton distributional patterns described for Deep Cove. At Deep Cove the bathymetric distributional patterns of the chiton population are presented by season in Fig. 6. They reveal that the relative numerical dominance of _T_. _rubra_ and the subordinate positions of _T_. _marmorea_ and _I_. _albus_ show little seasonal fluctuation in the shallow subtidal (7.5 meters). The causes for the slightly greater seasonal irregularities below 7.5 meters were not determined, but these irregularities may reflect only minor changes in a region of lower population density and/or may be artificially induced. The latter may be related to excess siltation and other forms of perturbation resulting from nearby scallop dragging, which occurs from late fall into early spring. Due to the extremely low density of chitons at mean low water, the variations at this depth were not statistically significant.

_Size Distribution_. The mean length and weight of the three species of chitons are presented by depth interval for Deep Cove (Fig. 7). Two features are evident: (1) chitons decrease in size with increasing depth, and (2) there is a marked size variation within each species of chiton. Also, at any depth interval, the mean size of _T_. _marmorea_ exceeds _T_. _rubra_, which exceeds _I_. _albus_.

At Cape Neddick, size distributions are presented

Figure 6. Bathymetric distribution of chiton population by season (Deep Cove).

Figure 6.

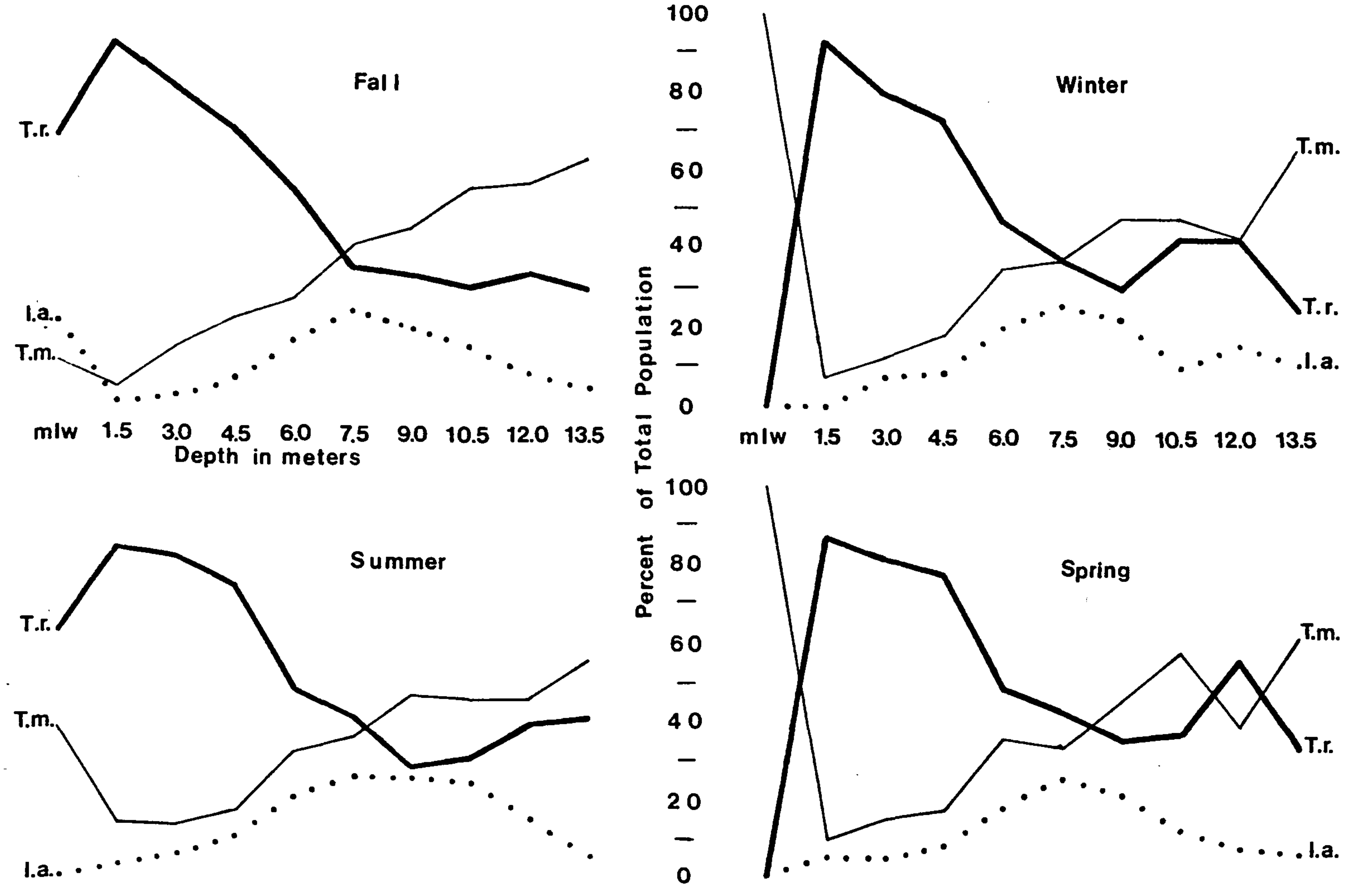
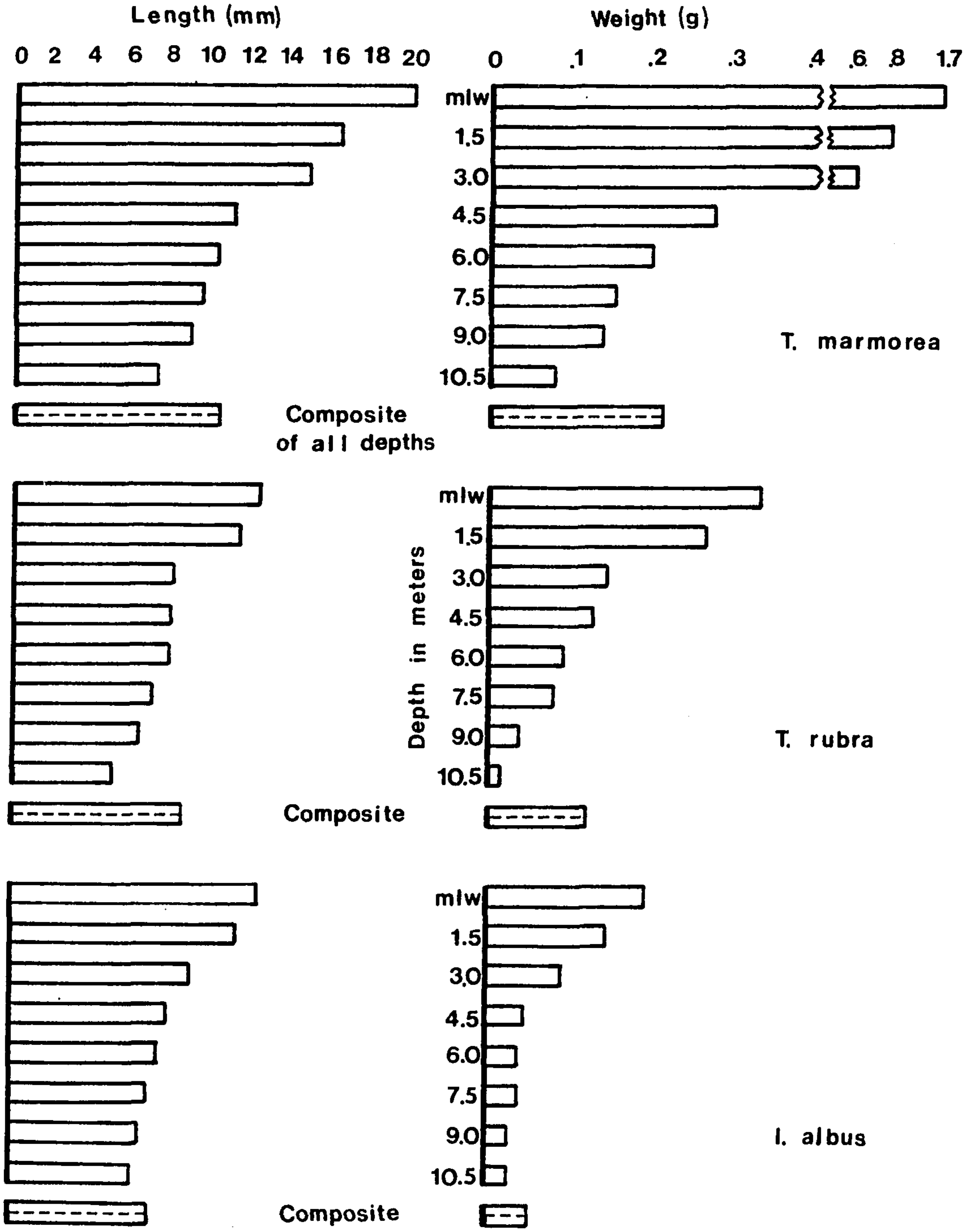

Fall
T.r.
I.a..
T.m.
mlw 1.5 3.0 4.5 6.0 7.5 9.0 10.5 12.0 13.5
Depth in meters
Winter
T.m.
T.r.
I.a.
100
80
60
40
20
0
Percent of Total Population
mlw 1.5 3.0 4.5 6.0 7.5 9.0 10.5 12.0 13.5
Summer
T.r.
T.m.
I.a..
Spring
T.m.
T.r.
I.a.
100
80
60
40
20
0

Figure 7. Mean length and weight of each species of chiton by depth interval (Deep Cove).

Figure 7.


Length (mm)
0 2 4 6 8 10 12 14 16 18 20
Weight (g)
0 .1 .2 .3 .4 .6 .8 1.7
mlw
1.5
3.0
4.5
6.0
7.5
9.0
10.5
T. marmorea
Composite of all depths
Depth in meters
T. rubra
Composite
I. albus
Composite

for the two depth intervals: 4.5 and 6 meters (Fig. 8). In a comparison of two similar depth intervals at two different sites at Cape Neddick, the sizes of _T. marmorea_ exceeded those of _T. rubra_, and the sizes of both species showed a decrease with increasing depth. At comparable depth intervals, _T. rubra_ and _T. marmorea_ were larger at Cape Neddick than at Deep Cove.

The mean length and weight of each species of chiton at Deep Cove is presented in Table 5. The size relationships are most clearly represented by the weight. The mean lengths and weights of _T. marmorea_ greatly exceeded those of _T. rubra_ and _I. albus_. The mean lengths of _T. rubra_ were slightly larger than _I. albus_, but the mean weights were substantially larger for _T. rubra_. Since the data for Cape Neddick was based on a limited number of depth intervals, the sites were not compared. Monthly and seasonal size distributions were plotted for each species, but no indication of the population structure or duration of life of the chitons could be determined.

The presence of a sexual dimorphism in size among the species of chitons was investigated (Table 6). There was no significant difference in the length or weight between the sexes of the chitons. This condition persisted at all depth intervals in Deep Cove.

_Population Density_. The density of the total chiton population averaged over 600 individuals/m$^2$ between mean low water and 10.5 meters at Deep Cove. At Cape

Figure 8. Mean length and weight of each species of chiton by depth interval (Cape Neddick).

Figure 8.

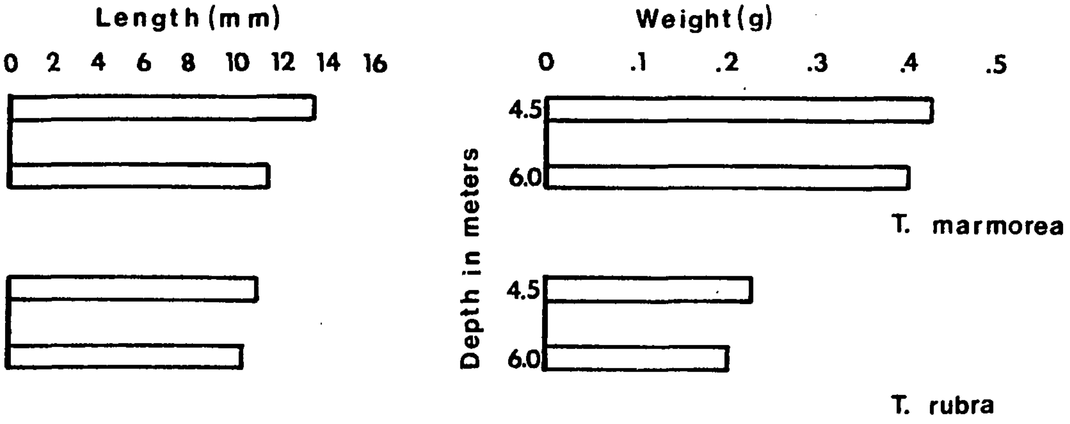

Length (mm)
0 2 4 6 8 10 12 14 16
Weight (g)
0 .1 .2 .3 .4 .5
Depth in meters
4.5
6.0
T. marmorea
4.5
6.0
T. rubra

Table 5. Mean length and weight of each species of chiton.

Deep Cove

| Species | Mean Length (mm) | Mean Weight (g) | Sample Size |
|---|---|---|---|
| *Tonicella rubra* | 8.7 | 0.13 | 2143 |
| *Tonicella marmorea* | 10.5 | 0.22 | 1154 |
| *Ischnochiton albus* | 7.2 | 0.04 | 524 |

Cape Neddick

| Species | Mean Length (mm) | Mean Weight (g) | Sample Size |
|---|---|---|---|
| *Tonicella rubra* | 9.5 | 0.19 | 997 |
| *Tonicella marmorea* | 12.2 | 0.40 | 336 |

Table 6. Mean length and weight of each species of chiton by sex.

Deep Cove

| | MALE | | | FEMALE | | |
|---|---|---|---|---|---|---|
| Species | Mean Length (mm) | Mean Weight (g) | Sample Size | Mean Length (mm) | Mean Weight (g) | Sample Size |
| *Tonicella rubra* | 9.3 | 0.15 | 937 | 8.9 | 0.13 | 1026 |
| *Tonicella marmorea* | 10.2 | 0.22 | 553 | 10.5 | 0.25 | 496 |
| *Ischnochiton albus* | 7.3 | 0.04 | 194 | 7.9 | 0.05 | 270 |

Cape Neddick

| | MALE | | | FEMALE | | |
|---|---|---|---|---|---|---|
| Species | Mean Length (mm) | Mean Weight (g) | Sample Size | Mean Length (mm) | Mean Weight (g) | Sample Size |
| *Tonicella rubra* | 10.4 | 0.19 | 467 | 10.1 | 0.19 | 515 |
| *Tonicella marmorea* | 13.0 | 0.43 | 157 | 13.7 | 0.50 | 124 |

Neddick it was less than 70 individuals/m$^2$ at 4.5 and 6 meters. At Deep Cove the density rose sharply from a low of 16 individuals/m$^2$ at mean low water to a peak exceeding 1000 individuals/m$^2$ by 6 meters (Fig. 9), and it declined with increasing depth, except for a plateau at 9 to 10.5 meters. The high density at 6 meters was substantiated by one year of independent (1/4m$^2$) quadrat samples. This difference in density between Deep Cove and Cape Neddick appears to be the result of predation and is discussed under the role of predation in determining population structure.

The densities of the component species are presented for Deep Cove in Fig. 10. _T_. _rubra_ illustrates a rapid rise in density from mean low water to 1.5 meters followed by a more gradual rise to a peak density of just under 600 individuals/m$^2$ at a depth of 4.5 meters. The density declined with increasing depth but was interrupted by a plateau between 9 and 10.5 meters. In marked contrast, the density of _T_. _marmorea_ increased gradually from mean low water to a peak of over 300 individuals/m$^2$ at 6 meters. The density declined slightly to a plateau which extended between 7.5 to 10.5 meters before declining further. The density of _I_. _albus_ increased gradually to a peak of less than 200 individuals/m$^2$ at 6 meters and then declined.

At Cape Neddick the density of _T_. _rubra_ declined slightly from 52 (± 42) individuals/m$^2$ at 4.5 meters to

Figure 9. Mean density (± SD) of total chiton population by depth interval (Deep Cove).

Figure 9.

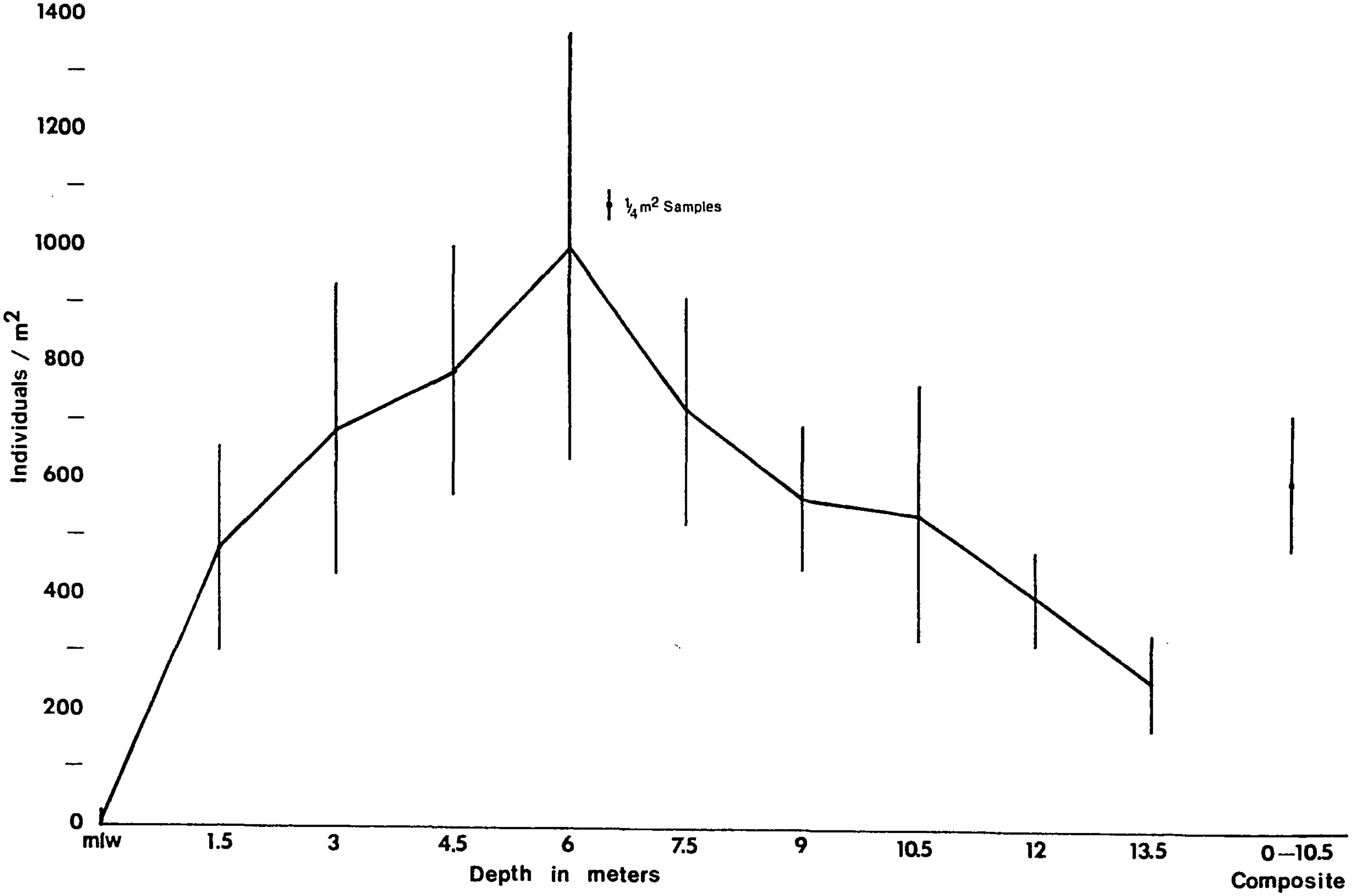
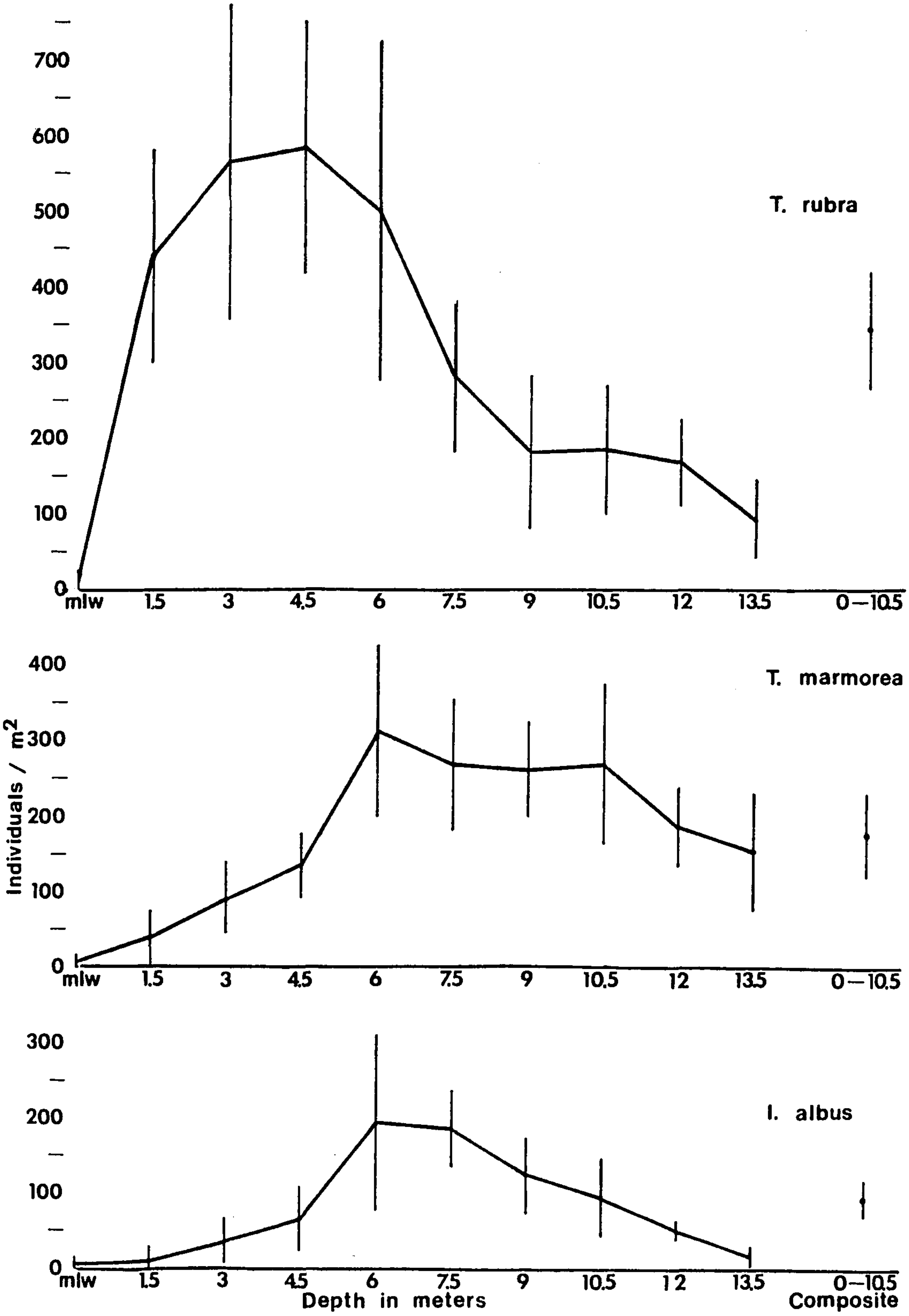

1400
1200
1000
800
600
400
200
0
Individuals / $m^2$
¼ $m^2$ Samples
mlw
1.5
3
4.5
6
7.5
9
10.5
12
13.5
0—10.5
Depth in meters
Composite

Figure 10. Mean density (± SD) of each species of chiton by depth interval (Deep Cove).

Figure 10.


700
600
500
400
300
200
100
0
mlw
1.5
3
4.5
6
7.5
9
10.5
12
13.5
0—10.5
T. rubra
400
300
200
100
0
T. marmorea
Individuals / m2
300
200
100
0
I. albus
Depth in meters
Composite

48 (± 28) individuals/$m^2$ at 6 meters. By contrast, the density of T. marmorea increased slightly from 15 (± 11) to 20 (± 14) individuals/$m^2$ with increasing depth. This reciprocal pattern was similar to that of Deep Cove, where the density of T. rubra declined below 4.5 meters and the T. marmorea population increased below 4.5 meters.

Seasonal changes in the densities of the chitons were evident in Deep Cove. The mean densities were 604 (± 108) in spring, 587 (± 183) in summer, 551 (± 139) in fall, and 484 (± 128) in winter. During spring, there was a general increase in density at most depth intervals (Fig. 11). During summer, stabilization of densities occurred at most depths. A decrease in density occurred during fall and continued into winter.

The seasonal variations in density were most pronounced in T. rubra above 7.5 meters (Fig. 12). Below 7.5 meters, the density fluctuated only slightly. The numbers of T. rubra rose sharply during spring, leveled off during summer, and declined during the subsequent seasons. The higher density during the summer probably reflected the growth and appearance of the remaining spring recruits.

The seasonal variations in density were most apparent in T. marmorea at the depths of greatest population concentration, below 4.5 meters (Fig. 13). Above 6 meters the density showed minor seasonal fluctuations. The density increased slightly at most depths during spring. A continued rise in density occurred in summer, and a de-

Figure 11. Mean density (± SD) of total chiton population by season (Deep Cove).

Figure 11.

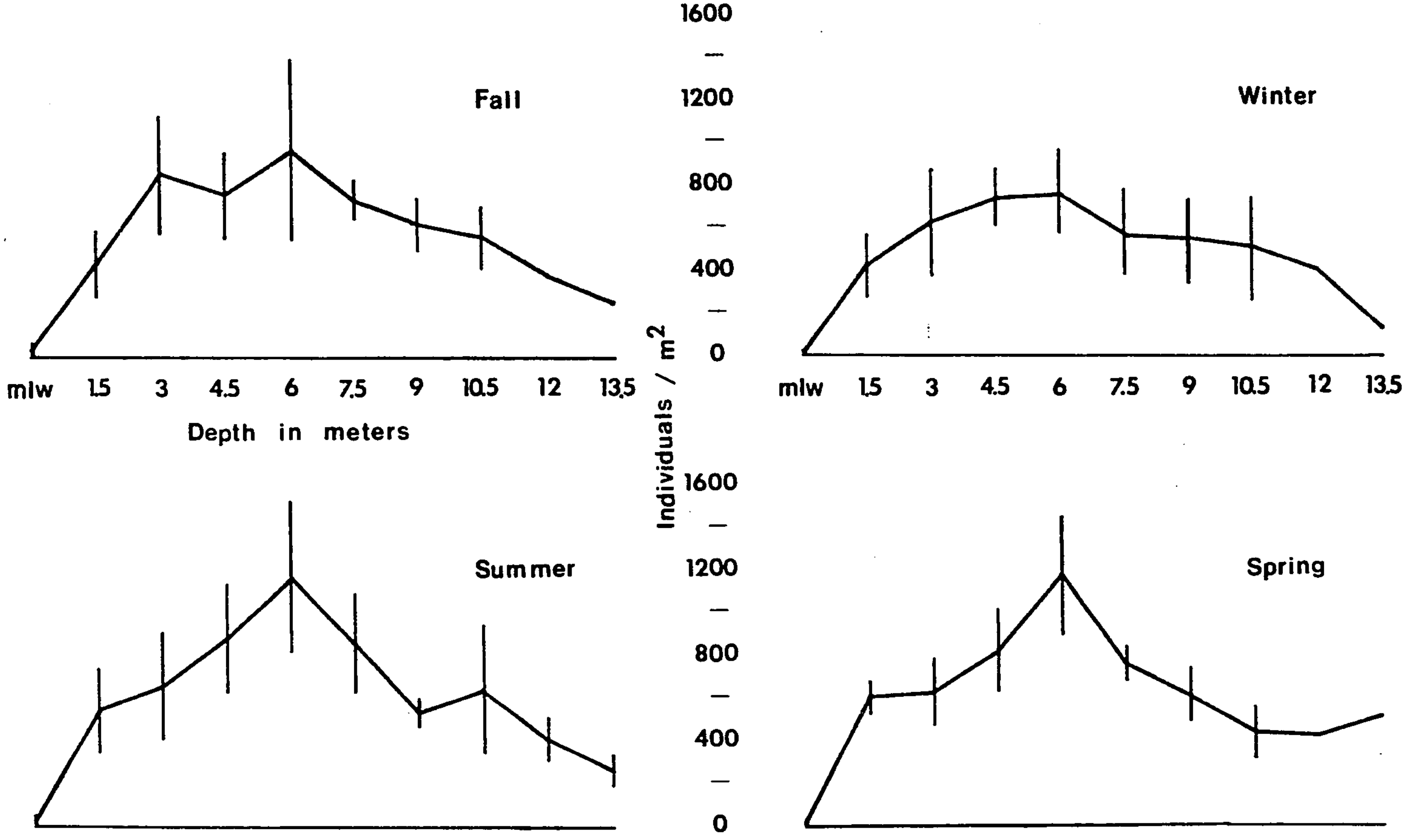

Fall
Winter
Summer
Spring
1600
1200
800
400
0
Individuals / m²
mlw
1.5
3
4.5
6
7.5
9
10.5
12
13.5
Depth in meters

Figure 12. Mean density (± SD) of <u>Tonicella rubra</u> by season (Deep Cove).

Figure 12.

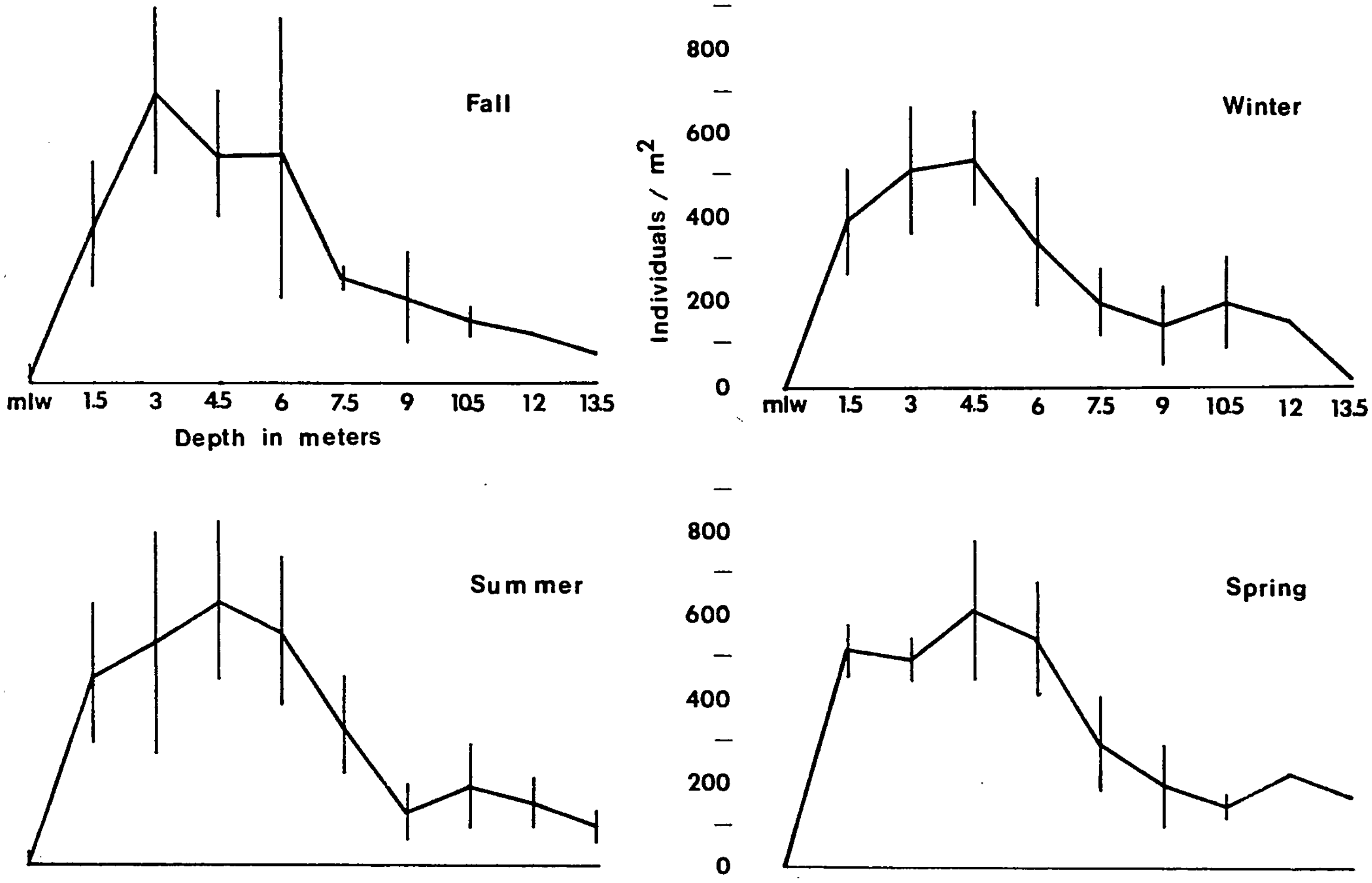
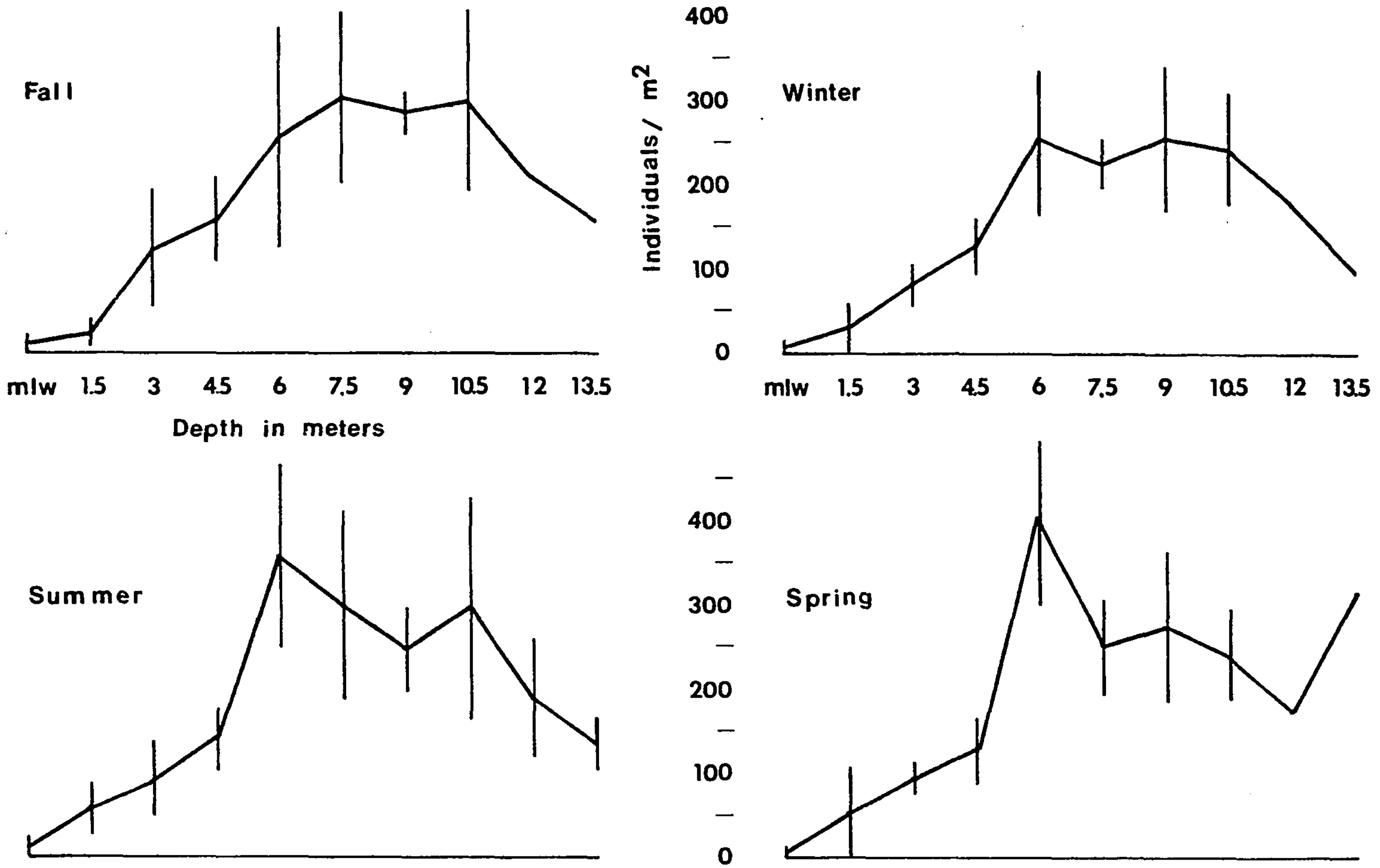

Fall
Winter
Summer
Spring
Individuals / m²
800
600
400
200
0
800
600
400
200
0
mlw
1.5
3
4.5
6
7.5
9
10.5
12
13.5
mlw
1.5
3
4.5
6
7.5
9
10.5
12
13.5
Depth in meters

Figure 13. Mean density (± SD) of *Tonicella marmorea* by season (Deep Cove).

Figure 13.


Fall
Winter
Summer
Spring
Individuals/ $m^2$
0
100
200
300
400
mlw
1.5
3
4.5
6
7.5
9
10.5
12
13.5
Depth in meters

cline followed during subsequent seasons. Population recruitment appeared first during late spring and increased during summer. The decline in density during winter was less severe for T. marmorea than for T. rubra.

The density of I. albus illustrated seasonal variations between 4.5 and 10.5 meters (Fig. 14); outside of these depths only minor seasonal fluctuations occurred. The population density increased during spring and summer. This was followed by a decline in fall and a stabilization in winter. I. albus showed the largest decline in population density during fall. The reason for this is unclear. The occurrence of T. rubra and I. albus at mean low water during fall, followed by their absence during winter and spring, was probably caused by extremely low air temperature coupled with spring tides and ice scouring.

## Encrusting Organisms

A list of the organisms encrusted on the dorsal surfaces of T. rubra, T. marmorea, and I. albus is presented in Table 7. Among the three species of chitons, I. albus was uniquely free of encrusting organisms except for an occasional filamentous green alga. The flora and fauna encrusted on T. rubra and T. marmorea were in some cases similar, but there were differences. The types of encrusting phyla were similar in Deep Cove and Cape Neddick, but the species composition differed.

A marked difference occurred in the frequency with

Figure 14. Mean density (± SD) of *Ischnochiton albus* by season (Deep Cove).

Figure 14.

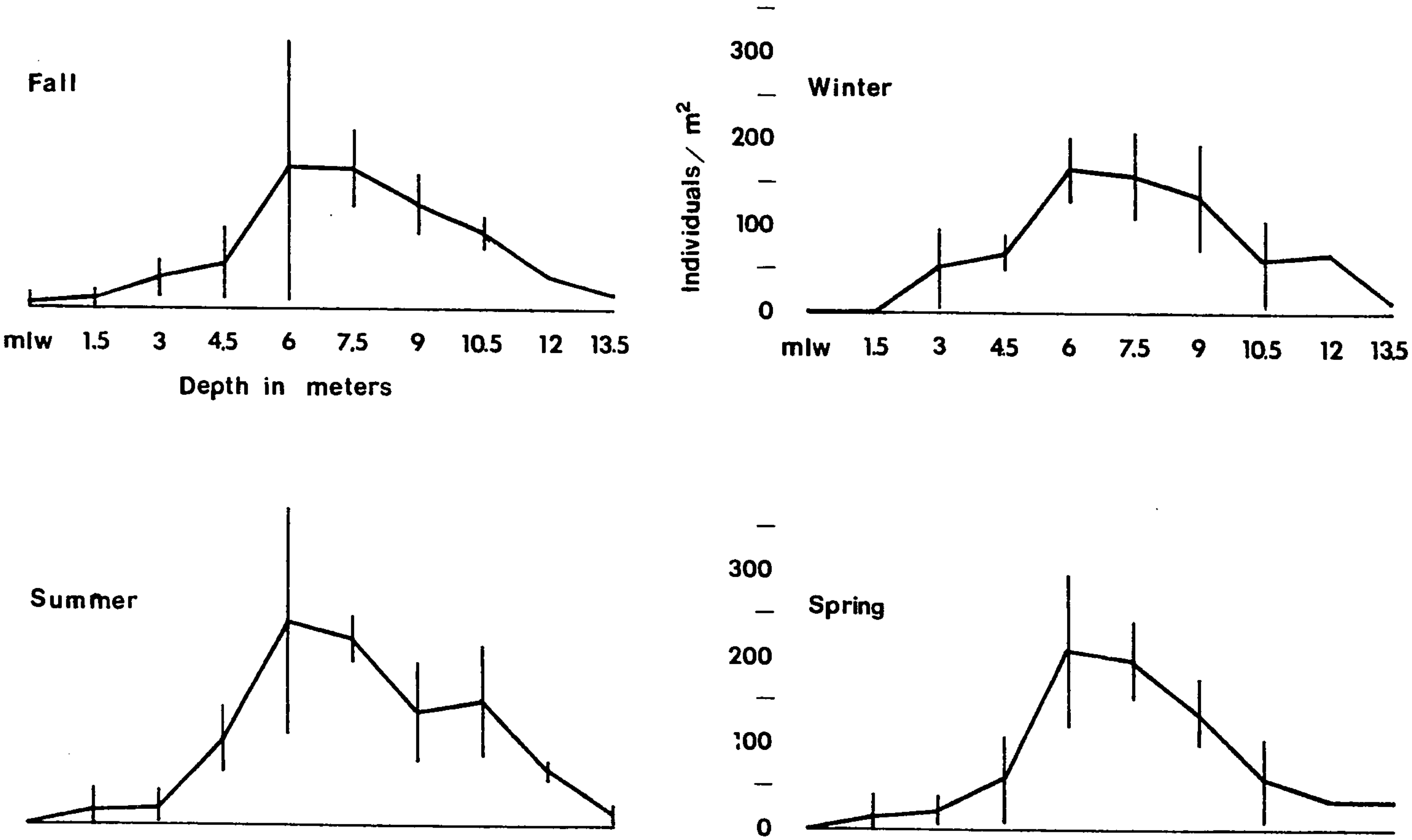

Fall
mlw
1.5
3
4.5
6
7.5
9
10.5
12
13.5
Depth in meters
Winter
300
200
100
0
Individuals / m$^2$
mlw
1.5
3
4.5
6
7.5
9
10.5
12
13.5
Summer
Spring
300
200
100
0

Table 7. Encrusting organisms found on each species of chiton.

| Types of Encrusting Organisms | Deep Cove | | | Cape Neddick | |
|---|---|---|---|---|---|
| | *T. rubra* | *T. marmorea* | *I. albus* | *T. rubra* | *T. marmorea* |
| Ectoprocta | | | | | |
| *Microporella ciliata* | + | - | - | - | - |
| *Bugula* sp. | + | - | - | - | - |
| Unid sp. | + | + | - | + | + |
| Cnidaria | | | | | |
| Hydrozoa | + | + | - | + | + |
| Anthozoa (anemones) | + | + | - | - | - |
| Annelida | | | | | |
| *Spirorbis borealis* & *S. spirillum* | + | - | - | + | + |
| Chordata | | | | | |
| *Molgula* sp. | + | - | - | - | + |
| *Boltenia echinata* | - | + | - | - | - |
| Rhodophyceae | | | | | |
| *Clathromorpha* sp. | + | + | - | + | + |
| Unid. filamentous sp. | - | + | - | - | + |
| Chlorophyceae | | | | | |
| *Ulva lactuca* | - | - | - | - | + |
| *Urospora* sp. | - | + | - | - | - |
| Unid. filamentous sp. | + | + | + | + | + |

which the specific encrusting phyla appeared on the different species of chitons (Table 8). This difference was readily observed at Deep Cove and at Cape Neddick. At Deep Cove the dominant encrusting forms were ectoprocts on _T. rubra_ and hydroids on _T. marmorea_. At Cape Neddick the dominant form on _T. rubra_ was serpulid worms, but it was hydroids on _T. marmorea_. As previously mentioned, the dominant form encrusted on _I. albus_ was a filamentous green alga.

The percentage of the chiton population encrusted at each depth interval is presented in Table 9. At Deep Cove the percentage of encrustation of the _Tonicella_ species peaked at 7.5 meters. The frequency of encrustation decreased with increasing or decreasing depth. Encrusting organisms were absent from _I. albus_ except at 9 meters.

The distribution of the encrusting organisms on the dorsal surface of the chitons is presented in Table 10. At Deep Cove the encrusted organisms on _T. rubra_ increased from anterior to posterior. Few organisms encrusted on the chiton girdle. At Cape Neddick this distributional pattern differed. The encrusted forms were greatest on the central shell plates and decreased anteriorly and posteriorly.

At Deep Cove, _T. marmorea_ had a fairly equal distribution of encrusting organisms over the shell plates. In general there was a slightly greater frequency of encrusting forms on the central plates, while greater en-

Table 8. The frequency of occurrence of encrusting phyla on each species of chiton.

| | Deep Cove | | |
|---|---|---|---|
| Encrusting Phyla | *T. rubra* | *T. marmorea* | *I. albus* |
| Ectoprocta | 71.1 % | 11.6 % | 0.0 % |
| Cnidaria (Hydrozoa) | 7.5 % | 59.4 % | 0.0 % |
| Annelida (Serpulidae) | 6.4 % | 0.0 % | 0.0 % |
| Chordata (Urochordata) | 0.5 % | 1.5 % | 0.0 % |
| Rhodophyceae | 14.0 % | 20.3 % | 0.0 % |
| Chlorophyceae | 0.5 % | 7.2 % | 100.0 % |

| | Cape Neddick | |
|---|---|---|
| Encrusting Phyla | *T. rubra* | *T. marmorea* |
| Ectoprocta | 5.0 % | 0.0 % |
| Cnidaria (Hydrozoa) | 5.0 % | 50.0 % |
| Annelida (Serpulidae) | 88.0 % | 33.0 % |
| Chordata (Urochordata) | 0.0 % | 0.0 % |
| Rhodophyceae | 0.0 % | 0.0 % |
| Chlorophyceae | 2.0 % | 17.0 % |

Table 9. The percent of encrusted forms in the chiton population by depth interval for Deep Cove.

| Depth in meters | *T. rubra* | *T. marmorea* | *I. albus* |
|---|---|---|---|
| MLW | 0.0 % | 0.0 % | 0.0 % |
| 1.5 | 4.0 % | 0.0 % | 0.0 % |
| 3.0 | 1.7 % | 3.9 % | 0.0 % |
| 4.5 | 3.4 % | 5.9 % | 0.0 % |
| 6.0 | 16.7 % | 9.0 % | 0.0 % |
| 7.5 | 29.4 % | 9.4 % | 0.0 % |
| 9.0 | 7.9 % | 2.4 % | 2.2 % |
| 10.5 | 3.0 % | 3.8 % | 0.0 % |

Table 10. Distribution of encrusting organisms on the dorsal surface of each species of chiton.

Deep Cove

| Species | Shell Plate Number<br>1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | Girdle |
|---|---|---|---|---|---|---|---|---|---|
| *T. rubra* | 1.8 % | 3.7 % | 4.8 % | 5.5 % | 14.3 % | 20.6 % | 19.1 % | 29.4 % | 0.7 % |
| *T. marmorea* | 4.9 % | 11.8 % | 10.8 % | 11.8 % | 15.7 % | 18.7 % | 13.7 % | 11.8 % | 9.8 % |
| *I. albus* | 0.0 % | 0.0 % | 50.0 % | 0.0 % | 50.0 % | 0.0 % | 0.0 % | 0.0 % | 0.0 % |

Cape Neddick

| Species | Shell Plate Number<br>1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | Girdle |
|---|---|---|---|---|---|---|---|---|---|
| *T. rubra* | 0.0 % | 17.0 % | 12.0 % | 17.0 % | 24.0 % | 12.0 % | 9.0 % | 7.0 % | 2.0 % |
| *T. marmorea* | 0.0 % | 0.0 % | 17.0 % | 33.0 % | 33.0 % | 17.0 % | 0.0 % | 0.0 % | 0.0 % |

crustation occurred on the mantle of T. marmorea than on the other two species of chitons. This probably resulted from an absence of mantle scales on T. marmorea, scales which are found on the other chitons. The distributional pattern of encrusted forms on T. marmorea from Cape Neddick was similar to Deep Cove with a more definitive concentration on the central plates. The distribution of organisms on I. albus revealed no pattern.

The percent of the total chiton population encrusted by flora and/or fauna is presented in Table 11. Similar patterns were evident for the Tonicella species at Deep Cove and Cape Neddick. T. rubra had a greater frequency of encrusted animal forms at both sites, while the frequency of encrusted forms of algae was slightly greater on T. marmorea at both sites. I. albus had a very low frequency of plant and no animal encrustation.

## Morphological Variations

Two types of morphological variations were found among the chiton shell plates. First was a fusion of adjacent plates to form an inflexible unit, and second was the absence of part of or more than one shell plate. Due to the analysis techniques used, investigation of the frequency of fused plates was not undertaken. Individuals with variation in shell plate number were found for all three species of chitons. All of the variants collected had less than the normal eight shell plates, 7 1/2, 7, or

Table 11. Percent of the total chiton population encrusted.

Deep Cove

| Species | Animal | Algae | Animal &/ or Algae |
|---|---|---|---|
| Tonicella rubra | 7.7 % | 1.2 % | 8.96 % |
| Tonicella marmorea | 4.4 % | 1.6 % | 6.0 % |
| Ischnochiton albus | 0.0 % | 0.4 % | 0.4 % |

Cape Neddick

| Species | Animal | Algae | Animal &/ or Algae |
|---|---|---|---|
| Tonicella rubra | 4.0 % | 0.1 % | 4.1 % |
| Tonicella marmorea | 1.5 % | 0.3 % | 1.8 % |

6. The occurence of a 7 1/2-plated chiton was first described by Oliver (1921). It, as the name implies, is missing either the right or left half of a shell plate. No nine-plated specimens, which have been reported for other species of chitons, were found. The distribution of the morphological variants among the chiton populations is presented in Table 12. In all but one case, the morphological variations comprised less than 1/2 of one percent of the total population.

An approximately equal proportion of the populations of *T. rubra* at Deep Cove and Cape Neddick were composed of variants. All of the variant forms from Cape Neddick were comprised of seven plates (Table 13). However, at Deep Cove the forms included 7 1/2, 7, and 6-plated individuals.

Unlike *T. rubra*, the proportion of variants in the populations of *T. marmorea* was twice as large at Deep Cove than at Cape Neddick (Table 13). At Deep Cove seven-plated individuals were much more common than six-plated specimens. Only seven-plated forms were found at Cape Neddick. No 7 1/2-plated forms were collected for *T. marmorea*.

Among the three species of chitons, variants were most common among populations of *T. rubra* and least common among *I. albus*. The 7 and 7 1/2-plated specimens were equally represented among *I. albus*, while the six-plated form was absent. The percent frequency of morphological

Table 12. Distribution of morphological variations among the three species of chitons.

| Species | Number of Shell Plates | Deep Cove | Cape Neddick |
|---|---|---|---|
| <u>Tonicella rubra</u> | 7 1/2 | 0.14 % | 0.00 % |
| | 7 | 0.46 % | 0.54 % |
| | 6 | 0.046% | 0.00 % |
| <u>Tonicella marmorea</u> | 7 1/2 | 0.00 % | 0.00 % |
| | 7 | 0.35 % | 0.21 % |
| | 6 | 0.087% | 0.00 % |
| <u>Ischnochiton albus</u> | 7 1/2 | 0.19 % | - |
| | 7 | 0.19 % | - |
| | 6 | 0.00 % | - |

Table 13. Percent of the total chiton population with less than eight shell plates.

| | Deep Cove | Sample Size | Cape Neddick | Sample Size |
|---|---|---|---|---|
| *Tonicella rubra* | 0.65 % | 2166 | 0.54 % | 1292 |
| *Tonicella marmorea* | 0.44 % | 1149 | 0.21 % | 487 |
| *Ischnochiton albus* | 0.38 % | 528 | - | - |

variants is presented by depth interval for Deep Cove in Table 14. It indicates that the occurrence of the variants is not related to depth.

## Behavior

Habitat Selection and Activity Patterns. *T. rubra* and *T. marmorea* are colored cryptically when found on rocks covered with red calcareous algae. During the diurnal hours, the majority of the chitons occupy the vertical faces and undersides of rocks. This zone is bounded by the terminated growth of calcareous algae on the upper edge and soft substrate on the lower edge. This zone often contains a variety of encrusting fauna including those forms which were frequently found on the chiton shell plates (see Encrusting Organisms). On rocks where the vertical faces terminate below the soft substrate, chitons orient in a linear fashion along the interface of the soft substrate. On occasion, chitons were found several centimeters below the surface of the soft substrate while still in contact with a rock surface.

Although the majority of the chitons were found within the zone described, they also occupy a variety of microhabitats either within or on the margins of this zone. The microhabitats differ depending on the age group of the chitons and differences in the local habitats. At Cape Neddick chitons were located under thickly-layered calcareous algae and along the sand-rock interface. Analysis of

Table 14. Percent of morphological variants by depth for Deep Cove.

| Depth in meters | *T. rubra* | *T. marmorea* | *I. albus* |
|---|---|---|---|
| MLW | 0.00 % | 0.00 % | 0.00 % |
| 1.5 | 0.87 % | 0.00 % | 0.00 % |
| 3.0 | 0.46 % | 1.30 % | 0.00 % |
| 4.5 | 0.84 % | 0.00 % | 1.70 % |
| 6.0 | 0.55 % | 1.10 % | 0.79 % |
| 7.5 | 1.26 % | 0.45 % | 0.00 % |
| 9.0 | 0.00 % | 0.00 % | 0.00 % |
| 10.5 | 0.00 % | 0.00 % | 0.00 % |
| 12.0 | 0.00 % | 0.00 % | 0.00 % |
| 13.5 | 0.00 % | 0.00 % | 0.00 % |

feeding habits and encrusting organisms found on the adult chitons from Deep Cove showed that *T. rubra* often frequented undersides of rocks, *T. marmorea* frequented the sides of rocks distinctly above the soft substrate interface, and the microhabitat of *I. albus* extended to the crevices on the upper rock surface. The microhabitat of young *T. rubra* was located at the base of the papillae of the calcareous alga *Lithothamnium* sp., and young *I. albus* were found on the undersides of bivalve shells.

The chitons did not show a consistent diurnal behavior pattern. Individuals could be found crossing upper rock surfaces during peak diurnal hours. Chitons also occupied a variety of isolated hard substrates in muddy areas. These included bottles and shells of living scallops, hermit crabs, and gastropods.

The occurrence of chitons on isolated hard objects on muddy bottoms led to an isolation experiment to determine if these objects were populated solely by larval chitons or perhaps by migrating adults. The experiment consisted of establishing an "island" of chiton-free rocks which was separated from the remaining rocky substrate and chiton population by a meter ring of silty mud. Within two months adult chitons were found on the "island," and their number increased during the subsequent months. Thus, chitons are not restricted to the site of larval settling but are capable of migrating into areas where the rocks are not contiguous. The semi-soft substrate is not a barrier to migration.

The nocturnal behavior of the chitons was observed in August 1972 at Deep Cove. During a twelve-hour period from before sunset to after sunrise, the subtidal behavior was observed at 1.5-hour intervals. Within one hour after sunset, large and small chitons representing all three species migrated from lower rock surfaces to upper surfaces of rocks. This activity increased to a peak around midnight, when the chitons were extremely numerous on all rock surfaces. Thereafter, a slow decline in the number of exposed chitons followed, and by 0400 only small individuals were noticeable on upper rock surfaces. The observation of, first, the large chitons returning to the undersides of rocks just before dawn and, then, the later return by young chitons suggested a stronger photonegative behavior in older chitons. A few chitons were still visible at sunrise at 0530, but they were gone by 0700.

Homing Behavior. Indirect evidence of homing behavior appears to exist for *T. rubra* and to a lesser extent for *T. marmorea*. On repeated occasions at sites in New Hampshire and southern Maine, *T. rubra* was removed from a rock surface covered with viable calcareous algae. Removal and examination of the chitons revealed that the calcareous algae under the chitons were either absent or white, the latter indicating a nonviable condition. A closer inspection of the home depression revealed no radular markings, which suggests that the depressions were not caused by feeding. The lack of growth or death of the calcareous algae under the chitons indicates that, at least during diurnal hours, the animals had occupied this position for an extended period of time. No more than one chiton was ever observed to occupy a single home depression. This absence of sharing, in a most limited sense, is suggestive of territorial behavior. The home depression behavior was found less frequently for _T_. _marmorea_ primarily because of the lower frequency of occurrence of this species in New Hampshire and southern Maine. It is feasible, though unlikely, that mild depressions, i.e., homes, were created by some other organism and later taken over by chitons. Technical difficulties prevented further investigations of homing behavior and the frequency of occurrence of this behavior. The major obstacle was the marking of subtidal specimens without their removal from home depression which reportedly interrupts or destroys the homing instinct.

## Discussion

It is generally accepted that the three species of chitons have an arctic-boreal distribution. Gould (in Binney, 1870) and Johnson (1934) reported the southernmost western Atlantic distribution of these species as Connecticut.

The distribution of T. rubra extends from northern Canada and Labrador (Whiteaves, 1901; Johnson, 1934) to Greenland (Fabricius, 1780) and the White Sea (Middendorff, 1849; Yakovleva, 1952) in the eastern Atlantic. T. rubra extends southward along Norway (Sars, 1878) to parts of Great Britain (Forbes and Hanley, 1850) and the Baltic Sea (Thiele, 1928). Dall (1878) reported that T. rubra ranged from Kamchatka, in the northwest Pacific, northward beyond the Bering Straits; Dall (1921) reported its range extended from the Arctic Ocean to Monterey, California. Taki (1938) reported the presence of T. rubra as far south as Hokkaido and the Sea of Japan in the northeast Pacific. Additional authors have substantiated both Pacific and Atlantic distributions. In contrast, Yakovleva (1952) reported T. rubra as an exclusively boreal North Atlantic species that does not extend to the eastern coast of North America.

The arctic-boreal distributions of T. marmorea and I. albus are similar to those described for T. rubra. Along the New England coast, T. marmorea has been reported as far south as Connecticut by Gould (in Binney, 1870) and Massachusetts Bay by Johnson (1934). The southern extent of *I. albus* is listed as Cape Cod by Gould (in Binney, 1870) and Massachusetts Bay by Johnson (1934). The report by Yakovleva (1952) of *I. albus* extending southward along the east coast of the United States and into the Caribbean is questionable. The source of the error may be the chiton *Chaetopleura apiculata* (Say, 1830), which has a superficial appearance similar to *I. albus* and a distribution extending from Massachusetts to the Caribbean (Abbott, 1974).

Several authors (Couthouy, 1838; Gould, in Binney, 1870; Blaney, 1904; Balch, 1906; Yakovleva, 1952; Christiansen, 1954) reported *T. rubra*, *T. marmorea*, and *I. albus* on subtidal rock substrates at diverse geographic locations. Yakovleva (1952) reported *T. marmorea* commonly occurs on *Laminaria* holdfasts. *T. marmorea* was not found on holdfasts. Gould (in Binney, 1870) reported the association of *T. rubra* with rocks and kelp, and the findings of this study support that report.

On subtidal, algal-covered rocks, the cryptic coloration of the chitons frequenting calcareous algae was noted by Yakovleva (1952) and Fischer-Piette and Franc (1960). While cryptic coloration was observed for the two species of *Tonicella* at Deep Cove and Cape Neddick, *I. albus* was not found on white calcareous algae as described by Fischer-Piette and Franc (1960).

*T. rubra*, *T. marmorea*, and *I. albus* occasionally utilized crevices or galleries in thickened calcareous algae. This behavior, which was more frequent at Cape Neddick, is similar to that described for *Acanthochitona* in France (Benard, 1960). The more frequent occurrence of this behavior at Cape Neddick may be the result of two factors. First, the more stable and permanent rock formations at Cape Neddick allow for a longer period of uninterrupted algal growth and the resultant thick deposits; and, second, chitons occupying these galleries and crevices were less prone to fish predation, particularly from the wrasse *Tautogolabrus adspersus*.

Barnes (1972) described an integral association between *Tonicella lineata* and calcareous algae in the northeastern Pacific. This chiton is dependent on calcareous algae for food and successful larval metamorphosis. Despite the fact that *T. rubra*, *T. marmorea*, and *I. albus* are found associated with calcareous algal-covered rocks, they do not show the specific substrate association described for *T. lineata*. In fact, the majority of the animals spend the diurnal period on rock surfaces, e.g., undersides of rocks, devoid of this algae. In addition, the occurrence of chiton populations (1) on isolated hard substrates (shells and bottles) in muddy environments, (2) on rock substrates free of calcareous algae, and (3) on glass succession slides suspended from floats points even more strongly to the lack of dependency of the three species of chitons, and most probably their larvae, upon the presence of calcareous algae.

The ability of chitons to survive in areas having a high silt content, to burrow under soft substrates while maintaining contact with rock surfaces, and to cross limited distances of soft substrate in order to populate new areas is not widely recognized. This behavior was observed on many occasions. This ability indicates that the movements of these chitons are not restricted to areas with contiguous rocks. Further, this capability allows chitons to populate substrates unsuccessfully colonized by settling larval forms or to repopulate areas which have become devastated by factors such as heavy predation or local environmental mishaps such as scallop dragging. Crozier (1918a) reported that chitons distributed along a beach in Bermuda were often buried under sand but always in contact with rocks. This behavior is in contrast to the generally accepted concept that chitons cannot survive in areas of soft substrate due to clogging of gills.

Yakovleva (1952) reported that the minimum salinity and temperature required for survival by the three species of chitons were 32 $^{o}/oo$ and +1.2 C. However, these same species were found surviving at Cape Neddick at a salinity of 28.8 $^{o}/oo$ and a water temperature of $-3^{o}$ C. In addition, the salinities at Deep Cove and at Cape Neddick were below 32 $^{o}/oo$ during most seasons. _T. marmorea_ and _T. rubra_ survived without signs of stress, i.e., increased oxygen consumption, at salinities above 24.5 $^{o}$/oo, and T. rubra withstood osmotic stress and showed no appreciable mortality until the salinity dropped below 21 $^{o}$/oo (Langer, unpublished). The subtidal physical factors, i.e., temperature and salinity, encountered by the chitons during seasonal extremes were clearly within their range of tolerance and did not approach the condition of stress. However, no judgment can be made on the degree of influence imparted by heavy wave action during storms at Cape Neddick. Fager (1968) and Connell (1972) emphasized the effects of variations in water movement and its resultant mechanical stress and siltation on subtidal epifaunal populations.

Tonicella lineata is found predominantly in the low and mid intertidal zone along the northern Pacific Coast (Barnes, 1972). In contrast, T. rubra, T. marmorea, and I. albus are essentially absent from all but the lowest fringe of the intertidal zone of New England. Several factors indicate that temperature and/or salinity partially limit the intertidal occurrence and survival of these chitons. The water temperature and particularly the air temperature ranges are far more extreme in New England than those experienced by West Coast chitons. Observations at several sites in Maine and New Hampshire have indicated an annual population recruitment to the low intertidal zone and tide pools in late spring. However, with the onset of summer and rising temperatures, the chiton population in this region disappears. During late fall, occasional specimens are found in the low intertidal. However, when the lower intertidal zone is exposed to extremely low air temperatures (-32° C) during spring tides in winter, the chitons disappear. The occurrence of ice floes and wave-borne objects are common at Deep Cove. The degree of destructive, i.e., abrasive and crushing, nature of such items on chitons in the littoral fringe is not known. But, the destructive influence of wave-borne objects on sessile, intertidal forms and the resultant patchiness of various populations is established in the literature (Dayton, 1971; Connell, 1972). In the field the chitons were found to survive under rocks covered with sea ice in water temperatures below -3° C, but specimens entrapped in ice for more than a few hours suffered heavy mortality (personal observation). More work is needed in this area to clarify the physical and biological factors, e.g., bird and crab predation, which influence the distribution of the chitons in the intertidal zone.

Predation on chitons is well established in the literature. Chiton predators include echinoderms (Yakovleva, 1952; Feder, 1959; Mauzey, 1966; Mauzey _et al_., 1968; Paine, 1969; Menge, 1970; Robilliard, 1971; Barnes, 1972; O'Brien, 1972), arthropods (Fischer-Piette and Franc, 1960; Thorne, 1968), molluscs (Arey and Crozier, 1919; Pilson and Taylor, 1961), fishes (Gould in Binney, 1870; Yakovleva, 1952; Fischer-Piette and Franc, 1960;

Randall, 1967; Jillet, 1968), mammals (Drake, 1896; Arey and Crozier, 1919) and, possibly, birds (Glynn, 1970; anon., 1973).

Fish predation on T. rubra, T. marmorea, and I. albus has been documented in the literature on many occasions since Gould (in Binney, 1870). Several commercially valuable bottom-feeding fish are known to feed on these chitons. These include the cod (Gadus morhua), haddock (Melanogrammus aeglefinus), hake (Urophycis chuss), and winter flounder (Pseudopleuronectes americanus) along the New England coast (M. Hill, personal communication). Fischer-Piette and Franc (1960) reported I. albus was eaten by two European flatfish, Pleuronectes vulgaris and Solea vulgaris.

The high density of the wrasse Tautogolabrus adspersus at Cape Neddick and its absence at Deep Cove is the most conspicuous difference in these two sites which indicates the wrasse's role as a chiton predator at Cape Neddick. According to Bigelow and Schroeder (1953), this wrasse is rarely reported north of Mount Desert, and the lowest known temperature for successful breeding of this fish is 13-13.5° C. The highest temperature recorded in Deep Cove was 12.5° C. I have observed this fish near Cobscook Bay, but it appears to choose a habitat with a community composition (e.g., large macroscopic algae) different from that of Deep Cove.

In contrast to Cape Neddick, the most conspicuous predatory fish at Deep Cove is the winter flounder Pseudopleuronectes americanus. Four years of observation reveals it to be a seasonally occurring predator in the shallow subtidal. Its selective feeding behavior indicates that it is a significant chiton predator at Deep Cove; whereas at Cape Neddick, the winter flounder chooses alternative prey and thus appears to be a minor predator on chitons.

Asteroid predation by Leptasterias littoralis on T. rubra was first reported by O'Brien (1972). Similarly, Leptasterias hexactis, a possible ecological equivalent on the Pacific Coast of North America, is reported to feed on the chiton Tonicella lineata (Barnes, 1972) and fills a similar niche.

Berry (1907), Taki (1938), Fischer-Piette and Franc (1960), and Boyle (1970) have reported for several species of chitons that young (e.g., small) individuals are found in deeper water and older (e.g., larger) individuals frequent shallow water. However, Berry (1951) and others did not find this to be the case for all species of chitons. Barnes (1972) found the largest individuals of T. lineata occupied the low littoral, whereas the small individuals were equally distributed over the littoral zone.

A limited number of studies have dealt with chiton density, and all but one of these studies have been restricted to intertidal forms. The numerical dominance of T. rubra was reported by Balch (1906), who estimated the subtidal density of *T. rubra* from Blue Hill Bay as 10 times greater than *T. marmorea*. Glynn (1970) found the maximum density for *Acanthopleura* to be 17 individuals/m$^2$ and 30 individuals/m$^2$ for *Chiton* sp. These two tropical species are substantially larger in size than *T. rubra*, *T. marmorea*, or *I. albus*. Glynn (1970) reported seasonal variations in chiton density due to predation and other causes of mortality. *T. rubra*, *T. marmorea*, and *I. albus* have also shown seasonal variations in density for similar reasons. Boyle (1970) found chiton densities of 228 individuals/m$^2$ in the low littoral of New Zealand. Greenfield (1972) found that densities of *Acanthopleura* sp. in the littoral of Tanzania rarely exceeded 10 individuals/m$^2$. It is difficult to draw any valid comparisons between the chiton densities presented in the literature and those presented for *T. rubra*, *T. marmorea*, and *I. albus* in Figs. 9 and 10. The reasons include the following: (1) the former represent intertidal forms; (2) they are of generally larger size; and (3) they are influenced by a different set of physical and biological factors than the subtidal forms studied here.

The substantial difference in population density between Deep Cove, 600 individuals/m$^2$, and Cape Neddick, less than 70 individuals/m$^2$, appears to be the result of predation. In spite of a higher diversity of predators at Deep Cove, the greater predator density and the longer duration (temporal) of seasonal predation at Cape Neddick results in more intense predation pressure on chitons at Cape Neddick (Table 3).

Several types of nonparasitic associations involving chitons have been reported in the literature. Many of these have dealt with animals occurring on the ventral surface and pallial groove (Holleman and Hand, 1962; Brattegard, 1968; Glynn, 1968; Helfman, 1968; Webster, 1968; Vader, 1972). No such non-parasitic associations were found for the three chiton species. However, several obvious cases of parasitism were observed. (1) A poorly preserved, worm-like parasite was found burrowed between two shells of a _T. rubra_. It caused significant tissue damage and malformation of the adjacent shell plates. (2) Internal parasites were obtained from _I. albus_. (3) Small bore holes were occasionally found in the shell plates of all species.

A diversity of organisms has been reported encrusting on chiton shell plates. Arey and Crozier (1919) suggested that serpulid and barnacle encrustations altered the photonegative behavior of _Chiton_. Bryozoans were reported on chiton shell plates by Adegoke (1967). Boring fauna have been reported to weaken chiton shell plates (Tucker and Giese, 1959; Bullock and Boss, 1971). MacGinitie and MacGinitie (1968) described a method by which _Cryptochiton stelleri_ rids its mantle tissue of settling organisms by using 1 mm spicules and mucous secretion on the dorsal surface.

The types of encrusting organisms, their frequencies of occurrence, and distribution on the dorsal surface of the chitons differed for each species of chiton. These data suggested differences in behavior and microhabitats among the chitons.

The dominant species of encrusting organisms found on the chiton shell plates reflected the dominant encrusting fauna and flora at either Deep Cove or Cape Neddick (Table 8). The predominant encrusting phyla found on *T. rubra* at Deep Cove and Cape Neddick were forms most frequently found on the undersides of rocks. Those forms, predominant on *T. marmorea*, were common on the sides and upper surfaces of rocks. *I. albus* had an algal form most commonly found on upper rock surfaces. *T. rubra* frequented the undersides of rocks and therefore had the characteristic encrusting forms, e.g., ectoprocts and serpulids, of that microhabitat. *T. marmorea* predominated on the sides of rocks covered with hydroids and was encrusted with them. *I. albus* was most often found on upper rock surfaces. Its presence in this position would account for the occurrence of green algae which has a high light requirement. Further support of this horizontal stratification by the chiton species is presented in the Feeding Biology section.

The reasons for the highest frequency of encrustation among the *Tonicella* populations occurring above 7.5 meters (Table 9) are not clear; however, they may involve several factors, including population structure patterns at different depths and physical factors like cobble size. The former would influence the encrustation frequency if a significant age (size) difference existed between depth intervals, e.g., older chitons would have a longer exposure to encrusting organisms than younger chitons. However, the deep water chiton populations are smaller and therefore, most probably, are of a younger age.

Cobble size might be the more significant factor, assuming equal distribution of the larval stages of encrusting forms. Since there is less cobble and it is smaller in deeper water, less substrate would be available to settling larvae, hence the greater frequency of encrustation on an alternative hard substrate -- the chiton shell plates.

The lower frequency of encrusted forms on the anterior shell plate of T. rubra at Deep Cove (Table 10) was brought about not by selective settling of the encrusting organisms, but perhaps by abrasion. Theoretically, the abrasion was the result of this chiton's frequent burrowing through the substrate and/or by dorsal contact with opposing rock surfaces while frequenting the undersides or crevices of rocks. This condition would occur more frequently at Deep Cove because of the smaller cobble size and greater proportion of semi-soft substrate than at Cape Neddick, where substantially larger cobble size would lead to less frequent contact with semi-soft substrate.

These observations and suppositions lend support to the foregoing microhabitat discussion and gain support in the Feeding Biology section.

By contrast, the distribution pattern characterized by the highest density of encrusting organisms occurring on the central plates of *T. marmorea* at Deep Cove and Cape Neddick and on *T. rubra* at Cape Neddick suggests a preference by larval encrusting forms for settling on higher projections. Possibly planktonic feeding organisms like hydroids would settle on higher projections, e.g., central shell plates, to facilitate successful feeding.

Finally, all chiton populations at Deep Cove had a substantially higher percent of total encrustation than at Cape Neddick (Table 11). This could be attributed to the higher chiton population density at Deep Cove and to differences in community composition at the species level.

The reports of morphological variations in chiton shell plate numbers are not uncommon in the literature. Over 35 authors have reported such variations from diverse geographic locations. These have been partially summarized by Taki (1932), Fischer-Piette and Franc (1960), and Burghardt and Burghardt (1969). Blaney (1904), according to Taki (1932), reported a 6-plated *T. rubra*. However, I found no mention of this specimen in Blaney's (1904) original paper.

The role of severity of the environment in causing morphological variations among the chitons was considered. Logically, if the variants were influenced by surf-related factors, then there would be a greater frequency of occurrence at Cape Neddick and in the shallowest water. The occurrence of the morphological variants (percent of the population) was less frequent at the more severe Cape Neddick site than at Deep Cove (Tables 12 and 13). In addition, the occurrence of variants showed no relationship to depth at Deep Cove (Table 14). This indicates an unlikely relationship between the variants and surf-related physical severity.

The variants did show the greatest percent frequency at the levels of largest population concentration (Table 14). If the variant forms were random genetic mutants, then it logically follows that they are most frequent where the population density is greatest. However, the survival of the mutants may have been selected against at the more severe site, Cape Neddick, and therefore this would reduce their appearance in the samples. No explanation can be attached to the following: (1) occurrence of 7 1/2- and 6-plated individuals at Deep Cove and their conspicuous absence from Cape Neddick, (2) predominance of one type of morphological variation over another, (3) higher frequency of occurrence of variant specimens in one species of chiton as opposed to another, and (4) conspicuous absence of any 9-plated individuals among these three species of chitons.

This study is the first report of morphological variations among _T_. _marmorea_ and _I_. _albus_ and substantiates the occurrence of morphological variants for _T_. _rubra_. This study also includes statistical analysis and a comparison of their frequency of occurrence.

The study of chiton behavior has oriented principally around light-related activity patterns. Photonegative behavior is documented for many chitons (Heath, 1899; Crozier and Arey, 1918; Hoffman, 1930; Evans, 1951; Douglas, 1952; Matthews, 1953; Christiansen, 1954; Giese, Tucker and Boolootian, 1959; Glynn, 1970). The most thorough investigation of photic sensitivity and other taxes was conducted by Evans (1951) on _Lepidochitona_ _cinereus_.

A weak photonegative behavior was evident in _T_. _rubra_, _T_. _marmorea_, and _I_. _albus_. During diurnal hours, the chitons were inactive and occupied a zone of low light intensity. The chitons do frequent upper rock surfaces when such surfaces are covered with silty mud or during inclement weather when light intensity is low. The active behavior displayed during the nocturnal hours further supports a nocturnal behavior pattern. Steneck and Vadas (personal communication) have also observed these chitons on corallines at night.

Unlike the two activity peaks per night described for tropical chitons by Glynn (1970), only one nocturnal peak was evident for _T_. _rubra_, _T_. _marmorea_, and _I_. _albus_. Arey and Crozier (1919) reported that older chitons had less intense photonegative behavior. This phenomenon may be due to erosion of the shell plates along with the embedded photoreceptors, or it may be due to reduced light penetration caused by a covering of encrusting organisms. Representatives of the three chitons were observed on upper rock surfaces during diurnal hours. This behavior could not be attributed to a particular age group or to the presence of encrusting fauna on the shell plates.

Aggressive interspecific behavior was reported for the intertidal limpet Lottia gigantea by Stimson (1970). No territorial behavior has been documented for chitons. Among the three species studied, the chitons were frequently observed to contact and crawl over each other with no apparent change in behavior.

In view of the homescar observations and their implication of homing behavior, territoriality should be investigated.

Homing is a complex behavioral pattern which is characteristic of a variety of intertidal molluscs and is reported to occur among a few chitons (Arey and Crozier, 1919; Johns, 1960; Thorne, 1968). Essentially, homing behavior consists of a single home position or depression from which an animal leaves to forage and to which it consistently returns during periods of non-activity. The physical and/or chemical methods by which a chiton reorients to its home are reviewed by Thorne (1968).

A logical concern about homing behavior was the lack of home depressions at Deep Cove and adjacent northern sites. Two considerations may in part be responsible for this condition. First, the high density of chitons and possibly selective predation may have masked or locally suppressed this behavior. Since most chitons generally frequent the undersides of hard rocks (igneous) where no calcareous algae is present, home depressions cannot easily be recognized. The second consideration involves the degree of exposure and impact of storms on the environment. At sites where home depressions were observed, occasional severe storms reorganize and upset the shallow subtidal rock substrate. The upset of the rock substrate allows for the establishment of "homes" by chitons on bare rock. The bare rock surrounding the chitons is subquently colonized by calcareous algae and thus results in home depressions. Home depressions are not evident on old well-established calcareous algae on immovable rock walls at Cape Neddick. In addition, Deep Cove and the northern adjacent sites are not subjected to storms of sufficient force to reorganize or upset the subtidal rock substrate. Hence, the calcareous algae covering the rocks at Deep Cove and adjacent sites is old and well-established. New bare rock situations and the potential home depressions are not present at these sites. This discussion is speculative, and further work in this area is needed.

## Summary

1. This study describes and compares the ecology and habitats of three species of chitons, *T. rubra*, *T. marmorea*, and *I. albus*, from two widely-separated sites in the Gulf of Maine. These chitons commonly frequent calcareous algal-covered rock substrates in the subtidal zone of Deep Cove and Cape Neddick. Physically, Deep Cove was characterized by having strong current action; in contrast, Cape Neddick often featured surf-related physical stress.

   The two species of *Tonicella* showed cryptic coloration when found on calcareous algae. The three species of chitons also occupied isolated, hard substrates free of calcareous algae and were found under silty mud in contact with rocks. Occasionally, these species utilized crevices or galleries as microhabitats in the thickened calcareous algae.

2. A comparison of the two communities revealed a major difference in algal cover. The limited macroscopic algal composition at Deep Cove is the result of reduced light and grazing by the herbivorous sea urchin *Strongylocentrotus droebachiensis*. Chitons were not found to influence the subtidal algal composition of either community. The flora and fauna showed seasonal variations in occurrence, composition, and density.

3. The lower physical extremes of temperature and salin-

ity were greater than reported in the literature, but laboratory studies showed that the extremes did not reach the absolute tolerance limits of these chitons. The effects of rigorous water movements were not fully determined.

4. The three species of chitons are primarily limited to the subtidal zone. The absence of significant populations of intertidal chitons is postulated to be the result of exposure to temperature extremes encountered during the summer and winter in conjunction with spring tides.
5. The major fish, echinoderm, and arthropod predators were identified and their spatial and temporal distributions recorded for Deep Cove and Cape Neddick. The winter flounder and the asteroid <u>Leptasterias littoralis</u> shaped the subtidal size distribution pattern and the species distribution pattern of the three chiton species at Deep Cove. At Cape Neddick the key chiton predator was the cunner <u>Tautogolabrus adspersus</u>. Its absence from Deep Cove is the most conspicuous difference between the two sites and is postulated to account for the great difference in chiton density.
6. Analysis of the chiton population by species revealed the numerical dominance of <u>T</u>. <u>rubra</u> $>$ <u>T</u>. <u>marmorea</u> $>$ <u>I</u>. <u>albus</u> at Deep Cove and <u>T</u>. <u>rubra</u> $>$ <u>T</u>. <u>marmorea</u> at Cape Neddick.
7. Bathymetric patterns of species occurrence were pre-

sented for each specific population at Deep Cove. The key findings were that _T. rubra_ was the dominant species to 7.5 meters, and its percent composition of the population declined with increasing depth. _T. marmorea_ rose with increasing depth and became the dominant species below 7.5 meters. _I. albus_ was most significant at 7.5 meters and decreased with changes in water depth.

8. Monthly sampling established that seasonal stability of the bathymetric patterns of species distribution occurred for the chitons to the 9 meter depth interval.
9. The size relationship among the species _T. marmorea_ > _T. rubra_ > _I. albus_ was established. The mean size of the chitons decreases with increasing depth.
10. Sexual dimorphism in size was not found for any of the three species of chitons.
11. A comparison of sites revealed a significantly lower chiton density at Cape Neddick. This was attributed to the limited geographical distribution of a major chiton predator _Tautogolabrus adspersus_ and the much lower spatial and probably temporal occurrence of chiton predators at Deep Cove.
12. Slight seasonal adjustments in chiton density were attributed to (1) changes in the seasonal carrying capacity of the environment and (2) seasonal recruitment of young chitons into the population.
13. A study was conducted on the type and distribution of

the encrusting organisms found on the dorsal surface of the chitons. The flora and fauna found encrusted on the chitons differed both among the individual chiton species and between sites. The types of encrusting organisms and their distribution within the habitat revealed differences in the microhabitats frequented by the three species of chitons. The percent frequency of encrustation among the chitons was, from the highest to the lowest, *T. rubra*, *T. marmorea*, and *I. albus*.

14. Two or more types of morphological variations in shell plate number (6, 7, 7 1/2) were recorded for each species of chiton. The frequency and distribution of the variations appeared to be unrelated to physical (surf-related) severity of the environment. The frequency of distribution of the variants among the chiton species was *T. rubra*> *T. marmorea*> *I. albus*.
15. The three species of chitons demonstrated a weak photonegative behavior.
16. During diurnal hours, the chitons most commonly frequented vertical faces and undersides of rocks but also utilized a variety of microhabitats within the crevices and galleries of the calcareous algae.
17. Observations and experiments were conducted which showed that adult chitons were capable of migrating across silty mud zones to populate isolated hard substrates.

18. Evidence was presented suggesting that homing behavior occurred in both species of *Tonicella*.

# FEEDING BIOLOGY

## Introduction

Classically, chitons have been described as herbivorous scrapers, but an increasing amount of literature suggests that some are omnivorous or seasonally carnivorous. MacGinitie and MacGinitie (1949), Fischer-Piette and Franc (1960), and Hyman (1967) summarized the polyplacophoran diet as herbivorous, based on the early observations of Heath (1899; 1903; 1907), Milligan (1916), Arey and Crozier (1919), Crozier (1921), Simroth and Hoffman (1929), and Fretter (1937). Subsequent authors (Barnawell, 1960; McLean, 1962a; Arakawa, 1963; Boolootian, 1964; Thorne, 1968; Craig *et al*., 1969; Glynn, 1970; Barnes, 1972; Greenfield, 1972) have verified these results, particularly for intertidal chitons, and identified the algal contents of several species of chitons as belonging to the phyla Cyanophyceae, Chrysophyceae, Chlorophyceae, Rhodophyceae, and Phaeophyceae.

Carnivorous habits have been reported predominantly among subtidal chitons. The presence of foraminiferans was reported in stomach contents from *I. albus* by Yakovleva (1952) and in other chitons (Christiansen, 1954; Kues, 1974). Plate (1901) found sponge spicules in the stomach contents of a chiton. Others (von Siegfried, 1954; Barnawell, 1960; McLean, 1962a; Kues, 1974) confirmed chiton predation on sponges. Mestayer (1920) recorded chiton predation on gastropod egg masses. Chitons have been found to eat arthropods (Barnawell, 1960; McLean, 1962a; Boolootian, 1964), molluscs (Barnawell, 1960; Boolootian, 1964), annelids (Barnawell, 1960; McLean, 1962a), hydroids (Barnawell, 1960), and bryozoans (Giese *et al*., 1959).

This section is a study of the feeding biology of *T. rubra*, *T. marmorea*, and *I. albus*. The elements include (1) an analysis of diet composition for each species of chiton; (2) the influence of depth and season on diet; (3) an intraspecific comparison of diet at two study sites; and (4) an interspecific comparison of diet among the three species of chitons.

## Materials and Methods

A general description of the sampling, preservation, and digestive tract separation techniques was presented earlier. Specifically, microscopic scanning of wet-mount slide preparations was conducted on stomach and intestinal contents. Identification and records were made for prey species found in each chiton digestive tract. Following the method used by Barnawell (1960), subjective estimations were made of the percent volumes of algal and animal material present. After pooling the data for analysis, statistical evaluation of percentages, as described in Sokal and Rohlf (1969), was used to compare differences between percentages and to adjust for variability in sample size. The confidence level of statistical significance was 95%.

## Results

### Intraspecific Diet Analysis

Diet analysis was based on examination of 2518 digestive tracts from T. rubra, T. marmorea, and I. albus (Table 15). The difference in the proportion of chitons lacking gut contents from the two sites was not significant.

A list of chiton prey species is presented in Table 16. It has not been determined whether nematodes found in the gut were prey or intestinal parasites. Among the protozoans found in chiton diets, foraminiferans outnumbered sessile ciliates. Identification of sponges of the genus Halisarca as prey was not based on gut contents. Since these sponges lack spicules, identification was based on repeated field observations in which chitons were found in contact with this, as well as other, species of sponges.

The sizes of calcareous sponge spicules and complete algal filaments in the chiton gut indicate occasional ingestion of young organisms. The Chlorophyceae, Rhodophyceae, and Phaeophyceae found in chitons were almost exclusively of filamentous construction; whereas the

Table 15. Chiton digestive tracts examined and their state.

| | Deep Cove | Cape Neddick |
|---|---|---|
| *Tonicella rubra* | 937 examined<br>29 empty (3 %)<br>908 w/ identifiable contents (97 %) | 494 examined<br>28 empty (6 %)<br>466 w/ identifiable contents (94 %) |
| *Tonicella marmorea* | 595 examined<br>15 empty (3 %)<br>580 w/ identifiable contents (97 %) | 223 examined<br>13 empty (6 %)<br>210 w/ identifiable contents (94 %) |
| *Ischnochiton albus* | 269 examined<br>5 empty (2 %)<br>264 w/ identifiable contents (98 %) | |

Table 16. Occurrence of chiton prey.

| | Deep Cove | | | Cape Neddick | |
|---|---|---|---|---|---|
| Prey Species | *T. rubra* | *T. marmorea* | *I. albus* | *T. rubra* | *T. marmorea* |
| Protozoa | | | | | |
| *Follicullina* sp. | + | + | + | + | + |
| *Zoothamnium* sp. | + | + | + | + | + |
| Unid. Tintinnid | + | + | + | + | + |
| Unid. Suctorian | + | + | + | + | + |
| Unid. Foraminiferan ssp. | + | + | + | + | + |
| Porifera * | + | + | + | + | + |
| Calcispongiae | | | | | |
| *Clathrina coriacea* | | | | | |
| *Leucosolenia botryoides* | | | | | |
| Demospongiae | | | | | |
| *Halichondria panicea* | | | | | |
| *Haliclona oculata* | | | | | |
| *Halisarca* sp. | | | | | |
| *Microciona prolifera* | | | | | |
| *Pellina sitiens* | | | | | |
| Cnidaria | | | | | |
| Hydrozoa | | | | | |
| *Sertularella* sp. | - | + | - | - | - |
| *Thuiaria* sp. | - | - | - | + | - |
| Unid. Campanularid sp. | + | + | + | + | + |
| Anthozoa | | | | | |
| *Gersemia rubiformis* | - | +(?) | - | - | - |

Table 16 (continued).

| | Deep Cove | | | Cape Neddick | |
|---|---|---|---|---|---|
| Prey Species | *T. rubra* | *T. marmorea* | *I. albus* | *T. rubra* | *T. marmorea* |
| Nematoda | + | + | + | + | + |
| Mollusca | | | | | |
| Bivalvia | + | + | + | + | + |
| *Hiatella arctica* | | | | | |
| Mytilidae | | | | | |
| Gastropoda | - | +(?) | - | + | - |
| Rotifera | | | | | |
| *Lepadella* sp. | + | - | - | - | - |
| Unid. sp. | + | + | + | + | + |
| Kinorhyncha | | | | | |
| *Echinoderes* sp. | + | - | - | - | - |
| Unid. sp. | - | + | - | - | - |
| Arthropoda | | | | | |
| Ostracoda | | | | | |
| *Loxoconcha* sp. | - | - | - | - | + |
| Unid. ssp. | + | + | + | + | + |
| Harpacticoid Copepoda | - | + | - | - | + |
| Amphipoda | - | - | - | - | + |
| Unid. Larval Arthropod | + | + | + | + | + |
| Unid. Arthropod Appendages | + | + | + | + | + |

Table 16 (continued).

| | Deep Cove | | | Cape Neddick | |
|---|---|---|---|---|---|
| Prey Species | *T. rubra* | *T. marmorea* | *I. albus* | *T. rubra* | *T. marmorea* |
| Annelida | | | | | |
| Polychaete Setae | + | + | + | + | - |
| Ectoprocta | - | - | +(?) | - | +(?) |
| Trochophore Larva | + | - | - | - | - |
| Chlorophyceae | | | | | |
| *Ulva lactuca* | - | - | - | + | - |
| Unid. Filamentous ssp. | + | + | + | + | + |
| Rhodophyceae | | | | | |
| *Callithamnion* sp. | - | - | - | - | + |
| *Erythrotrichia carnea* | - | - | - | - | + |
| *Rhododermis elegans* | + | + | - | - | - |
| Unid. Filamentous ssp. | + | + | + | + | + |
| Phaeophyceae | | | | | |
| *Ectocarpus* sp. | - | - | - | + | + |
| Unid. Filamentous ssp. | + | + | + | + | + |
| Chrysophyceae ** | + | + | + | + | + |
| *Achnanthes longipes* | | | | | |
| *Biddulphia aurita* | | | | | |
| *Coscinodiscus* sp. | | | | | |

Table 16 (continued).

| | Deep Cove | | | Cape Neddick | |
|---|---|---|---|---|---|
| Prey Species | *T. rubra* | *T. marmorea* | *I. albus* | *T. rubra* | *T. marmorea* |
| Chrysophyceae (continued) | | | | | |
| *Fragillaria* sp. | | | | | |
| *Grammatophora marina* | | | | | |
| *Gyrosigma* sp. | | | | | |
| *Isthmia* sp. | | | | | |
| *Licmophora abbreviata* | | | | | |
| *Navicula* sp. | | | | | |
| *Nitzschia longissima* | | | | | |
| *N. seriata* | | | | | |
| *N. reversa* | | | | | |
| *Rhabdonema adriaticum* | | | | | |
| *Rhizosolenia hebetata* | | | | | |
| *R. setigera* | | | | | |
| *Schroderella delicatula* | | | | | |
| *Striatella unipunctata* | | | | | |
| *Surirella* sp. | | | | | |
| *Thalassionema nitzschioides* | | | | | |
| *Thalassiosira gravida* | | | | | |
| *T. nana* | | | | | |
| *Thalassiothrix longissima* | | | | | |

* Prey identification based on spicules and recorded at phylum level.

**Prey recorded at phylum level.

Chrysophyceae, or diatoms, were primarily solitary species. Diatom tests occurring in the gut were usually devoid of contents or were broken with contents partially intact. This seems to indicate digestion of diatoms by chitons.

The presence of carbonate compounds in the gut was determined by use of hydrochloric acid. Several possible sources were foraminiferan tests, calcareous sponge spicules, serpulid tubes, ectoproct skeletons, and calcareous algae (Lithothamnium, Lithophyllum, and Clathromorphum). There is no evidence to indicate that calcareous (coralline) algae were a food source, but some ingestion may have occurred during rasping of epiphytes and epifauna. Based on the large volumes of detritus ingested by the three species of chitons, the feasibility of bacteria as a food source exists. However, the methods employed in this study did not allow for investigation of this possibility.

Tonicella rubra, Deep Cove. In order of decreasing occurrence, the Chrysophyceae, Porifera, and Protozoa constituted the major portion of the chiton diet (Table 17). The remaining portion of the diet was comprised of ten phyla. This diversity of prey was indicative of a grazing omnivore.

While the three major diet components showed some seasonal variability (Table 18), the greatest change occurred in terms of total prey diversity (Fig. 15). The timing of these variations appeared to correspond to seasonal availability of prey.

Table 17. Frequency of occurrence of prey phyla in chiton digestive tracts from Deep Cove.

| Prey Phyla | *T. rubra* | $P \leq 0.05$* | *T. marmorea* | $P \leq 0.05$ | *I. albus* | $P \leq 0.05$ |
|---|---|---|---|---|---|---|
| Porifera | 38.6 % | + | 55.3 % | + | 33.7 % | + |
| Protozoa | 14.8 % | + | 24.7 % | + | 28.8 % | + |
| Arthropoda | 1.7 % | + | 4.1 % | + | 15.9 % | + |
| Nematoda | 1.7 % | + | 4.3 % | + | 2.7 % | - |
| Mollusca | 0.4 % | - | 0.7 % | - | 0.8 % | + |
| Rotifera | 0.1 % | + | 0.5 % | + | 1.9 % | + |
| Cnidaria | 0.3 % | + | 0.5 % | + | 0.4 % | - |
| Kinorhyncha | 0.1 % | - | 0.2 % | + | 0.0 % | + |
| Annelida | 0.2 % | - | 0.2 % | - | 0.0 % | - |
| Ectoprocta | 0.0 % | - | 0.0 % | + | 0.4 % | + |
| | | | | | | |
| Chrysophyceae | 79.5 % | + | 85.5 % | + | 86.7 % | + |
| Phaeophyceae | 2.5 % | + | 4.0 % | - | 3.8 % | + |
| Chlorophyceae | 1.5 % | + | 2.4 % | + | 3.8 % | + |
| Rhodophyceae | 2.8 % | + | 2.0 % | - | 1.1 % | + |
| Unid. Algae | 0.1 % | - | 0.3 % | - | 0.4 % | - |

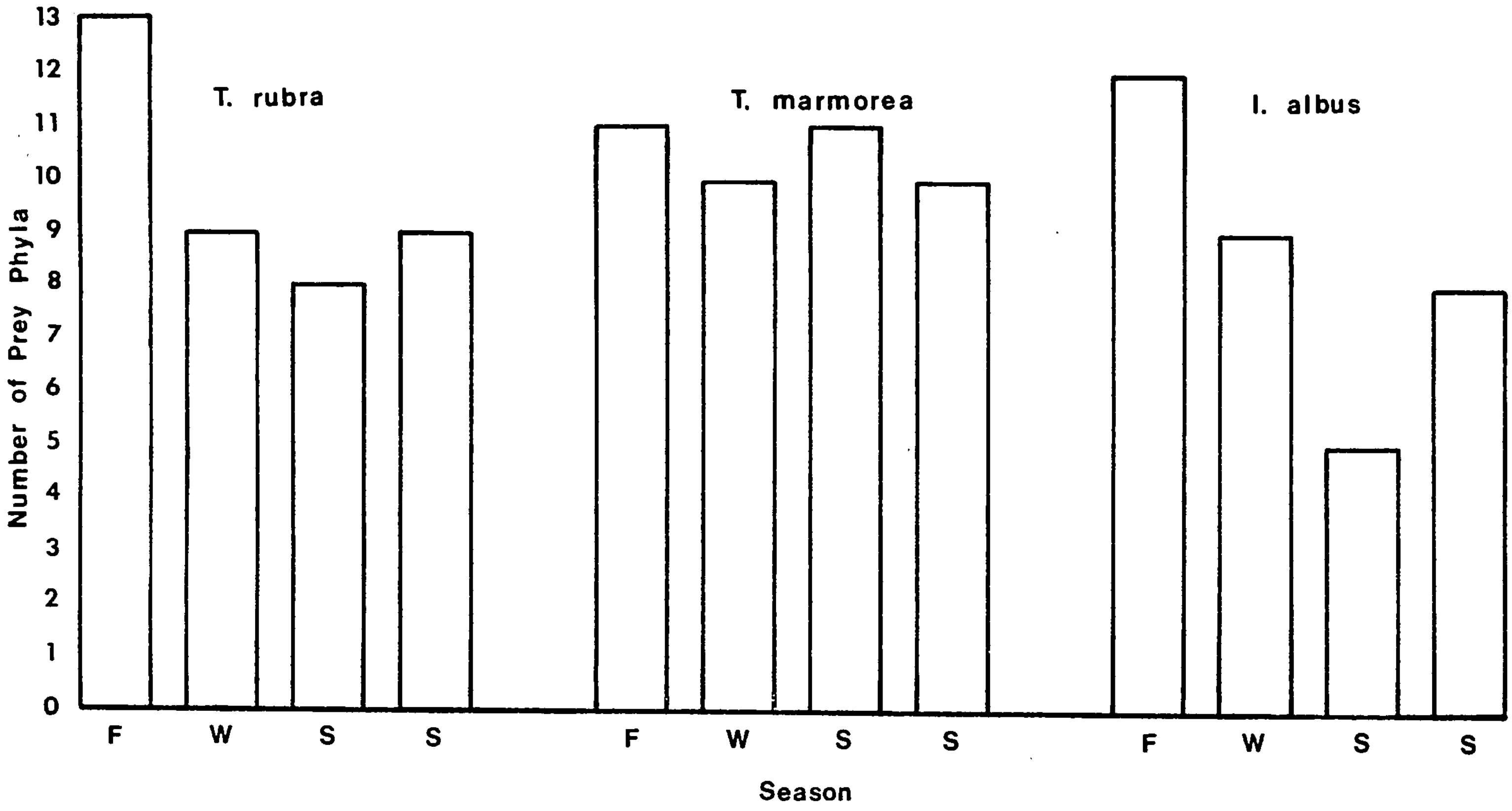
* Significant at 95 % level (+); Nonsignificant at 95 % level (-).

Table 18. <u>Tonicella</u> <u>rubra</u>: Frequency of occurrence of prey phyla by season (Deep Cove).

| Prey Phyla | Spring | P≤ 0.05 | Summer | P≤ 0.05 | Fall | P≤ 0.05 | Winter | P≤ 0.05 |
|---|---|---|---|---|---|---|---|---|
| Porifera | 23.8 % | + | 25.2 % | + | 50.3 % | - | 47.0 % | + |
| Protozoa | 6.7 % | + | 10.2 % | + | 19.1 % | + | 13.2 % | - |
| Arthropoda | 1.1 % | + | 1.5 % | - | 1.7 % | + | 2.6 % | + |
| Nematoda | 0.0 % | + | 1.0 % | + | 2.4 % | - | 2.1 % | + |
| Mollusca | 0.0 % | + | 1.0 % | - | 0.7 % | - | 0.4 % | + |
| Rotifera | 0.0 % | - | 0.0 % | + | 0.4 % | + | 0.0 % | - |
| Cnidaria | 1.1 % | + | 0.0 % | + | 0.4 % | + | 0.0 % | - |
| Kinorhyncha | 0.0 % | - | 0.0 % | + | 0.4 % | + | 0.0 % | - |
| Annelida | 0.0 % | - | 0.0 % | + | 0.4 % | + | 0.0 % | - |
| | | | | | | | | |
| Chrysophyceae | 77.2 % | - | 77.7 % | - | 77.8 % | + | 83.3 % | + |
| Phaeophyceae | 1.7 % | + | 3.9 % | + | 1.7 % | + | 3.0 % | + |
| Chlorophyceae | 2.8 % | + | 1.9 % | + | 0.4 % | + | 1.7 % | + |
| Rhodophyceae | 0.6 % | + | 4.9 % | + | 3.8 % | + | 1.7 % | + |
| Unid. Algae | 0.0 % | - | 0.0 % | + | 0.4 % | + | 0.0 % | - |

Figure 15. Numerical diversity of prey phyla in the chiton diets by season (Deep Cove).

Figure 15.


T. rubra
T. marmorea
I. albus
Number of Prey Phyla
0
1
2
3
4
5
6
7
8
9
10
11
12
13
F
W
S
S
F
W
S
S
F
W
S
S
Season

Increasing depth showed no clear cut influence on the diet of T. rubra (Table 19). Diatoms decreased slightly, while Protozoa increased with increases in depth. The marked variation in diet at mean low water is insignificant due to low sampling density.

The total volume ingested by T. rubra was divided among three components: algae, animal material, and detritus. Detritus is the fraction not identifiable as algae or animal matter and often containing silicate grains, coal, and radular teeth. The coal is not endemic to the region. Its source is spillage from cargo ships at a time when coal was imported during the early twentieth century. The percent volume of algae ingested far exceeded the animal component, establishing a herbivorous habit for the omnivorous T. rubra (Table 20).

The algal, animal, and detrital components showed volumetric variations reflecting seasonal abundance. Fluctuations in the volume of algae ingested paralleled the seasons of high and low abundance (Table 21). The volume of animal material consumed remained low, except during fall (Table 22).

The volumetric relationships of the algal and animal components are presented by depth interval in Tables 23 and 24. The only significant fluctuation in the algal component of the diet occurred above 6 meters, while the animal component was not influenced by depth. The reason for the fluctuation in algae is not clear but may be re-

Table 19. <u>Tonicella rubra</u>: Frequency of occurrence of prey phyla by depth interval (Deep Cove).

| | Depth in meters | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Prey Phyla | MLW * | 1.5 | 3.0 | 4.5 | 6.0 | 7.5 | 9.0 | 10.5 |
| Porifera | 33.0 % | 58.3 % | 28.8 % | 37.9 % | 32.1 % | 41.8 % | 30.0 % | 39.3 % |
| Protozoa | 0.0 % | 19.0 % | 8.6 % | 7.9 % | 10.4 % | 19.4 % | 24.0 % | 19.6 % |
| Arthropoda | 0.0 % | 3.6 % | 0.9 % | 1.1 % | 3.0 % | 1.0 % | 0.0 % | 0.0 % |
| Nematoda | 33.0 % | 3.0 % | 0.9 % | 1.1 % | 1.5 % | 0.0 % | 2.0 % | 0.0 % |
| Mollusca | 0.0 % | 1.2 % | 1.4 % | 0.0 % | 0.0 % | 2.0 % | 0.0 % | 0.0 % |
| Rotifera | 0.0 % | 0.0 % | 0.0 % | 0.0 % | 0.0 % | 0.0 % | 2.0 % | 3.6 % |
| Cnidaria | 0.0 % | 1.2 % | 0.0 % | 0.0 % | 0.0 % | 1.0 % | 0.0 % | 1.8 % |
| Kinorhyncha | 0.0 % | 0.0 % | 0.0 % | 0.0 % | 0.0 % | 0.0 % | 2.0 % | 0.0 % |
| Annelida | 0.0 % | 0.6 % | 0.0 % | 0.0 % | 0.0 % | 1.0 % | 0.0 % | 0.0 % |
| | | | | | | | | |
| Chrysophyceae | 100.0 % | 92.3 % | 77.9 % | 83.1 % | 71.0 % | 79.6 % | 74.0 % | 60.7 % |
| Phaeophyceae | 33.0 % | 6.0 % | 1.8 % | 1.1 % | 3.0 % | 2.0 % | 0.0 % | 0.0 % |
| Chlorophyceae | 0.0 % | 1.8 % | 0.9 % | 2.8 % | 0.7 % | 2.0 % | 2.0 % | 0.0 % |
| Rhodophyceae | 33.0 % | 4.8 % | 3.2 % | 2.8 % | 0.7 % | 3.1 % | 0.0 % | 1.8 % |
| Unid. Algae | 0.0 % | 0.0 % | 0.5 % | 0.0 % | 0.0 % | 0.0 % | 0.0 % | 0.0 % |

* Insignificant due to low sampling density.

Table 20. Percent volumes of algal and/or animal material in the chiton diets (Deep Cove).

| Food Material | *T. rubra* | $P \leq 0.05$* | *T. marmorea* | $P \leq 0.05$ | *I. albus* | $P \leq 0.05$ |
|---|---|---|---|---|---|---|
| Algae | 7.2 % | + | 16.2 % | - | 13.6 % | + |
| | + | | + | | - | |
| Animal | 2.3 % | + | 5.1 % | + | 10.7 % | + |
| Algae and Animal | 9.5 % | + | 21.3 % | - | 24.3 % | + |
| Detrital Component | 90.5 % | + | 78.7 % | - | 75.6 % | + |

* Significant at 95 % level (+); Nonsignificant at 95 % level (-).

Table 21. Estimated percent volumes of algae in the chiton diets by season (Deep Cove).

| Season | *T. rubra* | P≤ 0.05 | *T. marmorea* | P≤ 0.05 | *I. albus* | P≤ 0.05 |
|---|---|---|---|---|---|---|
| Spring | 5.3 % | + | 11.7 % | - | 13.2 % | + |
| | + | | + | | - | |
| Summer | 8.3 % | + | 17.4 % | - | 15.8 % | + |
| | - | | - | | - | |
| Fall | 8.3 % | + | 17.3 % | - | 17.3 % | + |
| | + | | + | | + | |
| Winter | 6.3 % | - | 6.8 % | + | 9.6 % | + |
| | - | | + | | + | |

Table 22. Estimated percent volumes of animal material in the chiton diets by season (Deep Cove).

| Season | *T. rubra* | $P \leq 0.05$ | *T. marmorea* | $P \leq 0.05$ | *I. albus* | $P \leq 0.05$ |
|---|---|---|---|---|---|---|
| Spring | 1.5 % | + | 3.3 % | + | 10.0 % | + |
| | - | | - | | + | |
| Summer | 1.6 % | + | 4.5 % | - | 5.7 % | + |
| | + | | + | | + | |
| Fall | 3.8 % | + | 9.0 % | + | 17.3 % | + |
| | + | | + | | + | |
| Winter | 1.9 % | + | 4.1 % | + | 11.0 % | + |
| | - | | - | | - | |

Table 23. Estimated percent volumes of algae in the chiton diets by depth interval (Deep Cove).

| Depth in meters | *T. rubra* | $P \leq 0.05$ | *T. marmorea* | $P \leq 0.05$ | *I. albus* | $P \leq 0.05$ |
|---|---|---|---|---|---|---|
| MLW | 43.3 % | - | 65.0 % | + | 5.0 % | + |
| | + | | + | | + | |
| 1.5 | 12.9 % | - | 12.5 % | + | 31.5 % | + |
| | + | | - | | - | |
| 3.0 | 5.0 % | + | 15.9 % | - | 18.1 % | + |
| | + | | - | | - | |
| 4.5 | 8.9 % | + | 12.8 % | - | 15.2 % | + |
| | + | | - | | - | |
| 6.0 | 4.9 % | + | 13.7 % | - | 15.0 % | + |
| | - | | - | | - | |
| 7.5 | 4.3 % | + | 16.2 % | + | 12.1 % | + |
| | - | | + | | - | |
| 9.0 | 4.8 % | + | 11.3 % | + | 11.1 % | + |
| | - | | + | | - | |
| 10.5 | 3.7 % | + | 7.9 % | - | 10.3 % | + |

Table 24. Estimated percent volumes of animal material in the chiton diets by depth interval (Deep Cove).

| Depth in meters | *T. rubra* | $P \leq 0.05$ | *T. marmorea* | $P \leq 0.05$ | *I. albus* | $P \leq 0.05$ |
|---|---|---|---|---|---|---|
| MLW | 1.7 % | - | 3.5 % | + | 75.0 % | + |
| | - | | - | | + | |
| 1.5 | 3.1 % | + | 6.2 % | + | 18.5 % | + |
| | + | | - | | - | |
| 3.0 | 1.5 % | + | 6.0 % | + | 13.3 % | + |
| | - | | - | | - | |
| 4.5 | 2.0 % | + | 4.4 % | + | 7.6 % | + |
| | - | | - | | - | |
| 6.0 | 2.4 % | + | 4.1 % | + | 8.4 % | + |
| | - | | - | | - | |
| 7.5 | 2.7 % | + | 5.4 % | + | 11.7 % | + |
| | - | | - | | - | |
| 9.0 | 3.9 % | - | 6.2 % | - | 9.7 % | + |
| | - | | - | | - | |
| 10.5 | 2.2 % | + | 4.8 % | + | 11.6 % | + |

lated to abundance and local current factors.

Tonicella rubra, Cape Neddick. The diet composition was essentially the same at both sites (Tables 17 and 25). The major difference being that Protozoa occurred more frequently than Porifera at Cape Neddick; whereas at Deep Cove, Porifera exceeded Protozoa.

The occurrence and the diversity of prey showed seasonal variations (Table 26 and Fig. 16). During winter and spring, sponges were eaten more frequently than protozoans; while during summer and fall, the situation was reversed. At Cape Neddick, T. rubra consumed more algae than animal material (Table 27). The herbivorous bias of T. rubra is evident at both Deep Cove and Cape Neddick.

Volumetric variations in the basic diet components showed seasonal fluctuations (Table 28). The variations of algae ingested reflected seasonal abundance, except during fall. This decline corresponded to rise in the animal material consumed, illustrating a change from a herbivorous habit to a carnivorous habit (Table 29).

In summation, the feeding habits of T. rubra from Deep Cove and Cape Neddick are similar and appear to depend on seasonal availability of food.

Tonicella marmorea, Deep Cove. The Chrysophyceae, Porifera, and Protozoa were the major prey of T. marmorea (Table 17). The wide diversity of prey was indicative of a grazing omnivore. While a seasonal variation in the frequency of occurrence of specific prey was evident

Table 25. Frequency of occurrence of prey phyla in chiton digestive tracts from Cape Neddick.

| Prey Phyla | *T. rubra* | $P \leq 0.05$* | *T. marmorea* |
|---|---|---|---|
| Protozoa | 43.9 % | + | 68.2 % |
| Porifera | 33.0 % | - | 36.2 % |
| Nematoda | 2.6 % | + | 6.7 % |
| Arthropoda | 3.0 % | + | 10.2 % |
| Mollusca | 3.4 % | - | 6.7 % |
| Rotifera | 0.9 % | + | 6.2 % |
| Cnidaria | 0.6 % | - | 1.4 % |
| Annelida | 0.2 % | - | 0.0 % |
| Ectoprocta | 0.0 % | - | 0.5 % |
| | | | |
| Chrysophyceae | 69.1 % | - | 75.2 % |
| Phaeophyceae | 5.6 % | + | 13.8 % |
| Chlorophyceae | 3.4 % | - | 5.7 % |
| Rhodophyceae | 2.4 % | - | 3.8 % |
| Unid. Algae | 3.2 % | - | 4.8 % |

* Significant at 95 % level (+); Nonsignificant at 95 % level(-).

Table 26. *Tonicella rubra*: Frequency of occurrence of prey phyla by season (Cape Neddick).

| Prey Phyla | Spring | $P \leq 0.05$ | Summer | $P \leq 0.05$ | Fall | $P \leq 0.05$ | Winter | $P \leq 0.05$ |
|---|---|---|---|---|---|---|---|---|
| Protozoa | 24.5 % | + | 52.4 % | + | 55.5 % | + | 43.2 % | + |
| Porifera | 25.4 % | + | 13.1 % | + | 38.5 % | + | 48.3 % | + |
| Nematoda | 0.8 % | + | 0.0 % | + | 4.7 % | - | 3.4 % | + |
| Arthropoda | 1.6 % | + | 7.2 % | + | 2.1 % | - | 2.6 % | - |
| Mollusca | 0.0 % | + | 2.4 % | + | 8.1 % | + | 1.7 % | + |
| Rotifera | 0.0 % | - | 0.0 % | + | 2.0 % | + | 0.9 % | + |
| Cnidaria | 0.0 % | - | 0.0 % | + | 0.7 % | + | 1.7 % | + |
| Annelida | 0.0 % | + | 1.2 % | + | 0.0 % | - | 0.0 % | - |
| | | | | | | | | |
| Chrysophyceae | 61.0 % | + | 79.8 % | + | 60.1 % | + | 81.0 % | + |
| Phaeophyceae | 4.2 % | - | 3.6 % | + | 8.8 % | + | 4.3 % | - |
| Chlorophyceae | 5.1 % | - | 7.1 % | + | 2.0 % | - | 0.7 % | + |
| Rhodophyceae | 0.0 % | + | 3.6 % | - | 4.7 % | + | 0.9 % | - |
| Unid. Algae | 0.0 % | + | 11.9 % | + | 3.4 % | + | 0.0 % | - |

Figure 16. Numerical diversity of prey phyla in the chiton diets by season (Cape Neddick).

Figure 16.

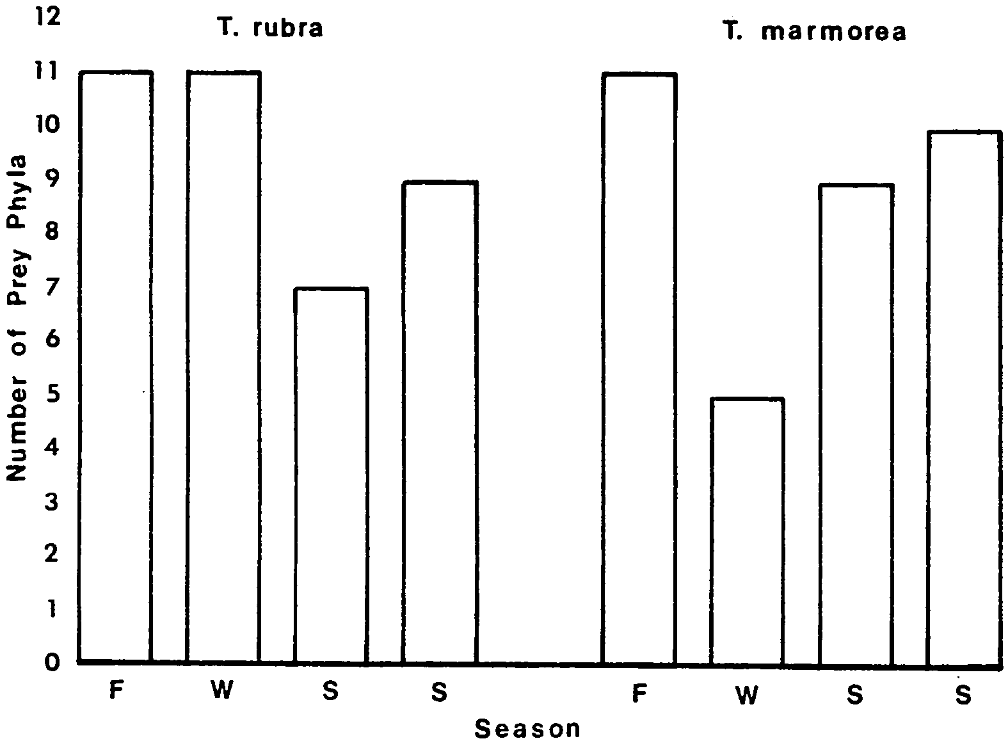

T. rubra
T. marmorea
Number of Prey Phyla
0
1
2
3
4
5
6
7
8
9
10
11
12
F
W
S
S
F
W
S
S
Season

Table 27. Percent volumes of algal and/or animal material in the chiton diets (Cape Neddick).

| Food Material | *T. rubra* | $P \leq 0.05$* | *T. marmorea* |
|---|---|---|---|
| Algae | 9.6 % | + | 11.8 % |
| | + | | + |
| Animal | 7.5 % | + | 15.4 % |
| Algae and Animal | 17.1 % | + | 27.2 % |
| Detrital Component | 82.8 % | + | 72.8 % |

* Significant at 95 % level (+).

Table 28. Estimated percent volumes of algae in the chiton diets by season (Cape Neddick).

| Season | *T. rubra* | $P \leq 0.05$ | *T. marmorea* |
|---|---|---|---|
| Spring | 4.7 % | + | 11.4 % |
| | + | | + |
| Summer | 19.9 % | - | 18.6 % |
| | + | | + |
| Fall | 6.6 % | + | 9.1 % |
| | + | | - |
| Winter | 10.9 % | - | 9.8 % |
| | + | | - |

Table 29. Estimated percent volumes of animal material in the chiton diets by season (Cape Neddick).

| Season | *T. rubra* | $P \leq 0.05$ | *T. marmorea* |
|---|---|---|---|
| Spring | 1.8 % | + | 8.1 % |
| | + | | + |
| Summer | 9.9 % | + | 13.8 % |
| | + | | + |
| Fall | 13.5 % | + | 22.4 % |
| | + | | + |
| Winter | 4.3 % | - | 5.4 % |
| | + | | - |

(Table 30), the diversity of prey phyla showed no seasonality (Fig. 15). Depth had no effect on dietary habits (Table 31). Among the basic components, ingestion of algae exceeded animal, thus indicating a herbivorous habit (Table 20).

The percent volumes of algae and animal ingested showed seasonal variation in prey abundance (Table 21 and 22). A decline in the algae consumed occurred below 7.5 meters (Table 23). The other variation, occurring at mean low water, is not significant due to low density. Minor fluctuations in animal material consumed proved unrelated to changes in depth (Table 24).

The diet composition was similar to that at Deep Cove (Table 16). The major difference was that the protozoans were the second most frequent prey, and poriferans third (Table 25).

The most significant seasonal variation in diet occurred during fall, when Protozoa became the predominant prey (Table 32). Unlike at Deep Cove, the diversity of prey showed seasonal variations (Fig 16).

_Tonicella marmorea_, _Cape Neddick_. Superficially, _T. marmorea_ appeared to ingest more animal than algal material at Cape Neddick (Table 27) and in this way differed from the herbivorous habit described for Deep Cove (Table 20). However, from a seasonal perspective _T. marmorea_ maintained herbivorous habit during all but fall (Tables 28 and 29).

Table 30. *Tonicella marmorea*: Frequency of occurrence of prey phyla by season (Deep Cove).

| Prey Phyla | Spring | $P \leq 0.05$ | Summer | $P \leq 0.05$ | Fall | $P \leq 0.05$ | Winter | $P \leq 0.05$ |
|---|---|---|---|---|---|---|---|---|
| Protozoa | 15.1 % | + | 29.3 % | + | 32.6 % | + | 23.2 % | + |
| Porifera | 40.3 % | + | 57.1 % | + | 72.0 % | + | 54.9 % | + |
| Nematoda | 0.6 % | + | 10.2 % | + | 1.5 % | + | 4.9 % | + |
| Arthropoda | 6.3 % | + | 4.1 % | + | 1.5 % | + | 4.2 % | + |
| Mollusca | 0.6 % | + | 2.0 % | + | 0.0 % | + | 0.7 % | - |
| Rotifera | 0.0 % | - | 0.0 % | + | 1.5 % | - | 0.7 % | + |
| Cnidaria | 0.6 % | - | 0.7 % | + | 1.5 % | + | 0.0 % | + |
| Kinorhyncha | 0.6 % | + | 0.0 % | - | 0.0 % | - | 0.0 % | + |
| Annelida | 0.0 % | - | 0.0 % | + | 0.8 % | + | 0.0 % | - |
| | | | | | | | | |
| Chrysophyceae | 80.5 % | + | 94.6 % | + | 90.9 % | + | 76.1 % | + |
| Phaeophyceae | 3.8 % | + | 6.8 % | - | 3.0 % | + | 2.1 % | + |
| Chlorophyceae | 2.5 % | + | 1.4 % | + | 2.3 % | - | 2.1 % | - |
| Rhodophyceae | 1.2 % | + | 0.7 % | + | 5.3 % | + | 2.1 % | + |
| Unid. Algae | 0.0 % | - | 0.0 % | + | 1.5 % | + | 0.0 % | - |

Table 31. *Tonicella marmorea*: Frequency of occurrence of prey phyla by depth interval (Deep Cove).

|  | Depth in meters |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|
| Prey Phyla | MLW * | 1.5 | 3.0 | 4.5 | 6.0 | 7.5 | 9.0 | 10.5 |
| Porifera | 50.0 % | 57.7 % | 63.8 % | 56.6 % | 50.8 % | 62.5 % | 56.0 % | 43.9 % |
| Protozoa | 0.0 % | 19.2 % | 18.9 % | 21.7 % | 20.6 % | 25.9 % | 34.1 % | 25.6 % |
| Arthropoda | 50.0 % | 7.7 % | 3.4 % | 6.0 % | 1.6 % | 2.7 % | 5.5 % | 4.9 % |
| Nematoda | 0.0 % | 3.8 % | 3.4 % | 6.0 % | 4.0 % | 5.4 % | 3.3 % | 3.6 % |
| Mollusca | 0.0 % | 0.0 % | 1.7 % | 0.0 % | 0.0 % | 0.9 % | 3.3 % | 0.9 % |
| Rotifera | 0.0 % | 0.0 % | 1.7 % | 0.0 % | 1.6 % | 0.0 % | 0.0 % | 0.0 % |
| Cnidaria | 0.0 % | 0.0 % | 0.0 % | 0.0 % | 0.0 % | 0.9 % | 1.1 % | 1.2 % |
| Kinorhyncha | 0.0 % | 0.0 % | 0.0 % | 0.0 % | 0.8 % | 0.0 % | 0.0 % | 0.0 % |
|  |  |  |  |  |  |  |  |  |
| Chrysophyceae | 100.0 % | 84.6 % | 94.8 % | 89.2 % | 88.1 % | 94.6 % | 68.1 % | 78.0 % |
| Phaeophyceae | 0.0 % | 3.8 % | 5.2 % | 3.6 % | 5.6 % | 0.9 % | 5.5 % | 3.6 % |
| Chlorophyceae | 50.0 % | 0.0 % | 3.4 % | 3.6 % | 1.6 % | 3.6 % | 0.0 % | 2.3 % |
| Rhodophyceae | 0.0 % | 0.0 % | 1.7 % | 0.0 % | 0.8 % | 1.8 % | 6.6 % | 2.3 % |
| Unid. Algae | 0.0 % | 0.0 % | 0.0 % | 1.2 % | 0.8 % | 0.0 % | 0.0 % | 0.0 % |

* Insignificant due to low sampling density.

Table 32. *Tonicella marmorea*: Frequency of occurrence of prey phyla by season (Cape Neddick).

| Prey Phyla | Spring | $P \leq 0.05$ | Summer | $P \leq 0.05$ | Fall | $P \leq 0.05$ | Winter | $P \leq 0.05$ |
|---|---|---|---|---|---|---|---|---|
| Protozoa | 55.1 % | + | 68.1 % | + | 77.4 % | + | 52.4 % | - |
| Porifera | 24.5 % | - | 25.5 % | + | 48.4 % | + | 33.0 % | + |
| Nematoda | 10.2 % | + | 2.1 % | + | 8.6 % | + | 0.0 % | + |
| Arthropoda | 16.3 % | + | 8.5 % | + | 5.4 % | + | 0.0 % | + |
| Mollusca | 0.0 % | + | 6.4 % | - | 11.8 % | + | 0.0 % | - |
| Rotifera | 0.0 % | - | 0.0 % | + | 12.9 % | + | 4.8 % | + |
| Cnidaria | 4.1 % | - | 2.1 % | + | 0.0 % | - | 0.0 % | + |
| Ectoprocta | 0.0 % | - | 0.0 % | + | 1.1 % | + | 0.0 % | - |
| | | | | | | | | |
| Chrysophyceae | 75.5 % | - | 76.6 % | - | 73.1 % | + | 81.0 % | - |
| Phaeophyceae | 2.0 % | + | 12.8 % | + | 20.9 % | + | 14.3 % | + |
| Chlorophyceae | 10.2 % | - | 8.5 % | + | 3.2 % | + | 0.0 % | + |
| Rhodophyceae | 2.0 % | + | 6.4 % | + | 4.3 % | + | 0.0 % | + |
| Unid. Algae | 0.0 % | + | 17.0 % | + | 2.2 % | + | 0.0 % | - |

A comparison of the feeding habits of _T. marmorea_ at Deep Cove and at Cape Neddick reveals basic similarities in diet composition (adjusted to seasonal abundance). However, differences in food priorities and quantities, as well as the carnivorous habit during fall, are most likely related to habitat and microhabitat variability and differences in local prey abundance.

The three basic components of the diet showed seasonal fluctuations (Fig. 25). The percent volume of algae exceeded the animal matter in spring and summer, while percent volumes of animal material exceeded or equalled the algae consumed during fall and winter. The algal volumes consumed did reflect seasonal abundance (Table 21). However, the percent volumes of animal ingested did not reflect seasonal abundance patterns during summer (Table 22). The reason for this is not clear.

The percent volumes of algae ingested demonstrated a slight but insignificant decrease with water depth (Table 23). The fluctuations in the quantities of animal material consumed showed no relationship to increases in depth (Table 24).

_Ischnochiton albus_, _Deep Cove_. The frequency of occurrence of the nine animal and four algal phyla comprising the diet of _I. albus_ is presented in Table 17. Four prey phyla composed the major portion of the diet. The order of decreasing frequency was the Chrysophyceae, Porifera, Protozoa, and Arthropoda. The remaining prey phyla were represented by low frequencies of occurrence. The diversity of prey phyla is characteristic of a grazing omnivore.

Seasonal fluctuations in the frequencies of occurrence of the prey phyla were distinct (Table 33). The arrangement of the four major prey phyla in order of decreasing frequency changed with every season. The prey phyla consumed show marked fluctuations, reflecting seasonal abundance (Fig. 15).

The species composition within the prey phyla displayed fluctuations in frequency of occurrence unrelated to increases in depth (Table 34). The data representing mean low water are not significant due to low sampling density.

The differences in the volumes of algal and animal material consumed were not significant, thus indicating an omnivorous diet (Table 20). These same components showed seasonal fluctuations. The algal component exceeded the animal matter consumed in spring and summer, while the reverse occurred during fall and winter (Tables 21 and 22). The algae consumed slightly decreased with increasing depth (Table 23), but this did not occur for animal material (Table 24).

Table 33. *Ischnochiton albus*: Frequency of occurrence of prey phyla by season (Deep Cove).

| Prey Phyla | Spring | P≤ 0.05 | Summer | P≤ 0.05 | Fall | P≤ 0.05 | Winter | P≤ 0.05 |
|---|---|---|---|---|---|---|---|---|
| Protozoa | 17.6 % | + | 60.3 % | + | 23.1 % | + | 18.0 % | - |
| Porifera | 17.6 % | + | 24.1 % | + | 68.0 % | + | 38.5 % | + |
| Nematoda | 0.0 % | + | 5.2 % | + | 10.0 % | + | 1.5 % | + |
| Arthropoda | 23.1 % | - | 24.1 % | + | 4.0 % | + | 21.5 % | + |
| Mollusca | 0.0 % | - | 0.0 % | + | 4.0 % | + | 0.0 % | + |
| Rotifera | 0.0 % | - | 0.0 % | + | 4.0 % | + | 1.5 % | + |
| Cnidaria | 0.0 % | - | 0.0 % | + | 2.0 % | - | 1.5 % | + |
| Ectoprocta | 0.0 % | - | 0.0 % | + | 2.0 % | + | 0.0 % | - |
| | | | | | | | | |
| Chrysophyceae | 89.0 % | + | 96.6 % | + | 92.0 % | + | 83.1 % | + |
| Phaeophyceae | 0.0 % | + | 1.7 % | + | 4.0 % | + | 0.0 % | - |
| Chlorophyceae | 5.5 % | + | 1.7 % | + | 4.0 % | - | 3.0 % | + |
| Rhodophyceae | 0.0 % | - | 1.7 % | - | 2.0 % | - | 1.5 % | + |
| Unid. Algae | 0.0 % | + | 1.7 % | + | 0.0 % | - | 0.0 % | - |

Table 34. Ischnochiton albus: Frequency of occurrence of prey phyla by depth interval (Deep Cove).

| | Depth in meters | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Prey Phyla | MLW * | 1.5 | 3.0 | 4.5 | 6.0 | 7.5 | 9.0 | 10.5 |
| Porifera | 100.0 % | 50.0 % | 20.0 % | 20.5 % | 32.8 % | 39.5 % | 37.2 % | 31.8 % |
| Protozoa | 100.0 % | 50.0 % | 33.3 % | 17.9 % | 32.8 % | 31.6 % | 30.2 % | 45.5 % |
| Arthropoda | 50.0 % | 33.3 % | 13.3 % | 17.9 % | 11.5 % | 22.4 % | 9.3 % | 18.2 % |
| Nematoda | 0.0 % | 33.3 % | 6.7 % | 7.7 % | 0.0 % | 0.0 % | 2.3 % | 0.0 % |
| Mollusca | 0.0 % | 16.7 % | 0.0 % | 0.0 % | 0.0 % | 0.0 % | 0.0 % | 9.1 % |
| Rotifera | 100.0 % | 0.0 % | 0.0 % | 0.0 % | 3.3 % | 1.3 % | 0.0 % | 0.0 % |
| Cnidaria | 0.0 % | 0.0 % | 0.0 % | 0.0 % | 0.0 % | 0.0 % | 0.0 % | 4.5 % |
| Ectoprocta | 50.0 % | 0.0 % | 0.0 % | 0.0 % | 0.0 % | 0.0 % | 0.0 % | 0.0 % |
| | | | | | | | | |
| Chrysophyceae | 100.0 % | 100.0 % | 73.3 % | 76.9 % | 95.1 % | 93.4 % | 81.3 % | 72.7 % |
| Phaeophyceae | 0.0 % | 0.0 % | 0.0 % | 20.5 % | 1.6 % | 1.3 % | 0.0 % | 0.0 % |
| Chlorophyceae | 0.0 % | 16.7 % | 6.7 % | 5.1 % | 3.3 % | 5.3 % | 0.0 % | 0.0 % |
| Rhodophyceae | 50.0 % | 0.0 % | 0.0 % | 0.0 % | 0.0 % | 1.3 % | 2.3 % | 0.0 % |
| Unid. Algae | 0.0 % | 0.0 % | 0.0 % | 2.6 % | 0.0 % | 0.0 % | 0.0 % | 0.0 % |

* Insignificant due to low sampling density.

# Discussion

## Interspecific Diet Analysis

The diets of *T. rubra*, *T. marmorea*, and *I. albus* encompassed a wide diversity of phyla and a large number of species. A comparison of the diets is presented in Table 35. Although a large number of chiton prey have been reported (Giese *et al.*, 1959; Barnawell, 1960; McLean, 1961; Boolootian, 1964), the occurrences of the two phyla, Rotifera and Kinorhyncha, as well as most of the species identified in this study, have not previously been reported as food of chitons.

A large portion (75%) of the stomach contents of *T. rubra*, *T. marmorea*, and *I. albus* was composed of detritus (unidentified organic and inorganic material). Although limited data are presented, the detritus was chiefly composed of inorganic materials. Substantial quantities of sand and other detritus have been reported in the stomach contents of several species of chitons (Barnawell, 1960; McLean, 1961; Boolootian, 1964; Kues, 1974). In a recent study Kues (1974) found even larger quantities of detritus in the stomach of a deep water chiton than what I present for *T. rubra*. Although it is not unusual for a grazing omnivorous chiton to ingest detritus, the large portion ingested by *T. rubra*, *T. marmorea*, and *I. albus* suggests that the chitons may be utilizing bacteria as a food source.

Table 35. General Diet Comparison.

| Qualitative Comparison of Chiton Diets | Deep Cove | Cape Neddick |
|---|---|---|
| Diversity of prey phyla | Tm = Tr = Ia * | Tm = Tr |
| Frequencies of occurrence of the three primary prey phyla | Chrysoph.> Porifera> Protozoa (Tm, Tr & Ia) | Chrysoph.> Protozoa> Porifera (Tm, Tr) |
| Frequencies of occurrence: | | |
| Chrysophyceae | Ia = Tm > Tr | Tm = Tr |
| Porifera | Tm > Tr > Ia | Tm = Tr |
| Protozoa | Ia > Tm > Tr | Tm > Tr |
| Arthropoda, Rotifera, Nematoda and Phaeophyceae | Ia > Tm > Tr | Tm > Tr |
| Seasonal Analysis | | |
| Frequencies of occurrence of the three primary prey phyla | Chrys.>Porif.>Prot. (all seasons: Tm & Tr)<br>Chrys.>Arth.>Porif. = Prot. (spring: Ia)<br>Chrys.>Prot.>Arth. = Porif. (summer: Ia)<br>Chrys.>Porif.>Prot.>Arth. (fall: Ia)<br>Chrys.>Porif.>Arth.>Prot. (winter: Ia) | Chrys.>Prot.>Porif. (all seasons: Tm)<br>Chrys.>Prot.>Porif. (summer & fall: Tr)<br>Chrys.>Porif.>Prot. (winter & spring: Tr) |
| Largest diversity of prey phyla | Fall (Tm, Tr & Ia) | Fall & Winter (Tm)<br>Fall (Tr) |
| Lowest diversity of prey phyla | Spring (Tm, Tr & Ia) | Spring (Tm)<br>Winter (Tr) |

Table 35 (continued).

| | Deep Cove | Cape Neddick |
|---|---|---|
| Range in prey phyla diversity | 11 - 10 (Tm)<br>13 - 8 (Tr)<br>12 - 5 (Ia) | 11 - 5 (Tm)<br>11 - 7 (Tr) |
| Quantitative Comparison of Chiton Diets | | |
| Combined volume of algae & animal | Ia = Tm>Tr (2:1) | Tm>Tr (15:1) |
| Algal volume | Ia = Tm>Tr (2:1) | Tm>Tr (1.2:1) |
| Animal volume | Ia>Tm>Tr (4:2:1) | Tm>Tr (2:1) |
| Proportion of algal volume to animal volume | Algae>Animal (3:1) (Tm & Tr)<br>Algae = Animal (Ia) | Algae>Animal (13:1) (Tr)<br>Animal>Algae (1.3:1) (Tm) |
| Seasonal Analysis | | |
| Combined volume of algae & animal | Ia>Tm>Tr (all seasons) | Tm>Tr (spring, summer & fall)<br>Tm = Tr (winter) |
| Largest combined volume | Fall (Tm, Tr & Ia) | Summer & Fall (Tm)<br>Summer (Tr) |
| Smallest combined volume | Winter (Tm & Ia)<br>Spring (Tr) | Winter (Tm)<br>Spring (Tr) |

Table 35 (continued).

| | Deep Cove | Cape Neddick |
|---|---|---|
| Range of estimated percent volumes of algae and animal ingested | 10.9 % - 26.3 % (Tm)<br>6.8 % - 12.1 % (Tr)<br>20.6 % - 34.6 % (Ia) | 15.2 % - 32.4 % (Tm)<br>6.5 % - 29.8 % (Tr) |
| Percent volumes of algae | Ia = Tm>Tr | Tm>Tr |
| Seasons of largest percent volume ingested | Summer & Fall (Tm, Tr & Ia) | Summer (Tm & Tr) |
| Seasons of smallest percent volume ingested | Winter (Tm & Ia)<br>Winter & Spring (Tr) | Fall (Tm)<br>Spring (Tr) |
| Percent volumes of animal | Ia>Tm>Tr | Tm>Tr |
| Seasons of largest percent volume ingested | Fall (Tm, Tr & Ia) | Fall (Tm & Tr) |
| Seasons of smallest percent volume ingested | Spring (Tm & Tr)<br>Summer (Ia) | Winter (Tm)<br>Spring (Tr) |
| Proportion of algae to animal | Algae>Animal (all seasons: Tm & Tr)<br>Algae>Animal (spring & summer: Ia)<br>Algae = Animal (fall: Ia)<br>Animal>Algae (winter: Ia) | Algae>Animal (winter, spring & summer: Tm & Tr)<br>Animal>Algae (fall: Tm) |

* Tm = *T. marmorea*; Tr = *T. rubra*; Ia = *I. albus*

The non-detrital portions of the diets of T. rubra and T. marmorea were composed predominantly of three phyla, Chrysophyceae, Porifera, and Protozoa; while the diet of I. albus included a fourth major phylum, Arthropoda. In 1916 Milligan observed T. rubra feeding on "minute brownish vegetable growth which existed on shells and stones...." If the minute vegetable growth is interpreted as being a diatom film, Milligan thus supports the findings of this study.

The ability of a chiton to feed on calcareous algae was reported by Lowenstam (1962). He believed that the hard goethite caps on the radular denticles allowed chitons to scrape deeply into substrates without suffering excessive wear to the radula. Barnes (1972) reported that a northeastern Pacific chiton, Tonicella lineata, fed primarily on calcareous algae and to a lesser extent on epiphytes. In contrast to these reports, I found a notable absence of calcareous algae and a predominance of epiphytes and epifauna in the chiton stomach contents. A further indication that T. rubra, T. marmorea, and I. albus are not as closely associated with or as dependent upon calcareous algae for food as T. lineata is the occurrence of chiton populations in areas devoid of calcareous algae (see Habitat Description). The dependency of T. lineata on calcareous algae extends beyond that of food. Barnes and Gonor (1973) clearly established the necessary presence of calcareous algae to obtain a larval settling response by _T. lineata_. To this consideration no comparison can be drawn, since larval settling response is beyond the scope of this study.

Caloric value of calcareous algae is exceedingly low in contrast to caloric value of diatoms (Paine and Vadas, 1969). Energy expenditure required to obtain an equal amount of nutrition from calcareous algae is substantially higher than the energy expenditure required for nutrition obtained from diatoms and epifauna. This fact, coupled with occurrence of diatoms in chiton stomach contents (Fretter, 1937; Giese _et al_., 1959; McLean, 1962a; Arakawa, 1963; Boolootian, 1964), suggests that diatoms are a far more favorable food source in terms of nutrition and energy expenditure than are calcareous algae. The findings of this study further support this supposition. On the other hand, (1) not all species select for nutritional value, and (2) if an animal becomes a specialist on calcareous algae, it may become very efficient at utilizing this resource as opposed to the ability of a general grazing omnivore.

Barnawell (1960) identified different diets among several coexisting species of the genus _Mopalia_. The diets of _T. rubra_, _T. marmorea_, and _I. albus_ were also found to differ in several ways (Table 35). The diet composition in terms of percent volumes of algae, animal material, and detritus differed for each species. In addition, the proportions of the specific prey phyla, as well as the proportions of algae to animal material, differed among the three species of chitons. In summary, while coexisting in the same habitat and feeding on the same prey species, the three species of chitons differ substantially in the amounts of each prey phyla that they consumed.

A seasonal shift to a carnivorous habit was described for Mopalia by Barnawell (1960). This occurred during winter and spring when algal abundance declined. A similar seasonal shift to a carnivorous diet occurred for T. rubra and T. marmorea at Cape Neddick. However, unlike the low algal abundance that caused the shift to a carnivorous habit for Mopalia, the seasonal shift to a carnivorous habit for T. rubra and T. marmorea occurred in the fall, when the algal abundance (e.g., diatoms) was still relatively high at Cape Neddick. A distinct shift to a carnivorous habit did not occur at Deep Cove. This condition at Deep Cove was probably due to the predominance of algae (diatoms) during all seasons and perhaps to a proportionately lower density and abundance of animal material in the habitat.

In summary, the habitat (Deep Cove vs. Cape Neddick) differences in prey abundance reflected the percent volume and frequency of occurrence of specific prey phyla in the diets of T. rubra and T. marmorea. The carnivorous habit, which occurred for T. rubra and T. marmorea during fall, reflects the greater relative abundance of animal material at Cape Neddick during this season. Further support is found in the greater abundance of protozoans as opposed to poriferans in the chiton diets at Cape Neddick; whereas, at Deep Cove, there was a greater abundance of poriferans in the chiton diets.

The three species of chitons showed the same seasonally adjusted changes. The seasonal adjustments in frequency of occurrence and percent volume of prey phyla appear to reflect seasons in which prey phyla were available and abundant. Seasonal abundance of most chiton prey was low during the winter and spring and high during summer and fall.

The diet composition of _T. rubra_, _T. marmorea_, and _I. albus_ showed no significant adjustments related to changes in depth. Diet variations were evident at mean low water, but these are not significant due to low number of gut analyses representing this level.

Community composition at the two habitats, Deep Cove and Cape Neddick, differed (see Habitat Description). In particular, subtidal macroscopic algae were prevalent at Cape Neddick but essentially absent at Deep Cove. However, the prey phyla composing the diets of _T. rubra_ and _T. marmorea_ and seasonal adjustments in diet composition were similar. The diets do show differences clearly related to greater abundance and/or availability of particular prey phyla at each site. These findings are supported by Giese _et al._ (1959) and Boolootian (1964), who reported that the diets of Mopalia and other species reflected prey abundance at different locales.

Differences in the frequency of occurrence and percent volumes of prey among the three species of chitons appear to be the result of either feeding preference and/or separate feeding levels, i.e., microhabitats. The presence of 14 prey phyla indicates that feeding preference or selectivity was not strongly developed. A discussion of the microhabitats follows.

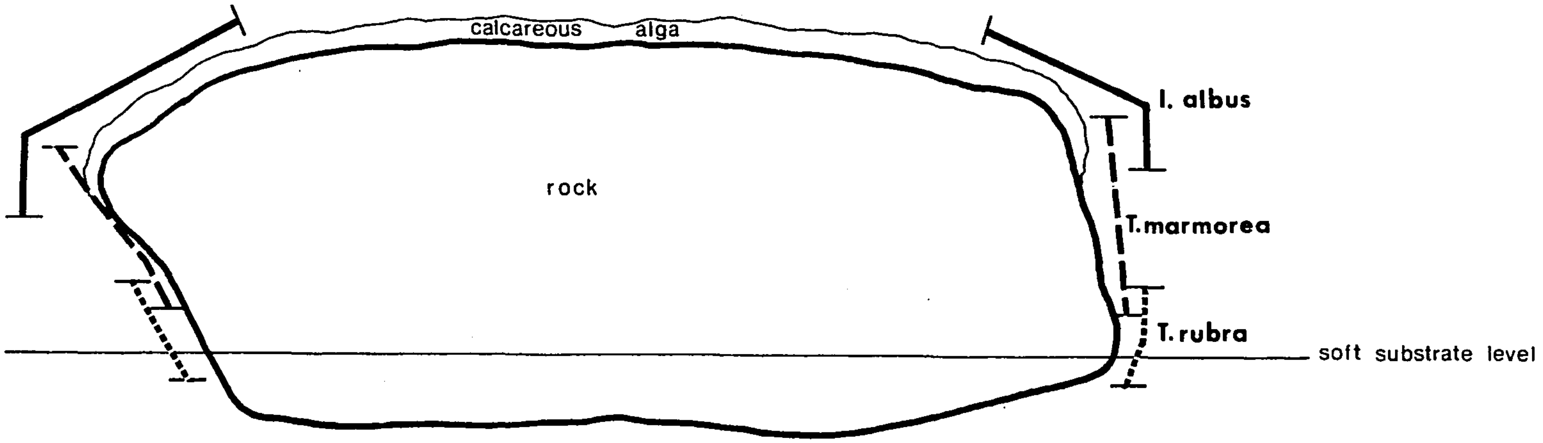
Microhabitat is used here to define the separate but overlapping horizontal feeding levels occupied by the three species of chitons. The microhabitats are presented for a hypothetical rock in Fig. 17. Adjustments in microhabitat occur for variations in shape of the rock. For example, the microhabitat of T. rubra includes undersides of rocks that touch the substrate and points of contact between contiguous rocks (Fig. 17).

The supposition of separate microhabitats is supported by the type and distribution of encrusting organisms on chiton shell plates (see Encrusting Organisms). Further support lies in the differences in the chiton diets which reflect differences in prey abundance in each microhabitat.

Spatial zonation observations described for other chiton species (Benard, 1960; McLean, 1962b; Glynn, 1970; Barnes, 1972) lend further support to the concept of separate microhabitats. However, these reports of spatial

Figure 17. Diagrammatic representation of the microhabitats of *Tonicella rubra*, *T. marmorea*, and *Ischnochiton albus* on a subtidal rock.

Figure 17.


calcareous alga
rock
I. albus
T. marmorea
T. rubra
soft substrate level

zonation were applied over a large portion of the intertidal and subtidal. Only Benard (1960) discussed the spatial zonation of the organisms (including the chiton, *Acanthopleura*) frequenting the various levels, e.g., galleries, of the calcareous alga *Lithophyllum incrustans*.

In general, the microhabitat of *T. rubra* is a horizontal zone at the base of the rock, the lower limit being slightly below the sand-rock interface (Fig. 17). The existence of this microhabitat is supported by diet characteristics and type and distributional pattern of encrusting organisms. Because of the greater proportion of detritus in the stomach contents of *T. rubra* than in the other species of chitons, it is apparent that this species frequently comes in contact with soft substrate. *T. rubra* spends much of its feeding time at or near the sand-rock interface.

The identification of the microhabitat of *T. rubra* is also supported by the encrusting organisms found on the chiton shell plates. The specific types of encrusted organisms on the plates of *T. rubra* from Deep Cove were most dense and most frequently found on the undersides of rocks or below the edge of the calcareous algal zone.

*T. marmorea* occupies a microhabitat above that of *T. rubra* (Fig. 17). The microhabitat of *T. marmorea* supports a higher proportion of algal and animal material than that of *T. rubra*. This higher proportion of algal and animal material is reflected in the diet of *T.*

marmorea. In addition, the substantially lower proportion of detritus in the stomach contents of T. marmorea indicates that it feeds in a zone above that of T. rubra and less frequently contacts the soft substrate.

The microhabitat of T. marmorea and its elevated position is identified by the encrusting forms inhabiting the chiton shell plates. The predominant encrusting form on T. marmorea was hydroids. These were most common on the sides of rocks. Furthermore, green and red algal species were more frequent on shell plates of T. marmorea than on T. rubra. The presence of these algal forms, which require a high light intensity, supports a separate microhabitat above that of T. rubra. The distribution of encrusted forms on T. marmorea gave no indication of directional abrasion that would indicate burrowing. This species was not observed to burrow, a behavior which was evident in T. rubra.

The microhabitat of I. albus appears to be located on or near the upper surface of the rock. The diet of this species had the lowest proportion of detritus and the highest proportion of algal and animal material. The proportion of animal material in the diet of I. albus was higher than in either of the two species of Tonicella. In addition, the presence of a fourth major prey phylum in the diet of I. albus indicates a separate feeding level. The prey of this phylum consisted primarily of arthropod larvae (barnacle?), and its presence suggests that the chiton feeding level is near the upper surface of the rock.

Only green algal filaments were found encrusted on I. albus. This algal form and its relatively high light requirement suggest that the I. albus microhabitat is at or near the upper rock surface.

The presentation of hypothetical microhabitats in Fig. 17 offers a visual perspective. It is apparent from observations of chiton behavior that these animals are not totally restricted to these microhabitats (see Behavior), and analyses of diets indicate the microhabitats probably overlap somewhat. For example, the diets of T. marmorea and I. albus differed with respect to the percent volume of animal material consumed but were similar in the percent volume of algae consumed. The microhabitats described here are probably most representative of diurnal and semidiurnal periods (see Behavior).

A detailed discussion of resource partitioning in ecological communities was presented by Schoener in 1974. In this study, several correlations between the dimensions of space, food, and time can be made; but the two most significant are (1) horizontal and vertical habitats and (2) food type and time. Species in a similar horizontal habitat often differ in vertical habitat, and these coexisting species of chitons do show different vertical habitats. In the latter pair of dimensions (i.e., food type and time), the separate diets of the three coexisting species of chitons support this concept (Table 17).

## Summary

1. The feeding biology of *T. rubra*, *T. marmorea*, and *I. albus* was investigated at two sites and intra- and interspecific comparisons were made.
2. Fourteen epifaunal and epiphytic phyla containing numerous species were identified as prey from gut analyses. Ingestion of calcareous algae was not found. The algal food was diatoms or filamentous growth forms.
3. Chiton guts contained large volumes of detritus, suggesting the possible use of microorganisms, e.g., bacteria, as a food source.
4. The three major prey phyla were the Chrysophyceae, Porifera, and Protozoa for *T. rubra* and *T. marmorea* with the addition of Arthropoda for *I. albus*.
5. The diets of *T. rubra* and *T. marmorea* were similar at both sites. Both were grazing omnivores; but *T. rubra* had a slight herbivorous habit, while *T. marmorea* had a strong herbivorous tendency. *I. albus* was a balanced omnivore.
6. The diets of the three species of chitons all showed seasonal variations, but depth-related variations were not found.
7. The intraspecific variations between sites were attributed to differences in local prey abundance and availability of prey.
8. Interspecific differences in diet were evident for

each species of chiton at each site.

9. The interspecific diet differences were attributed primarily to different feeding levels, i.e., microhabitats and, to a much lesser degree, to food selectivity.

# REPRODUCTIVE BIOLOGY

## Introduction

A significant portion of existing literature on reproductive habits and embryology of chitons is summarized by Hyman (1967). Many of the early workers (Clarke, 1855; Loven, 1856; Kowalevsky, 1879, 1882, 1883; Metcalf, 1892; Heath, 1899, 1905; and others) carefully recorded spawning behavior and embryological development of several species of chitons. Among these embryological studies, Lyngnes (1924) described egg morphology for *T. marmorea* and *I. albus*. Subsequent authors have established breeding records for many chitons and investigated factors that induce spawning. Orton (1920), Yonge (1940), Thorson (1946), Giese (1959) and Hedgpeth and Gonor (1969) have emphasized the particular importance of temperature in the timing of invertebrate reproductive cycles. Other factors which initiate spawning in chitons are tidal cycle and lunar phase (Grave, 1922; Brewin, 1942).

This study is primarily concerned with a determination of the breeding periods of *T. rubra*, *T. marmorea*, and *I. albus* in northern New England and a comparison of these with records from Norway for *T. rubra* (Christiansen, 1954) and *T. marmorea* (Lyngnes, 1924). The factors of temperature-induced breeding, depth, and possible temperature gradient are investigated. Data are also presented on sex ratios and sexual dimorphism in coloration.

## Materials and Methods

In addition to the general methods presented in the first section, annual reproductive cycles of *T. rubra*, *T. marmorea*, and *I. albus* were determined by measuring the gonad index, i.e., wet weight of the gonad divided by wet weight of the animal and multiplied by 100. This method for determining breeding period is further described by Giese (1959) and Boolootian (1964). Because of the small size of the three species of chitons, the gonad index was determined for all individuals from which a gonad weight could be obtained. The gonad indices were pooled to produce a monthly mean gonad index for each sex and for the species. Since very small and previously spawned individuals had no recordable gonad weights, these were eliminated from determination of the mean gonad index. The result was simply a reduction of the degree to which the gonad index declined after spawning.

## Results

### Gonad Size and Color

Just prior to spawning, the enlarged gonad comprises over one-half of the body cavity volume. After spawning, the gonads were so exhausted in *T. rubra* and *I. albus* that it was difficult to find a sufficient quantity of tissue for sex determination from a smear. There was no consistency as to minimum size at which the gametes of an individual species were identifiable. Among maturing chitons of similar size, the gametes of the male were usually recognizable before those of the female. This suggests earlier sexual maturity in the male. Only the gonad of the largest species, _T_. _marmorea_, was detectable throughout the breeding cycle. Gonads of _T_. _rubra_ and _T_. _marmorea_ were distinctly orange (salmon) in the female and white in the male, but these differences in color could not be detected externally, i.e., foot color. In contrast, no differences in gonad color could be detected between the sexes of _I_. _albus_.

## Breeding Season--Gonad Index

_Tonicella_ _rubra_. Gonad index data for _T_. _rubra_, _T_. _marmorea_, and _I_. _albus_ are presented in Table 36 and Fig. 18. At Deep Cove the highest mean gonad index was recorded for _T_. _rubra_ during late October. By late November the gonad index sharply declined, indicating that spawning had begun during early November. Spawning was completed in the males and nearly complete in the females by late December. After the completion of spawning, a period of quiescence occurred during winter in which no gonadal growth was evident. The duration of the rest period was approximately three months in females and five months in males. Renewed gonad development in

Table 36. Gonad Index Data.

Deep Cove

| Month | *T. rubra* | | | *T. marmorea* | | | *I. albus* | | |
|---|---|---|---|---|---|---|---|---|---|
| | ♂ | ♀ | ♂&♀ | ♂ | ♀ | ♂&♀ | ♂ | ♀ | ♂&♀ |
| August | 18.2 | 12.8 | 16.1 | 6.4 | 9.7 | 8.9 | * | 7.7 | 7.7 |
| September | 15.9 | 14.2 | 15.1 | 7.6 | 5.6 | 7.1 | 10.4 | 11.0 | 10.7 |
| October | 21.6 | 19.2 | 20.4 | 8.8 | 5.0 | 7.2 | 16.4 | 14.3 | 15.5 |
| November | 5.5 | 8.0 | 6.5 | 10.0 | 6.0 | 7.5 | 21.4 | 10.1 | 12.6 |
| December | 0.0 | 2.1 | 2.1 | 11.3 | 5.7 | 8.5 | 9.1 | 10.1 | 10.2 |
| January | 0.0 | 0.0 | 0.0 | 11.5 | 5.8 | 8.4 | * | 14.3 | 14.3 |
| February | 0.0 | 0.0 | 0.0 | 12.2 | 7.2 | 9.9 | 0.0 | 0.0 | 0.0 |
| March | 0.0 | 0.0 | 0.0 | 12.9 | 7.8 | 9.7 | 0.0 | 0.0 | 0.0 |
| April | 0.0 | 4.5 | 4.5 | 11.4 | 8.6 | 10.1 | 0.0 | 0.0 | 0.0 |
| May | 2.5 | 2.4 | 2.5 | 13.9 | 10.6 | 12.4 | * | * | * |
| June | 6.7 | 5.9 | 6.4 | 4.5 | 6.0 | 4.8 | 15.0 | 11.4 | 12.6 |
| July | 8.3 | 8.3 | 8.3 | 5.6 | 4.7 | 5.2 | 15.3 | 12.9 | 13.3 |

* Insufficient Data

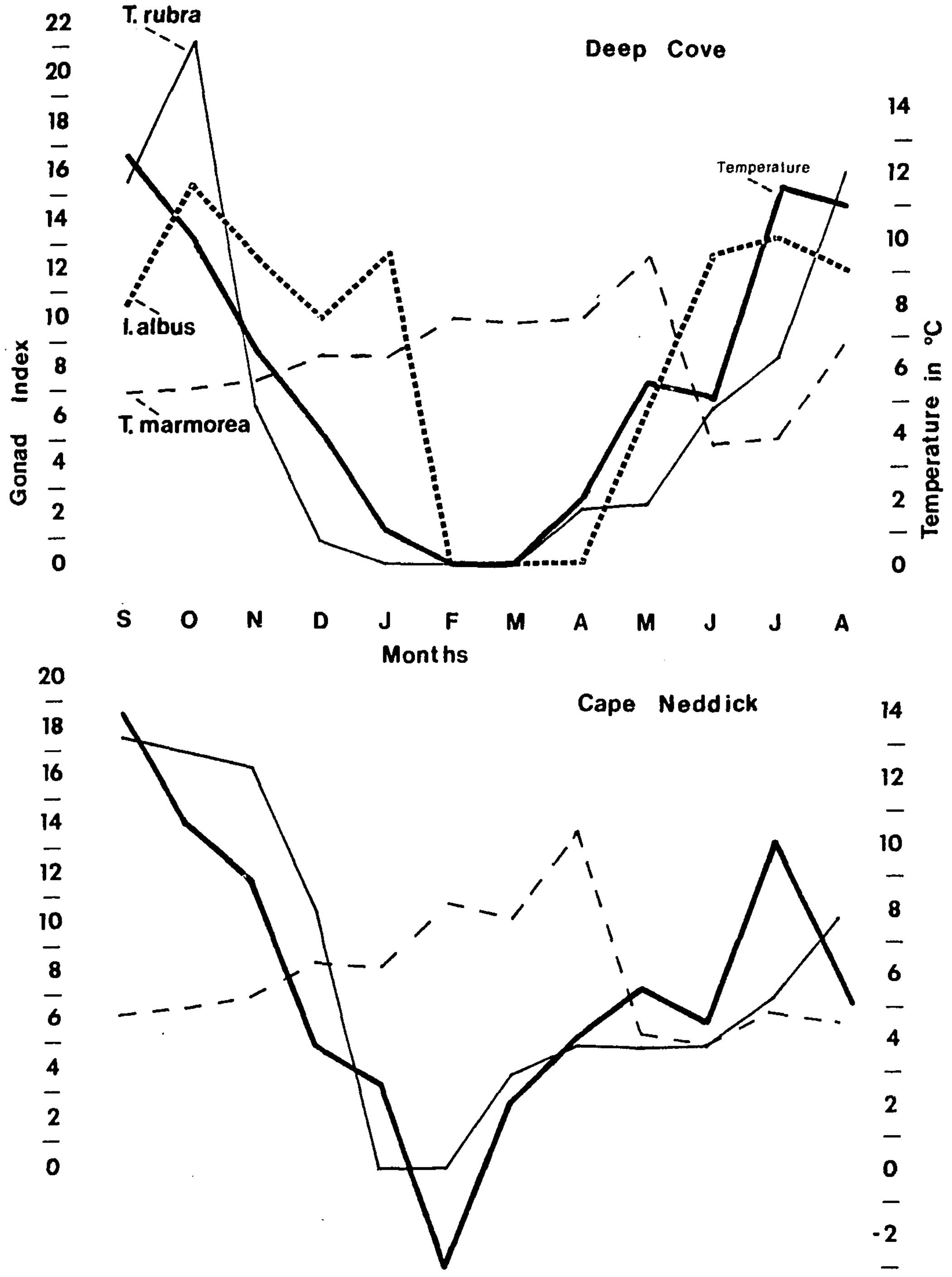
Table 36 (continued).

Cape Neddick

| | *T. rubra* | | | *T. marmorea* | | |
|---|---|---|---|---|---|---|
| Month | ♂ | ♀ | ♂&♀ | ♂ | ♀ | ♂&♀ |
| September | 19.8 | 15.8 | 19.6 | 4.7 | 5.1 | 4.9 |
| September | 18.8 | 12.9 | 15.4 | 9.2 | 5.6 | 7.6 |
| October | 18.6 | 13.2 | 15.9 | 9.1 | 3.6 | 6.8 |
| October | 20.1 | 16.5 | 17.9 | 12.6 | 10.9 | 12.3 |
| November | 21.1 | 16.8 | 18.6 | 9.9 | 3.6 | 8.0 |
| November | 15.0 | 13.8 | 14.3 | 8.1 | 4.0 | 5.9 |
| December | 10.2 | 15.8 | 14.0 | 11.6 | 4.7 | 8.3 |
| December | 7.1 | 7.3 | 7.3 | 10.2 | 6.8 | 8.5 |
| January | 0.0 | 0.0 | 0.0 | 8.2 | 7.5 | 7.7 |
| February | 0.0 | 0.0 | 0.0 | 6.3 | 11.4 | 10.7 |
| March | 2.7 | 4.6 | 3.7 | 15.3 | 5.5 | 10.1 |
| April | 4.3 | 5.5 | 5.1 | 9.9 | 17.2 | 15.6 |
| April | 4.0 | 5.8 | 5.0 | 15.9 | 10.3 | 11.8 |
| May | 5.2 | 4.4 | 4.6 | 5.5 | 5.5 | 5.5 |
| June | 4.8 | 4.8 | 4.8 | 4.3 | 5.4 | 5.0 |
| July | 6.6 | 6.9 | 6.7 | 6.9 | 5.7 | 6.6 |
| August | 10.2 | 7.5 | 8.7 | 6.2 | 3.9 | 5.2 |

Figure 18. Relationship between temperature and gonad index.

Figure 18.


T. rubra
Deep Cove
Temperature
I. albus
T. marmorea
Gonad Index
Temperature in °C
22
20
18
16
14
12
10
8
6
4
2
0
14
12
10
8
6
4
2
0
S
O
N
D
J
F
M
A
M
J
J
A
Months
Cape Neddick
20
18
16
14
12
10
8
6
4
2
0
14
12
10
8
6
4
2
0
-2

females coincided with the rise in water temperature during April. In May gonad growth in males began.

At Cape Neddick the gonad index data for T. rubra revealed that spawning began in late November and was completed by early January (Table 36). The rest period following spawning was of a two-month duration in both sexes. Renewed gonad development in both sexes at Cape Neddick also coincided with the rise in water temperature which occurred during March.

In T. rubra commencement of spawning, duration of the rest period, and renewed gonad development appeared to be temperature related. Spawning began at both sites when the water temperature declined below approximately 8° C, and spawning was completed when the water temperature dropped to 3-4° C. The duration of spawning was similar at Deep Cove and Cape Neddick. Termination of the rest period and the renewed gonad development began when the temperature increased to 2° C.

Tonicella marmorea. The highest mean gonad index was recorded for T. marmorea from Deep Cove during May (Table 36). The gonad index dropped by late June, indicating spawning had commenced by early June. Duration of spawning extended to approximately late July. Unlike the other two species of chitons, T. marmorea was not found to spawn all gametes from its gonads during its breeding period. Termination of spawning and duration of the rest period were not as distinct as that described for

T. rubra. The rest period of the females appeared to extend for several months following termination of spawning. By contrast, males appeared to have little or no rest period before renewed gonad development commenced.

At Cape Neddick spawning by T. marmorea took place from early May to late June. The rest period following spawning extended until December in the female, while in the male it was one month or less.

The breeding cycles of T. marmorea at Cape Neddick and Deep Cove were similar but differed slightly in timing. This difference in timing appeared to relate to water temperature. Renewed gonad development in the female correlated with declining water temperature.

Ischnochiton albus. Based on the decline in gonad index, I. albus began spawning by late January and completed spawning during February, when the water temperature reached the lowest point, $0^{\circ}$ C. A rest period for both sexes of 3-4 months followed spawning. Because of insufficient data, gonad indices were unavailable for May. Due to the relatively high gonad index recorded for both species for June, it is probable that renewed gonad development began in May, when the water temperature exceeded $3\text{-}4^{\circ}$ C.

A study of the relationship of depth and temperature gradient to spawning was investigated. It revealed that spawning commenced at all depths almost simultaneously and thus did not occur in a progressive pattern related to changes in depth. A depth-related temperature gradient was not found at Deep Cove due to the strong currents and vertical mixing.

During the spawning season, grouping behavior seemed evident for T. rubra at Cape Neddick, but similar behavior was not observed at the more densely populated site in Deep Cove. No such behavioral patterns were observed for T. marmorea or I. albus.

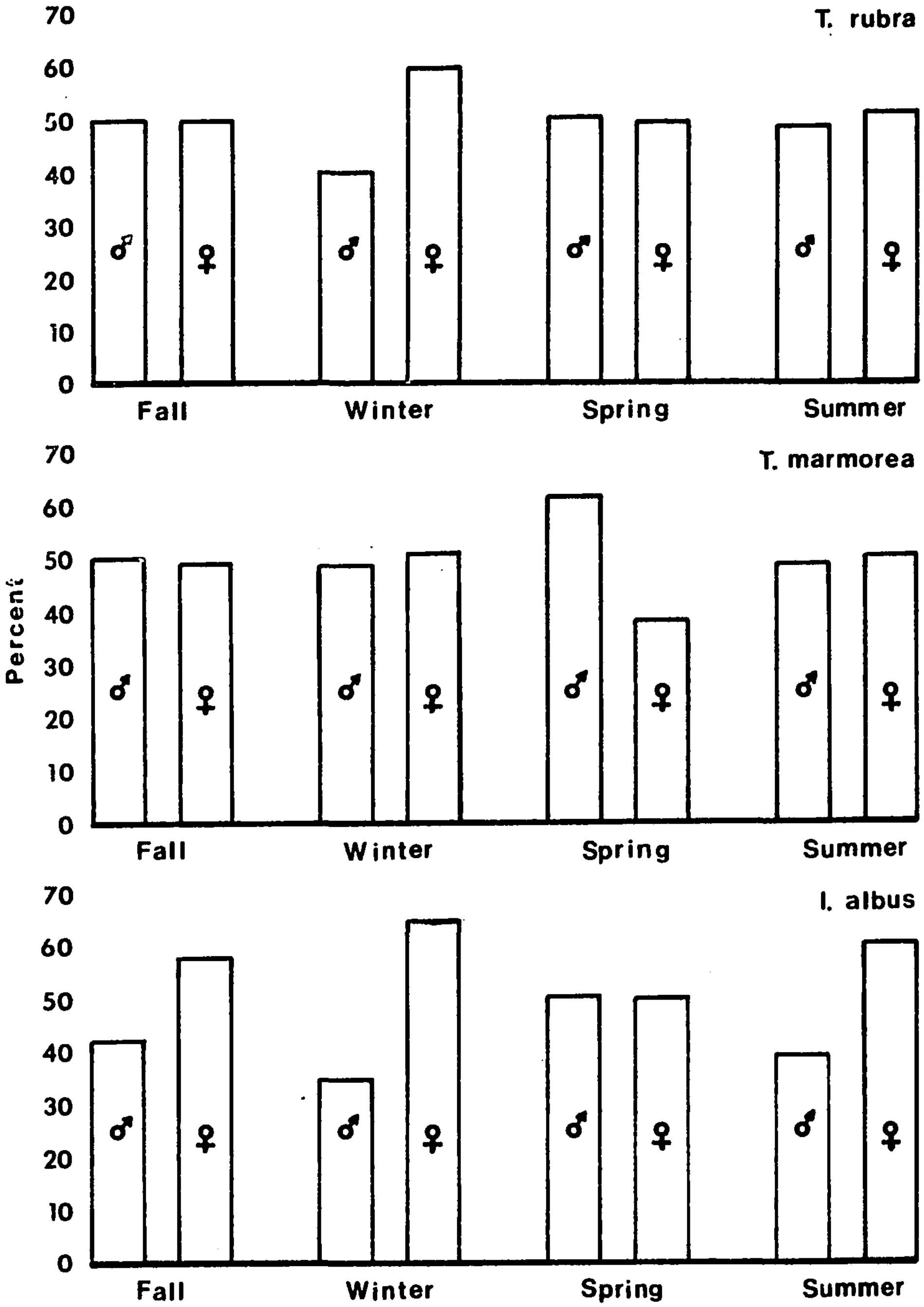
## Sex Ratios

The populations of T. rubra (1.08♀ : 1♂) and T. marmorea (0.86♂ : 1♀) had approximately the same sex ratio of 1:1. By contrast, the number of females in the population of I. albus (1.38♀ : 1♂) substantially exceeded the males. The distribution of the sexes showed no relationship to depth.

The three species of chitons illustrated seasonally consistent sex ratios except at breeding time (Fig. 19). T. rubra showed a marked decline in the number of males in the population after spawning. During spawning in late spring, T. marmorea showed a decrease in the proportion of females in the population. I. albus illustrated a slight decline in males during their winter breeding season. In the following spring a drop in the number of females occurred; this was the only period when the sex ratio for I. albus was balanced.

Figure 19. Sex ratios of each species of chiton by season (Deep Cove).

Figure 19.


70
60
50
40
30
20
10
0
T. rubra
♂
♀
Fall
Winter
Spring
Summer
Percent
T. marmorea
I. albus

## Discussion

Sex-correlated coloration of the gonad in which the males and females can be distinguished was described for chitons by Crozier (1920), Brewin (1942), Christiansen (1954), and Barnes (1972). Only Crozier and Brewin reported that the sexes could be distinguished by external foot color, and the former report was disputed by Glynn (1970). Sex-correlated coloration of the gonad was found for T. rubra and T. marmorea, but not for I. albus. In no case were the sexes distinguishable by external foot color.

The breeding time of T. rubra is supported by Christiansen (1954). She found that T. rubra spawned on 10 January in Norway. Unfortunately, she did not include temperature data for comparison with this study; but the timing of spawning by T. rubra in the Norwegian fjords did coincide with the terminal stages of spawning at Cape Neddick.

Lyngnes (1924) reported breeding by T. marmorea in Norway during summer. This supports the findings of this study where T. marmorea bred in June-July at Deep Cove.

No reports of breeding by I. albus were found in the literature.

The distinct annual breeding cycles demonstrated for T. rubra, T. marmorea, and I. albus are similar to those reported for most other species of chitons (Hewatt, 1938; Graham, 1941; Brewin, 1942; Ricketts and Calvin, 1948; MacGinitie and MacGinitie, 1949; Christiansen, 1954; Costello *et al*., 1957; Giese *et al*., 1959; Johns, 1960; Thorpe, 1962; Tucker and Giese, 1962; Boolootian, 1964; Nimitz, 1964; Monroe and Boolootian, 1965; Lawrence *et al*., 1965; Giese and Hart, 1967; Glynn, 1970). *T*. *rubra*, *T*. *marmorea*, and *I*. *albus* did not show spawning periods that extended over several months as described for other species by Grave (1922, 1932) and Korringa (1947).

Temperature-related spawning has been indicated for several invertebrates, including chitons (Orton, 1920; Yonge, 1940; Thorson, 1946; Giese, 1959). Hedgpeth and Gonor (1969) stated that temperature is the most important factor in coordinating the onset of breeding among invertebrates. While temperature-related spawning appears evident for *T*. *rubra*, *T*. *marmorea*, and *I*. *albus* (Fig. 18), this is not characteristic behavior of all chitons. In particular, intertidal species that are exposed to two temperature regimes, i.e., air and water, are often stimulated by a variety of factors, including lunar phase and tidal cycle (Grave, 1922, 1932; Brewin, 1942) or food availability (Murti and Nagabhushanam, 1968). These factors were not investigated; but the influence of depth was investigated, and it did not influence spawning at Deep Cove.

Grouping behavior at spawning time was reported for several chitons (Crozier, 1918a; Arey & Crozier, 1919). Heath (1899, 1905) suggested that this behavior may be involved in the inducement or onset of spawning. No evidence was found to support the latter statement, and grouping behavior was only tentatively identified for _T_. _rubra_ at Cape Neddick.

Reported sex ratios among chitons are variable. Crozier (1918a; 1918b), Magne (1937) in Fischer-Piette and Franc (1960), and Glynn (1970) reported greater numbers of males than females for several different chiton populations. By contrast, Pelseneer (1924), Christiansen (1954), and Glynn (1970) found more female than male chitons for other species. This study found an approximately equal sex ratio for _T_. _rubra_ and _T_. _marmorea_, while for _I_. _albus_ the sex ratio favored the females. The significance of the sex ratio difference reported for _I_. _albus_ is not known.

In the three species of chitons the variations in the sex ratios that occurred during breeding indicates a higher selective mortality for one sex or the other. The reasons for this unequal mortality are unclear but may relate to exhaustion of body reserves following breeding. In those populations where a decline of a specific sex followed breeding, e.g., males for _T_. _rubra_ and females for _T_. _marmorea_, that particular sex required a longer rest period before renewing gonad development. In addition, the males of _T_. _rubra_ commenced spawning at an earlier age and complete the annual spawning cycle before the female. The data suggest an earlier sexual maturity for males of _T_. _rubra_.

## Summary

1. The breeding cycles for _T_. _rubra_, _T_. _marmorea_, and _I_. _albus_ were determined using gonad index; and distinctly separate annual breeding periods were found.
2. Studies conducted at geographically separate sites suggest that the breeding periods of these chitons are temperature-related. _T_. _rubra_ spawned with decreasing temperature during late fall, _I_. _albus_ during mid-winter when the temperature was lowest, and _T_. _marmorea_ with increasing temperature during late spring.
3. The three species showed a rest period after spawning and before gonad redevelopment. The duration of this period differed both among the species and intraspecifically between the sexes.
4. The enlarged gonad, which comprised a large portion of the body cavity prior to breeding in all species, was completely exhausted during spawning in _T_. _rubra_ and _I_. _albus_, but not in _T_. _marmorea_.
5. Sex-correlated coloration of gonads was found for _T_. _rubra_ and _T_. _marmorea_ but was absent in _I_. _albus_. In the two former species, the gonad of the female was orange (salmon) and that of the male, white.

# FINAL DISCUSSION

This study is unique in that the biology of chitons was studied subtidally. The parameters acting on most intertidal populations are predominantly physical, whereas those acting on subtidal populations are biological (Connell, 1972). Predation appears to be the most significant biological factor determining the subtidal chiton population structure at Deep Cove and Cape Neddick.

The bathymetric population distribution was characterized by the predominance of _T_. _rubra_ in the shallow subtidal. Its dominance declined with increasing depth, whereas _T_. _marmorea_ showed a reciprocal increase. The smallest population in Deep Cove belonged to _I_. _albus_. A hypothesis for the bathymetric distribution of these chitons is as follows: the subtidal chiton population distribution above 6 meters is determined by the feeding habits of predators and the timing of chiton breeding periods.

The asteroid _Leptasterias_ _littoralis_ occurs in significant numbers from the low littoral zone to a depth of approximately 6 meters (Fig. 2 & Table 3). The distribution and maximum density of this asteroid overlaps the subtidal region where _T_. _rubra_ is dominant.

The female of _L_. _littoralis_ broods eggs in its oral region from late November until late April or early May (O'Brien, 1972). During this same winter period both sexes of the asteroid essentially cease feeding.

*T. rubra* spawns from November to December (Fig. 18). The resulting larvae settle during the period of low asteroid activity and occupy microhabitats at the base of the papillae of the calcareous alga *Lithothamnium* and in crevices in and under rocks. By early May, young *T. rubra* grow to a size exceeding the feeding capabilities of the newly released 1 mm asteroids. The location of the young chitons in various crevices and at the bases of papillae of *Lithothamnium* makes the young chitons inaccessible to adult asteroids when they become active in spring. *T. rubra* populations survive asteroid predation in the shallow subtidal zone at Deep Cove as a result of coordination of reproduction with the period of low asteroid predation and protected microhabitat selection by young chitons.

*I. albus* breeds from late January to late February (Fig. 18). Therefore, the young chitons have only a few months of growth before the onset of asteroid predation. Based on the size of young *I. albus* collected during July and the generally small adult size of this chiton, it is evident that the young *I. albus* are within the feeding capabilities of rapidly growing *L. littoralis* for a longer period of time than the larger species, *T. rubra* and *T. marmorea*. Only young *I. albus* were observed to frequent crevices and undersides of shells, where they are therefore less accessible to predatory asteroids. In summary, the _I_. _albus_ population suffers heavier asteroid predation than _T_. _rubra_ because of its later breeding time and smaller adult size.

_T_. _marmorea_ breeds from late May to June (Fig. 18). The larvae of this chiton settle after the release of young _Leptasterias_ and during the period of high asteroid predation. As a result, heavy asteroid predation occurs on young _T_. _marmorea_. This depresses the population size of _T_. _marmorea_ in the subtidal zone to a depth of 6 meters, where _L_. _littoralis_ is most dense.

Based on the timing of chiton breeding periods in relation to the timing of high asteroid predation and release of asteroid larvae by _L_. _littoralis_, _T_. _rubra_ is subjected to far less asteroid predation pressure than _I_. _albus_ or _T_. _marmorea_. This lower predation pressure is reflected in the higher abundance and distribution pattern of _T_. _rubra_ in the shallow subtidal zone of Deep Cove (Fig. 5).

In an apparent contradiction, the population of _T_. _marmorea_ exceeds that of _I_. _albus_ in the shallow subtidal zone. The spawning time of _I_. _albus_ should be more favorable to surviving asteroid predation than that of _T_. _marmorea_. _I_. _albus_' size is within the feeding capabilities of adult _L_. _littoralis_ during all stages of growth except for the largest adult size. By contrast, the size of *T. marmorea* exceeds the feeding capabilities of *L. littoralis* well before adult size is reached. In effect, *T. marmorea* escapes predation through size. The result is a larger population of *T. marmorea* and *I. albus* in the shallow subtidal of Deep Cove. This hypothesis is supported by studies on *Leptasterias hexactis* (Menge, 1970). He found a similar distinct relationship between predator and prey size.

The rationale for the population distribution patterns below 6 meters is less clear. A second species of predatory asteroid, *Leptasterias tenera*, frequented the deeper portions of the transect at Deep Cove (Fig. 2). The breeding and behavior characteristics of this less abundant asteroid, aside from chiton predation, were not elucidated. It is conceivable that *L. tenera* fills in part of the predatory role of *L. littoralis* on chitons in deeper water. Several additional factors--including available substrate; its mechanical composition; physical disturbance, e.g., siltation from nearby scallop dragging; nocturnal and seasonal fish predators--all complicate the analysis.

There was no evidence that the rationale presented for the chiton distribution patterns in the shallow subtidal can be applied to locales other than Deep Cove. The reasons for this are (1) those representatives of *L. littoralis* and *L. tenera* that occur in deeper water often attain larger sizes and, thus, are capable of feeding on larger chitons. (2) The geographic distribution of the two asteroid species did not extend to the shallow subtidal at Cape Neddick. (3) Other chiton predators, whose geographic distributions do not extend as far north as Deep Cove, alter chiton populations in other areas. (4) Predators which occur in low density and/or are seasonal in occurrence, such as fish, affect the chiton population only on a local or seasonal basis. (5) Finally, the particular habitat preference of these predators may also severely limit their influence.

The size distribution pattern at Deep Cove, characterized by large individuals in shallow water and small individuals in deep water, appears to be the result of two factors: predator distribution and substrate characteristics.

The principal chiton predators frequenting the deeper portions of the transect at Deep Cove are fishes, the winter flounder, and, to a lesser degree, the cod (Fig. 2). Gut analyses of the flounder clearly established its strong preference for large chitons.

Tyler (1971) reported that the winter flounder moves into the intertidal for 6-8 hours during high water, and he proposed that this zone is a major feeding area for northern populations of winter flounders. However, gut analyses and personal observations did not support his findings for the Cobscook Bay region. The major concentration of this predatory fish, and its resultant selective predation, occurs in the deeper water of the transect. Therefore, the distribution of this fish, coupled with its selective predation on large chitons, results in an altering of the deep water chiton population by eliminating the large and leaving the small individuals. Overlapping the effect of seasonally occurring fishes is the impact of the asteroid _L_. _tenera_. The degree of involvement of this low density asteroid is not clear.

_Leptasterias_ _littoralis_ is physically capable of feeding only on chitons below a certain size. This asteroid is primarily distributed in the shallow subtidal (< 6 meters) of Deep Cove (Fig. 2). Therefore, by being unable to feed on large chitons, this asteroid concentrates on small chitons. The result is an alteration of the shallow water chiton size distribution toward large individuals. This supposition is supported by Landenberger (1968), who found selective predator behavior can have important effects on age structure (size) of a prey population.

The predator-prey interaction just presented is intensified by a physical factor, substrate composition. The cobble substrate along the transect at Deep Cove decreases in size with increasing depth (Fig. 2). As a result, large chitons in deep water associated with small cobble are not afforded refuge and, therefore, are more frequently exposed to predation than chitons on the large cobble found in shallow water.

Among West Coast intertidal gastropods, two opposing examples of size distribution have been described. The largest individuals of two species of Acmaea were found to frequent the uppermost limit of their intertidal distribution (Frank, 1964). By contrast, Paine (1969) found that the gastropod Tegula migrated toward its lower distributional limit with advancing age. In both cases the migrations appear to be brought about by the high population densities and the resultant competition for food and space. In this study of subtidal chitons, no evidence was found to support a similar hypothesis for the chiton size distributions.

Haven (1972) found that competition limited the size and growth rates of intertidal limpets on the Pacific Coast. The algal growth characteristics, which substantially influenced the size of these intertidal gastropods, had a markedly different seasonal appearance than that of the low intertidal algae at Deep Cove. The diatom film, which is so important to the intertidal gastropods, has a seasonal growth pattern. Castenholz (1961) studied the seasonal appearance of intertidal diatoms and found that grazers can remove all diatoms in summer but not in winter. The latter assumption is based on reduced activity of the herbivores during winter. Aside from a seasonally occurring shallow-water colonial diatom species, the remaining diatom film in the subtidal at Deep Cove undergoes at least partial renewal with each tidal cycle. No evidence has been found to support the idea that subtidal chitons in Maine undergo the same pressures that limit the size and growth rate of intertidal limpets in California.

The seasonal variation in the total chiton population density at Deep Cove is the result of several factors. Larval recruitment is evident during spring, when the population density is highest. The gradual decline in population density during summer and fall reflects increased predation pressure. A sharp decline occurs in winter. This decline is probably the result of increased mortality due to a reduction in the overall carrying capacity of the environment and from a depletion of body reserves following breeding. The diet analysis data lends support to the supposition of a seasonally variable carrying capacity in that the most pronounced declines in population density occur at depth intervals of greatest population concentration. This supposition is characteristic of the winter breeding species _T_. _rubra_ and _I_. _albus_ and is supported by sex ratio data which indicates a marked mortality following spawning. Finally, death probably occurs at the shallowest depth intervals (mean low water and 1.5 meters) in winter due to exposure to very low air temperatures during extreme spring tides and from limited ice scouring.

The major predator influencing the chiton density at Cape Neddick is probably the fish _Tautogolabrus_ _adsper_-

_sus_. It is present as an active predator from early spring through late fall. The numerous young representatives of this common wrasse are particularly effective predators. These fish frequently pick at the hard substrates using their projecting teeth. This fish is absent from Deep Cove because of temperatures unfavorable for successful breeding. In addition, predatory crabs and lobsters are numerous at Cape Neddick during summer and fall but uncommon at Deep Cove.

At Deep Cove the chiton predators occur at a substantially lower density. The predators are also present for a shorter duration (usually one season) and appear to have a more restrictive bathymetric distribution. At Deep Cove the cunner is absent; but two fish predators, the winter flounder and the cod, frequent the deeper water. Chitons are a major prey of the winter flounder at Deep Cove, while at Cape Neddick the winter flounder chooses alternative prey and thus is relegated to the role of a lesser predator. The arthropod predators at Deep Cove are insignificant in their influence on chiton population density; but the echinoderm predators _L_. _littoralis_ and _L_. _tenera_ are significant. However, the asteroids are restricted both in feeding capability, with respect to prey size, and to bathymetric distribution.

According to Paine (1969), a "keystone species" is one of high trophic status which disproportionately affects the pattern of species occurrence, distribution, and density in a natural community. The cunner at Cape Neddick, and perhaps the winter flounder and Leptasterias littoralis at Deep Cove, might be considered to be "keystone species." It is evident that these predators exhibit demonstrative influence on the community structure at the respective sites of study, but further testing is necessary to verify this.

In summation it was found that in the benthic, marine environment of New England, three species of chitons are prominent inhabitants of calcareous algal-covered rocks of the subtidal zone. Their feeding behavior is somewhat similar to many littoral gastropods in that they scrape the diatom film covering the rocks. Neither their behavior nor their diet appears to be significantly influenced by species level differences in floral or faunal composition of widely separated communities. In agreement with the findings of Connell (1972), the upper limit of vertical distribution of the chitons appears to be determined principally by physical factors, particularly temperature. Unlike littoral forms, the lower limit of distribution was not clearly distinguished as biologically caused, but more often was due to substrate characteristics.

The reduction of niche overlap among the three chiton species by occupying separate microhabitats was elucidated through differences in diet composition and in associated encrusting organisms. While all three species were grazing omnivores, there were quantitative differences in diet composition. Support for this type of separation was found in Schoener's (1974) discussion of resource partitioning. In summary, these chitons show both spatial and dietary niche separations.

The trophic level of these roving scrapers was that of an omnivore. The chitons utilized only the smaller autotrophs and were in turn prey of low and high level heterotrophs. Some showed seasonal variations to herbivorous or carnivorous habits related to the changes in seasonal availability and abundance of food types. In contrast to the littoral, patellid gastropods which can severely influence the bottom algal composition (May, Bennett and Thompson, 1970), the non-selective chitons had no effect on the macroscopic algal composition and no obvious influence on benthic faunal diversity.

The interspecific differences in population size and species distribution and the intraspecific differences in the bathymetric size distribution, along with inherent seasonal variations, were dependent on several key biological and physical factors. Paine (1966) stated that local species diversity is directly related to the efficiency with which predators prevent the monopolization of the major environmental requisites by one species. At Cape Neddick, the role of the predator _T. adspersus_ severely limited chiton density. In contrast, absence of the cunner and the temporal restrictions on the replacement predators found in Deep Cove, allowed for a monopolization of the habitat by chitons.

The distributional patterns and bathymetric size distributions for the three species are dependent on biological factors, particularly predation. This agrees with the findings of other workers as reviewed by Connell (1972). Specifically, the selective survival of species is based on the temporal feeding patterns of predators, microhabitat selectivity by larval chitons, and the timing of the chiton breeding periods. In addition, the adult size of the two species at Deep Cove provided an escape from one predator, Leptasterias. Connell (1972) described a similar escape in size for Balanus cariosus. Finally, the bathymetric size distribution of the cobble at Deep Cove permitted selective protection of the chitons from predators at shallower depths. Inversely correlated with decreasing cobble size and depth is increased predation by visual predators, which suppresses chiton size.

In a manner similar to many terrestrial fauna, the factor in limiting population size other than predation appeared to be seasonal food abundance. The population size was depressed due to mortality in winter and spring to the level of the carrying capacity of the environment.

The purpose of this autoecological study was to describe the role of three co-occurring boreal chitons in subtidal rocky communities. Many of the aspects studied yielded positive insights into their ecology and the mechanisms that control their density and distribution patterns. This study provides a foundation for further experimental studies of these numerically important grazers and their role in shallow subtidal community dynamics. The author believes that further research in the following areas would add significantly to the knowledge of these chitons and their community role: embryology and early development, nocturnal and homing behavior, and population dynamics.

# LITERATURE CITED

Abbott, R. T. 1974. American Seashells. 2nd Edition. Van Nostrand Reinhold Company, New York, N. Y.

Adegoke, C. S. 1967. Bryozoan-Mollusk relationships. Veliger. 9(3):298-300.

Arakawa, K. Y. 1963. Studies on molluscan faeces. Publ Seto Mar Biol Lab. 11:185-208.

Arey, L. B. and W. Crozier. 1919. Sensory responses in *Chiton*. J Exp Zool. 29:157-260.

Balch, F. N. 1906. Remarks on certain New England chitons, with a new variety. Nautilus. 20:62-68.

Barnawell, E. P. 1960. Carnivorous habit among the Polyplacophora. Veliger 2(4):85-88.

Barnes, J. R. 1972. Ecology and reproductive biology of *Tonicella lineata*. Ph.D. Thesis. Oregon State University.

Barnes, J. R. and J. J. Gonor. 1973. The larval settling response of the lined chiton *Tonicella lineata*. Mar Biol. 20:259-264.

Benard, F. 1960. La faunale associee au *Lithophylum incrustans*. Phil des cuvettes de la region de Roscoff Bull Biol. March 1:89-102.

Berry, S. S. 1907. Molluscan fauna of Monterey Bay, California. I-IV. Nautilus. 21:17-52.

Berry, S. S. 1951. Notes on some British Columbian chitons. II. Proc Malacol Soc Lond. 28(6):213-229.

Bigelow, H. B. and W. C. Schroeder. 1953. Fishes of the Gulf of Maine. Fishery Bulletin. 74. U. S. Govt. Printing Office.

Blaney, D. W. 1904. Shell collecting days at Frenchman's Bay. Nautilus. 17:109-111.

Boolootian, R. A. 1964. On growth, feeding and reproduction in the chiton, *Mopalia mucosa* of Santa Monica Bay. Helgol Wiss Meeresunters. 11(3/4):186-199.

Boyle, P. R. 1970. Aspects of the ecology of a littoral chiton, *Sypharochiton pelliserpentis* (Mollusca: Polyplacophora). N Z J Mar Freshwater Res. 4(4):364-384.

Brattegard, T. 1968. Marine biological investigation in the Bahamas; on an association between *Acanthopleura granulata* and *Dynamene* spp. (Isopod). Sarsia 32:11-20.

Brewin, B. I. 1942. The breeding habits of *Cryptoconchus porosus* Burrow. Trans R Soc N Z. 72(2):186-190.

Bullock, R. and K. J. Boss. 1971. *Lithophaga aristata* in the shell-plates of chitons. Breviora. No.369, 10pp.

Burghardt, G. and L. Burghardt. 1969. Report on some abnormal chitons from California and British Columbia. Veliger, 12(2):228-229.

Carpenter, F. 1874. On the generic affinities of the New England chitons. Ann N H 13(4): 119-123.

Castenholz, R. W. 1961. The effect of grazing on marine littoral diatom populations. Ecology. 42:783-794.

Christiansen, M. E. 1954. The life history of *Lepidopleurus asellus*. Nyatt Mag Zool. 2:52-72.

Clarke, W. 1855. On the phenomena of the reproduction of chitons. Ann Mag Nat Hist. 16(2):446-449.

Connell, J. H. 1972. Community interactions on rocky intertidal shores. Ann Rev Ecol Syst. 3:169-192.

Costello, D. P., *et al*. 1957. Methods for obtaining and handling marine eggs and embryos. Marine Biol Lab, Woods Hole, Massachusetts. 247pp.

Couthouy, J. P. 1838. Descriptions of new species of mollusca and shells, and remarks on several polyps found in Massachusetts Bay. Boston J Nat Hist. Vol. II (1838-1839):53-111.

Craig, A. K., S. Dobkin, R. B. Grimm and J, B. Davidson. 1969. The gastropod, *Siphonaria pectinata*, a factor in destruction of beach rock. Am Zool. 9(3):895-901.

Crozier, W. 1918a. Growth and duration of life of *Chiton tuberculatus*. Proc Natl Acad Sci USA. 4:322-325.

Crozier, W. 1918b. Growth of *Chiton tuberculatus* in different environments. Proc Natl Acad Sci USA. 4:325-328.

Crozier, W. 1920. Sex-correlated coloration in Chiton. Am Nat. 54:84-88.

Crozier, W. 1921. Homing behavior in chitons. Am Nat. 55:276-281.

Crozier, W. and L. B. Arey. 1918. Reaction to shading in Chiton. Am J Physiol. 46:487-492.

Dall, W. H. 1878. Report on the limpets and chitons of the alaskan and arctic regions. Proc U S Natl Mus. 1: 53-126.

Dall, W. H. 1921. Summary of the marine shellbearing mollusks of the northwest coast of America, from San Diego to the Polar Sea, mostly contained in the collection of the U S National Museum. Smithsonian Institute, U S Natl Mus Bull. 112:1-127.

Dayton, P. K. 1971. Competition, disturbance and community organization: The provision and subsequent utilization of space in a rocky intertidal community. Ecol Monogr. 351-389.

Douglas, L. 1952. The photic responses of some chitons of Monterey Bay and vicinity. Adv Marine Invert Nat Hist Rept. 45. Zool Dept., Univ. of Calif Berkley (unpublished student report).

Drake, M. 1896. Notes on some shells of Puget Sound. Nautilus. 10.

Evans, F. 1951. Analysis of the behavior of Lepidochiton cinereus. J Anim Ecol. 20:1-10.

Fabricius, O. 1780. Fauna Groenlandica, Lipsae, J. G. Rothe. 452 pp.

Fager, E. W. 1968. A sand-bottom epifaunal community of invertebrates in shallow water. Limnol Oceanogr. 13: 448-464.

Feder, H. M. 1959. The food of the starfish, Pisaster ochraceus, along the California coast. Ecology. 40:721-724.

Fischer-Piette, E. and A. Franc. 1960. Classe des Polyplacophores in Grasse's Traite de Zoologie. 5:1701-1785.

Forbes, E. and S, Hanley. 1850. A history of British Mollusca. Vol. II, London. 557 pp.

Frank, P. W. 1964. The biodemography of an intertidal snail population. Ecology. 46:831-844.

Fretter, V. 1937. The structure and function of the alimentary canal of some species of Polyplacophora. Trans R Soc Edinb 59(4):119-164.

Giese, A. C. 1959. Reproductive cycles of some West Coast invertebrates. Publ Amer Ass Adv Sci. 55:625-638.

Giese, A. C., J. S. Tucker and R. A. Boolootian. 1959. Annual reproductive cycles of the chitons, *Katharina tunicata* and *Mopalia hindsii*. Biol Bull. 117(1):81-88.

Giese, A. C. and M. A. Hart. 1967. Seasonal changes in component indices and chemical composition in *Katharina tunicata*. J Exp Mar Biol Ecol. 1(1):34-46.

Glynn, P. W. 1968. Ecological studies on the association of chitons in Puerto Rico, with special reference to Sphaeromid Isopods. Bull Mar Sci. 18(3):572-626.

Glynn, P. W. 1970. Ecological studies of the Caribbean chitons *Acanthopleura granulata* Gmelin and *Chiton tuberculatus* Linné: Density, Mortality, Feeding, Reproduction and Growth. Smithson Contrib Zool. 66:1-21.

Gould, A. A. 1870. In W. G. Binney (ed.) Report on the Invertebrata of Massachusetts. University Press, Boston. 542 pp.

Graham, D. H. 1941. Breeding habits of twenty-two species of marine mollusca. Trans R Soc N Z. 71(2): 152-159.

Grave, B. H. 1922. An analysis of the spawning habits and spawning stimuli of *Chaetopleura apiculata*. Biol Bull. 42:234-256.

Grave, B. H. 1932. Embryology and life history of *Chaetopleura apiculata*. J Morphol. 54:153-160.

Greenfield, M. L. 1972. Feeding and gut physiology in *Acanthopleura spinigera* (Mollusca). Proc Zool Soc Lond. 166:37-47.

Haven, S. B. 1972. Competition for food between the intertidal gastropods *Acmaea scabra* and *A. digitalis*. Ecology. 54(1):143-151.

Heath, H. 1899. The development of Ischnochiton. Zool Jahrb; Abt Anat., Bd. 12:1-90.

Heath, H. 1903. The function of the chiton subradular organ. Anat Anz. 23:92-95.

Heath, H. 1905. The breeding habits of chitons on the California coast. Zool Anz. 29:390-393.

Heath, H. 1907. The gonad in certain species of chitons. Zool Anz. 32:10-13.

Hedgpeth, J. W. and J. J. Gonor. 1969. Aspects of the potential effect of thermal alteration on marine and estuarine benthos. Biological Aspects of Thermal Pollution: Proceedings of the National Symposium on Thermal Pollution: 80-118.

Helfman, E. S. 1968. A ctenostomatus ectoproct epizoic on the chiton, Ischnochiton mertensii. Veliger. 10(3):290-291.

Hewatt, W. G. 1938. Notes on the breeding seasons of the rock beach fauna of Monterey Bay, California. Proc Calif Acad Sci. 23:283-288.

Hoffman, H. 1930. Amphineura und Scaphopoda. Bronn's Klassen und Ordn Thier-Reichs Mollusca (Weichtiere) Bd. 3:135-453.

Holleman, J. T. and C. Hand. 1962. A new species, genus and family of marine flatworms (Turbellaria: Tricladida, Maricola) commensal with mollusks. Veliger. 5:20-22.

Hyman, L. H. 1967. The Invertebrates. Vol. VI. Mollusca I. McGraw-Hill Book Co., New York, N. Y.

Jillet, J. B. 1968. The biology of Acanthoclinus quadridactylus I. Age, growth and food. Aust J Mar Freshwater Res. 19(1):1-8.

Johns, P. M. 1960. Chiton pelliserpentis. A study in the taxonomy of a species in relation to its breeding biology and ecology. Unpublished M.Sc. Thesis, Univ. of Canterbury, N. Z.

Johnson, C. W. 1934. List of marine mollusca on the Atlantic coast from Labrador to Texas. Proc Boston Soc Nat Hist. 40(1):12-14.

Korringa, P. 1947. Relations between the moon and periodicity in breeding of marine animals. Ecol Monogr. 17:347-381.

Kowalevsky, A. 1879. Über die Entwickelung der Chitonen. Zool Anz. 37(2):469-473.

Kowalevsky, A. 1882. Weitere Studien uber die Entwickelung der Chitonen. Zool.Anz. 113(5):307-310.

Kowalevsky, A. 1883. Embryogenie du *Chiton polii* (Philippi). Ann Mus Hist Natur Marseille, Tom. 1. 5:1-46.

Kues, B. S. 1974. New occurrences of *Ischnochiton retiporosus* Carpenter, 1864, in the Eastern Pacific Ocean. Veliger. 16(4): 366.

Landenberger, D. E. 1968. Studies on the selective feeding in the Pacific starfish *Pisaster* in southern California. Ecology. 49:1062-1075.

Lawrence, A. L., J. M. Lawrence and A. C. Giese. 1965. Cyclic variation in the digestive gland and glandular oviduct of chitons. Science. 147:508-510.

Leloup, E. 1945. A propos de certains chitons du genre' *Tonicella* Carpenter 1873. Bull Mus Hist Nat Belge. 21(4):1-15.

Loven, S. 1856. Uber die Entwickelung von *Chiton*. Arch fur Naturgesch Berlin, Bd.1:206-210.

Lowenstam, H. A. 1962. Goethite in radular teeth of recent marine gastropods. Science. 137:279-280.

Lyngnes, R. 1924. Zur kenntnis der Einhullen der Chitoniden. Skr vid Selk. 20:1-15.

MacGinitie, G. E. and N. MacGinitie. 1949. Natural history of marine animals. McGraw-Hill Book Co., New York, N. Y.

MacGinitie, G. E. and N. MacGinitie. 1968. Notes on *Cryptochiton stelleri* (Middendorff). Veliger 11(1): 59-61.

McLean, J. H. 1961. Feeding behavior of the chiton *Placiphorella*. Ann Rep Amer Malacol Un. 28:39.

McLean, J. H. 1962a. Feeding behavior of Placiphorella. Proc Malacol Soc Lond. 35:23-26.

McLean, J. H. 1962b. Sublittoral ecology of kelp beds of the open coast area near Carmel, California. Biol Bull. 122:95-114.

Magne, A. 1937. Recherches sur l'activite sexuelle et la croissance de deux especés d Amphineures de bassin d'Arcachon Ischnochiton cinereus L. et Acanthochites discrepans Brown. Bull Sta Biol Arcachon. 34:147-159.

Matthews, G. 1953. Influence of behavioral factors on the ecology and orientation of Lepidochitona. Br J Anim Behav,I:79.

Mauzey, K. P. 1966. Feeding behavior and reproductive cycles in Pisaster ochraceus. Biol Bull. 131(1): 127-144.

Mauzey, K. P., C. Birkeland and P. K. Dayton. 1968. Feeding behavior of asteroids and escape responses of their prey in the Puget Sound region. Ecology. 49(4):603-619.

May, V., I. Bennett and T. E. Thompson. 1970. Herbivore-algal relationships on a coastal rock platform. Oecologia. 6:1-14.

Menge, B. A. 1970. The population ecology and community role of the predaceous asteroid, Leptasterias hexactis (Stimpson). Unpublished Ph.D. Thesis, University of Washington.

Mestayer, M. K. 1920. Note on a habit of the chiton, Cryptoconchus porosus (Burrow). Wellington N Z J Sci Technol. 3:117-118.

Metcalf, M. M. 1892. Preliminary notes upon the embryology of Chiton. Johns Hopkins Univ. Circ. 11: 79-80.

Middendorff, A. 1849. Beschreibung und Anatomie ganz neuer Oder fur Russland neuer Chitonen. Mem Acad Sci St Petersbourg, Pt. 2, Sci Natur. Series 6, Vol. 8.

Milligan, H. N. 1916. Behaviour of Chiton ruber. Zoologist, London. 20:467-468.

Monroe, H. C. and R. A. Boolootian. 1965. Reproductive biology in the chiton, Mopalia mucosa. Bull South Calif Acad Sci. 64(4):223-228.

Murti, K. G. and R. Nagabhushanam. 1968. Observations on the spawning and reproductive cycle of Chiton granoradiatus Leloup. Broteria. 37(64):223-233.

Nimitz, M. A. 1964. The reproductive physiology in chiton, Katherina. Ann Rep Amer Malacol Un. 31:50.

O'Brien, F. X. 1972. Some aspects on the biology of a brooding starfish, Leptasterias littoralis, (Stimpson) 1853. Ph.D. Thesis, University of New Hampshire.

Oliver, W. R. B. 1921. Variation in Amphineura. Trans Proc N Z Inst Wellington. 53:361.

Orton, J. H. 1920. Sea temperature, breeding and distribution in marine animals. J Mar Biol Assoc U K 12:339-366.

Paine, R. T. 1966. Food web complexity and species diversity. Am Nat. 100:65-75.

Paine, R. T. 1969. The Pisaster-Tegula interaction: prey patches, predator food preference and intertidal community structure. Ecology. 50:950-961.

Paine, R. T. and R. L. Vadas. 1969. Calorific values of benthic marine algae and their postulated relation to invertebrate food preference. Mar Biol. 4:79-86.

Pelseneer, P. 1924. La proportion relative des sexes chez les animaux et particulierement chez les mollusques. Acad Roy Belg Cl Sci. 8(2):1-258.

Pilson, M. E. Q. and P. B. Taylor. 1961. Hole drilling by Octopus. Science. 134:1366-1368.

Plate, L. H. 1901. Die Anatomie und Phylogenie der Chitonen. Zool Jahrb I Supplement heft 5. Fauna Chilensis 2, heft 2:281-600.

Randall, J. E. 1967. Food habits of reef fishes of the West Indies. Stud Trop Oceanogr. 5:665-847.

Ricketts, E. F. and J. Calvin. 1948. Between Pacific Tides. Stanford Univ. Press.

Robilliard, G. A. 1971. Feeding behavior and prey capture in an asteroid, Stylasterias forreri. Syesis. 4:191-195.

Sars, G. O. 1878. Bidrag til Kundskaben om norges arktiske Fauna. I. Mollusca regionis Arcticae Norvegiae Christiania. 8:1-466.

Schoener, T. W. 1974. Resource partitioning in ecological communities. Science. 185:27-39.

Simroth, H. and H. Hoffman. 1929. Amphineura und Scaphopoda, in Bronn's Klassen und Ordnungen. 3(1):1-511.

Sokal, R. R. and F. S. Rohlf. 1969. Biometry, the principles and practice of statistics in biological research. W. H. Freeman Co., San Francisco, Calif.

Stimson, J. 1970. Territorial behavior of the owl limpet, Lottia gigantea. Ecology. 51(1):113-118.

Taki, I. 1932. On some cases of abnormality of the shell-plates in chitons. Mem Coll Sci Kyoto. 8(1): 27-64.

Taki, I. 1938. Report of the biological survey of Mutsu Bay. 31. Studies on chitons of Mutsu Bay with general discussion on chitons of Japan. Sci Rep Tohoku Univ. 12(3):323-423.

Thiele, J. 1928. Beziehungen zwischen arktischen Loricaten, Gastropoden, Scaphopoden und Bivalven. Fauna Arctica. Bd. 5:1-628.

Thiele, J. 1929. Classis Loricata. Handbuch der Systematischen. Weichteirkunde. Vol.I(1):1-22.

Thorne, M. J. 1968. Studies on homing of the chiton, Acanthozostera gemmata. Aust J Mar Freshwater Res. 19(2):151-160.

Thorpe, S. R. 1962. A preliminary report on spawning and related phenomena in Californian chitons. Veliger. 4:202-210.

Thorson, G. 1946. Reproduction and larval development of Danish marine bottom invertebrates, with special reference to the planktonic larvae in the sound (Øresund). Meddelelser fre Kommissionen for Danmarks Fiskeri og Havundersøgelser Plankton Series. 4:1-523.

Tucker, J. S. and A. C. Giese. 1959. Shell repair in chitons. Biol Bull. 116(2):318-322.

Tucker, J. S. and A. C. Giese. 1962. Reproductive cycle of Cryptochiton. J Exp Zool. 150:33-43.

Tyler, A. V. 1971. Surges of winter flounder, Pseudopleuronectes americanus, into the intertidal zone. Fish Res Board Can J. 28(11):1727-1732.

Vader, W. 1972. Association between amphipods and molluscs: A review of published records. Sarsia 48:13-18.

von Siegfried, G. A. 1954. Aculifera Aplacophora u Aculifera Placophora im Gebiet der Nord und Ostsee. Kiel Meeresforsch. 10:261-271.

Webster, S. K. 1968. An investigation of the commensals of Cryptochiton stelleri in the Monterey Penisula area, California. Veliger. 11(2):121-125.

Whiteaves, J. F. 1901. Catalogue of marine invertebrates of Eastern Canada. Geol Surv Canada. Publ. 772.

Yakovleva, A. M. 1952. Armoured molluscs of the seas of USSR-Loricata. D.S.I.R. No. 53.

Yonge, C. M. 1940. The biology of reef building corals. Scientific Report, Great Barrier Reef Expedition, 1928. 29(1):353-391.