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The structure of subtidal algal and invertebrate assemblages at the Chatham Islands, New Zealand

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Abstract We examined the distribution and abundance of organisms on subtidal rocky reefs at nine sites around the Chatham Islands, a remote group 780 km east of southern New Zealand. We sampled five depth strata ranging from 1 to >16 m to identify spatial patterns in the abundance of algae and invertebrates and to assess their variation within and among sites. This information is used to discuss hypotheses concerning community structure at this remote locality. Several patterns were apparent. The immediate subtidal was occupied by the southern bull kelp *Durvillaea* spp. A suite of 11 fucal species were dominant to a depth of 10 m with an average abundance of 28 m^{-2} , while one species, *Carpophyllum flexuosum*, occurred mostly in deeper water. Only two laminarian species of algae were present at the islands. The indigenous *Lessonia tholiformis* was abundant at 2.5 to 15 m and was not found in deeper water, while the giant kelp *Macrocystis pyrifera* was abundant at two sites in 12 to 18 m. The commercially valuable abalone *Haliotis iris* was extremely abundant in shallow water, with an overall mean of 6 m^{-2} at 5 m. The sea urchin *Evechinus chloroticus* was common, but reached high densities only in small (< 25 m^2) patches. The characteristic urchin-dominated zones reported in kelp beds world-

wide were not seen. There was considerable site-to-site variation in the occurrence and abundance of individual species. Some differences between sites were associated with shelter from swell (e.g. *M. pyrifera* was found only in sheltered sites) and physical habitat (e.g. juvenile *H. iris* were found only beneath boulders inshore), but much of the variation could not be explained by physical or depth-related factors alone. We hypothesize that the differences in these kelp bed assemblages compared to mainland New Zealand are partially due to the high degree of endemism at the Chatham Islands. Local variation cannot be explained by herbivory, and is most likely the result of the various life-history characteristics of the major habitat-forming species, the large brown algae.

Introduction

Descriptions of the distribution and abundance patterns of organisms in subtidal habitats play an important role in understanding the organisation of near-shore marine communities. As hard-shore communities are described from more areas of the world, it is clear that there are few general patterns that occur over wide geographic scales. Consequently, it is unlikely that there are universally important structuring processes except in the broadest sense. In nearshore reef communities dominated by large brown algae, the life-history characteristics of resident algal species, grazing by invertebrates, especially echinoids, and the local regimes of physical disturbance have the major impacts on algal assemblages (Dayton 1985a; Schiel and Foster 1986). Large brown algae are of great importance because of their high productivity (Mann 1973), the habitats they provide for fish and sessile invertebrates (Choat and Ayling 1987; Carr 1989; Andrew and Jones 1990), and their competitive effects within and between species (Reed and Foster 1984). Without a knowledge of

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species assemblages, it is impossible to address broader questions concerning the structure of nearshore communities. How similar are communities within and between geographic areas? What life-history characteristics are shared by the major species? Do similar community structure and related species imply similar structuring processes?

Descriptions of subtidal reef communities have been done in most temperate and boreal regions. As for intertidal communities, however, study sites within regions tend to be few in number (Foster 1990). Consequently, it is not generally known whether the variability of assemblages within a geographic region is as great as that between wider areas (e.g. Foster and Schiel 1985, 1988). If the within-region variability is large, it has important consequences for interpreting biogeographic patterns and their putative causative processes.

The broadest pattern in subtidal algal assemblages is that laminarian algae dominate shores in the northern hemisphere, whereas fucal species are more numerous in the southern hemisphere (Schiel and Foster 1986; Underwood et al. 1991). Float-bearing kelps that form canopies on the sea surface can dominate nearshore reefs along the west coast of North America (Foster and Schiel 1985), Alaska (Dayton 1975; Duggins 1980), Chile (Santelices and Ojeda 1984 a, b), and Argentina (Barrales and Lobban 1975). Where such kelps do not occur, stipitate laminarians form characteristically dense stands, such as on shores along Nova Scotia (Chapman 1984), Japan and Britain (Kain 1979). Another broad pattern is that deforested patches resulting from grazing by echinoids occur in most temperate kelp forests (Harrold and Pearse 1987).

Nearshore reef assemblages in temperate Australia and New Zealand differ from those in other parts of the world. Dense beds of fucal algae dominate the shallow subtidal zone, and usually a single species of stipitate kelp, *Ecklonia radiata*, forms dense stands at middle depths (Womersley 1981; Choat and Schiel 1982; Underwood et al. 1991). The cosmopolitan giant kelp *Macrocystis pyrifera* occurs in the southern regions of both countries, but is abundant at only a few sites (Womersley 1954; Shepherd and Womersley 1971; Kingsford et al. 1989; Schiel 1990). In New Zealand, it is especially difficult to attain a comprehensive view of nearshore community structure because only a few regions have been described. Choat and Schiel (1982), for example, described the patterns of distribution and abundance of algae and invertebrates in northeastern New Zealand and provided a general context for many experimental studies (reviews in Andrew 1988; Jones 1988; Schiel 1988). General habitat descriptions by Schiel (1990), however, showed that assemblages of algae and invertebrates are different in many areas of southern New Zealand, where other species of laminarian and fucal algae dominate reefs. Furthermore, the characteristically large echinoid-dominated areas

common in northern New Zealand are rare in southern sites.

Many of the offshore islands of New Zealand are influenced by oceanic currents that do not strike the mainland (Heath 1985). These islands often have unique biotic components, lacking some prominent coastal species and possessing others that do not occur or are rare along the mainland (Choat and Schiel 1982; Choat and Ayling 1987; Choat et al. 1988; Kingsford et al. 1989; Nelson et al. 1991). They therefore offer excellent opportunities to examine local variability in assemblage structure and its potential effects on interpretations of community organisation.

The Chatham Islands are the most remote populated outpost of New Zealand, lying 780 km east of southern New Zealand. They are the centre of a deep-sea fishing industry and also possess rich inshore fisheries for rock lobsters and abalone. Because of the size of the local abalone fishery, at 292 t annually (Schiel 1992), and its dependence on inshore kelp production, the present study was undertaken to describe the inshore habitats and associations of algae and invertebrates. We describe their abundance patterns along depth gradients at several sites around the islands. These are discussed in the broader context of New Zealand inshore waters and other kelp forests of the world. Our goal was not only to achieve an understanding of the structure of these communities, but also to aid in the management of the abalone fishery and inshore areas.

Materials and methods

Study sites

The Chatham Islands group (44°S; 4°E; Fig. 1) forms part of a ridge of the Chatham Rise, which extends to a depth of 2400 m (Heath 1985). Extreme weather and sea conditions are frequent. A prevailing oceanic swell from the east refracts around the islands. South-westerly storms frequently occur in winter, causing swells of several metres in height. Surface-water temperatures around the islands range from ~8 to 17°C annually (Heath 1985).

There are two main islands in the group and several smaller islets. Chatham Island is approximately horseshoe-shaped and offers some protection from prevailing sea conditions along the margins of Petre Bay. Petre Bay itself and Hanson Bay on the eastern shore are comprised mostly of sandy beaches. There are also long stretches of sandy beach along the northern shore. The remainder of the island, all of Pitt Island, and the islets have rocky substrata along the shoreline. The southern part of Chatham Island along Pitt Strait has cliffs > 100 m high, and is usually exposed to extreme sea conditions. Pitt Island is bounded mostly by steep cliffs and has some protection along the western shore inside Mangere Island.

We sampled nine sites (Fig. 1), that were selected because they had extensive rocky reefs and were accessible in the prevailing sea conditions. The most sheltered sites were Ocean Bay and the two sites within bays at Pitt Island, while Cape L'Eveque was the most exposed. However, all sites can be subjected to extreme sea conditions at times. At the time of sampling (1 to 12 March 1987) there was an easterly swell of 3 m and severe sea conditions through Pitt Strait, limiting the number and location of accessible sites.

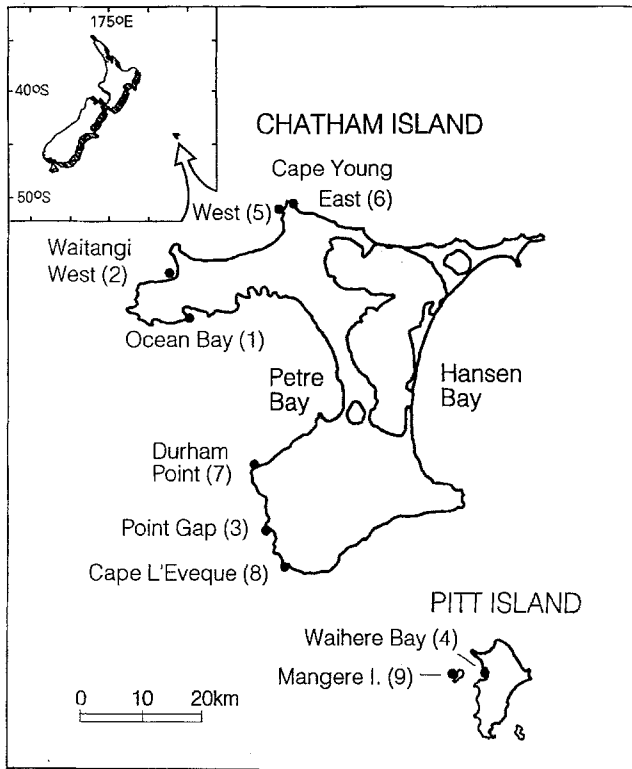


Fig. 1 Map showing position of Chatham Islands group, including Chatham Island, Pitt Island, and Mangere Island. Study sites are indicated by name and reference number

Sampling techniques

The nine sites were sampled at five depth strata: Depth 1, ≤ 1.5 m; Depth 2, 2 to 5 m; Depth 3, 6 to 9 m; Depth 4, 12 to 15 m; Depth 5, ≥ 16 m. Where sampling was limited by the swell, we concentrated our efforts in the middle depths. We intended to sample quantitatively from just below the intertidal fringe, but swell conditions made this impossible at most sites. We did not sample in Depth 5 at sites where the reef went to sand and gravel, or if there were no brown algae evident. Altogether, 33 depth strata were sampled at the nine sites.

We made quantitative estimates of the abundances of algae and invertebrates at each depth stratum, and also recorded size-frequency distributions of abalone and sea urchins, the major invertebrates. Quadrats (1 m^2) were placed by selecting random coordinates along a grid formed by two 30 m survey tapes set at right angles to each other. In each quadrat the data collected were: (1) counts of juvenile (< 20 cm in height) and adult laminarian and fucallean algae; (2) counts of mobile invertebrates (abalone, sea urchins, limpets, trochid and turbinid gastropods); (3) the sizes of abalone (shell length) and sea urchins (test diameter) using vernier calipers; (4) percentage cover of all algal species. Percentage cover was estimated using the random-point quadrat method of Foster (1975) using ten points within each quadrat. Because of vegetational layering, percentage cover within a quadrat could exceed 100%. The number of 1 m^2 quadrats sampled was usually ten at Depths 1 to 3, and five at Depths 4 and 5.

Many more species were encountered than can be accommodated in the descriptions in this paper. Species of larger algae are presented separately, but smaller species of algae are grouped into browns, greens, and reds. We identified algae according to Nelson et al. (1991). The most commonly encountered species and taxonomic authorities are listed in Table 1.

Table 1 Large and common species encountered during quadrat sampling at Chatham Islands. Algae identified from Nelson et al. (1991), invertebrates from Powell (1970)

Algae	Invertebrates
Laminariales	Echinoid
<i>Macrocystis pyrifera</i> (L.)	<i>Evechinus chloroticus</i> Val
<i>Lessonia tholiformis</i> Hay	
Fucales	Gastropods
<i>Carpophyllum maschalocarpum</i> Grev.	<i>Haliotis iris</i> Gmelin
<i>C. plumosum</i> Grev.	<i>H. australis</i> Gmelin
<i>C. flexuosum</i> Grev.	<i>H. virginea</i> Gmelin
<i>Marginariella boryana</i> Tandy	<i>Cookia sulcata</i> (Gmelin)
<i>M. urvilliana</i> Tandy	<i>Micrelenchus caelatus</i> Powell
<i>Cystophora distenta</i> J. Ag.	<i>M. dilatus</i> (Sowerby)
<i>C. scalaris</i> J. Ag.	<i>Trochus viridis</i> Gmelin
<i>C. torulosa</i> J. Ag.	<i>T. tiaratus</i> Quay & Gaimard
<i>Xiphophora gladiata</i> (Labill.)	<i>Maurea tigris chathamensis</i> (Dell)
<i>Landsburgia quercifolia</i> Harvey	<i>Cellana strigilis chathamensis</i> (Pilsbry)
<i>L. myricifolia</i> J. Ag.	<i>Radiacmea inconspicua</i> (Gray)
Durvillaeales	
<i>Durvillaea antarctica</i> Hariot	
<i>D. chathamensis</i> Hay	
Other brown algae	
<i>Halopteris</i> spp.	
<i>Glossophora kunthii</i> J. Ag.	
<i>Zonaria turneriana</i> J. Ag.	
Green algae	
<i>Codium fragile</i> (Suringar)	
<i>C. convolutum</i> (Dellow)	
<i>Ulva</i> spp.	
Red algae	
<i>Gigartina</i> spp.	
<i>Synarthrophyton schielianum</i> Woek. et Fost.	
Other non-geniculate corallines	
Geniculate corallines	

Analyses

Abundance data are presented as means (± 1 SE) for each site and depth. We assessed similarities of sites for all the organisms sampled, by means of cluster analysis on abundance data using Sorenson's index of dissimilarity and a group average fusion (UPGMA, McCune 1991). Overall patterns of key species were then summarized by depth. A correlation matrix was used to assess associations between species at different spatial scales (sites, depth, quadrats).

Results

Algae

Durvillaea chathamensis is a bull kelp endemic to the Chatham Islands and, along with *D. antarctica*, was abundant at all sites, forming a dense cover in the lower intertidal and shallow subtidal zone (< 2 m). Because of

the swell, we were able to measure the abundance of *Durvillaea* spp. only at Site 3. The average density at Site 3 was 2.7 plants (± 1.24) per m^2 , but this provided a canopy cover of 56%. In several other sites, particularly Durham Point (Site 7), Cape L'Eveque (8), Waihere Bay (4), and Mangere Island (9), *Durvillaea* spp. formed virtually a closed canopy in the immediate subtidal zone.

We found only two species of laminarian algae during the survey (Fig. 2). The giant kelp *Macrocystis pyrifera* formed forests at Waitangi West (Site 2) and Cape Young West (5), which are generally protected from the severe weather of the northeast and southwest. At 12 to 15 m (Depth 4), *M. pyrifera* occurred at 0.8 (± 0.13) plants m^{-2} at Waitangi West and 3.2 (± 1.45) at Cape Young West (Fig. 2A). Deeper plants were found only at Waitangi West ($\bar{x} = 1.4 \pm 0.40 m^{-2}$). Most plants reached the sea surface but had no more than five stipes. The higher densities of *M. pyrifera* at Site 5 produced a cover of attached holdfasts and basal fronds of only 12% of the substratum, whereas the lesser numbers at Site 2 produced a cover of 30% at 12 to 15 m (Depth 4) and 54% at > 16 m (Depth 5).

The other laminarian was *Lessonia tholiformis* which is endemic to the Chatham Islands. It occurred to 15 m depth at most sites. Average densities within a depth stratum ranged up to 11 m^{-2} but there was considerable site-to-site variation (Fig 2 B). The canopy of this species, formed ~ 1 m above the substratum, had a cover of $> 10\%$ at 2 to 5 m and 6 to 9 m (Depths 2 and 3) of Sites 1, 8, and 9. *L. tholiformis* was particularly dense at Site 8 where the cover was 65% at 2 to 5 m and 50% 12 to 15 m (Depth 4). Overall, the percentage cover largely reflected the abundance of plants, except at Depth 1 where the plants were small and provided little cover.

Despite intensive searches at all sites, the ubiquitous stipitate kelp of the New Zealand mainland, *Ecklonia radiata*, was not seen. It was recorded as present at the Chatham Islands in 1870, but has not been seen there in recent times (Nelson et al. 1991). Previous to our study, however, only a few subtidal sites had been searched.

We saw 11 species of fucalcan algae during the survey, primarily in shallow water (Table 1). *Xiphophora gladiata* was common at Ocean Bay (Site 1), Point Gap (Site 3), and Mangere Island. (Site 9), primarily at ≤ 1.5 m (Depth 1) but as deep as 9 m (Fig. 3A). Its cover reached 52% at Site 1 and 28% at Site 3 in ≤ 1.5 m depth.

The three *Carpophyllum* species are the common fucalcan along mainland New Zealand. *C. maschalocarpum* and *C. plumosum* are primarily shallow-water species, but occur as isolated plants to depths of ~ 20 m (Choat and Schiel 1982, Schiel 1990). At the Chatham Islands, both species were commonest at 2 to 5 m and 6 to 9 m (Depths 2 and 3; Figs. 3 B, C). *C. maschalocarpum* was particularly abundant at Waitangi West (Site 2), where it reached densities of

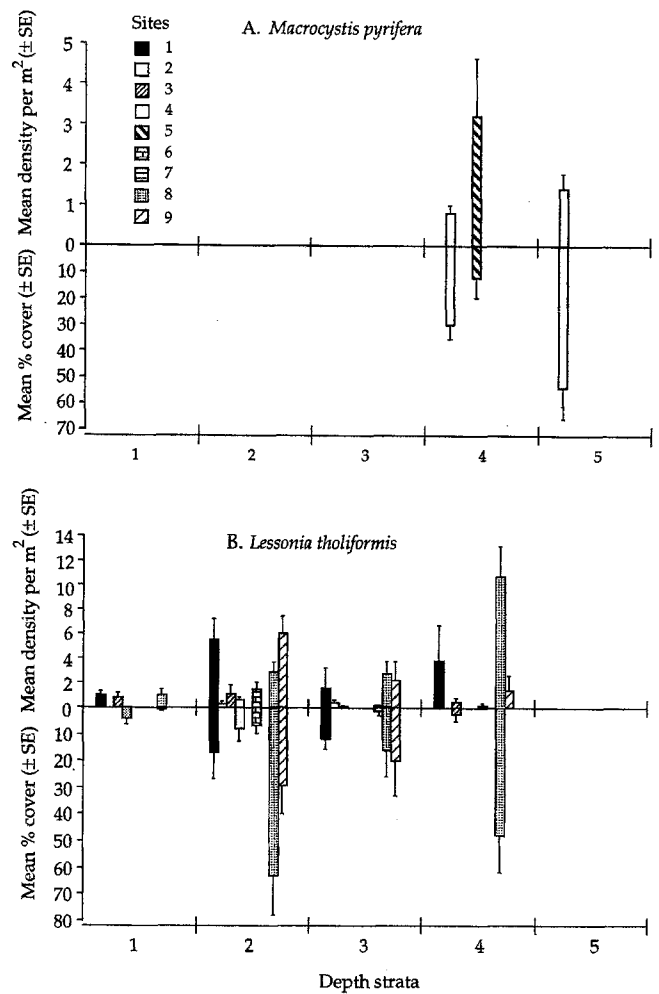


Fig. 2 *Macrocystis pyrifera* (A) and *Lessonia tholiformis* (B). Distribution of laminarian algae by site ($n = 9$) and depth stratum ($n = 5$; Depths 1–5 ≤ 1.5 , 2 to 5, 6 to 9, 12 to 15, ≥ 16 m, respectively). Abundance ($\bar{x} + 1$ SE) m^{-2} above x-axis, percentage cover ($\bar{x} + 1$ SE) below x-axis

37 m^{-2} and a cover $> 30\%$ at 2 to 5 m and 6 to 9 m (Depths 2 and 3). *C. plumosum* reached highest densities at Point Gap (Site 3) and Ocean Bay (Site 1). Average densities of 129 m^{-2} at Site 3, Depth 2 (2 to 5 m), produced a canopy of 59% cover, while a density of 38 m^{-2} at 6 to 9 m (Depth 3) at Site 1 had a canopy cover of 46% (Fig. 3 C).

Carpophyllum flexuosum occurred in the middle depths and beyond (Fig. 3 D). Some small plants were seen at 2 to 5 m and 6 to 9 m (Depths 2 and 3), reaching an average density of 29 m^{-2} at Waihere Bay (Site 4). However, the percentage cover of these plants was virtually zero, as plants were recent recruits. Overall, the greatest numbers and cover occurred in Depths 4 and 5 (12 to 16+ m). In deeper water, *C. flexuosum* was particularly abundant at Ocean Bay (Site 1), Cape Young East (Site 6), Durham Point (Site 7), and Mangere Island (Site 9). Average densities at Depth 4 (12 to 15 m) ranged from 16 to 42 plants m^{-2} , with

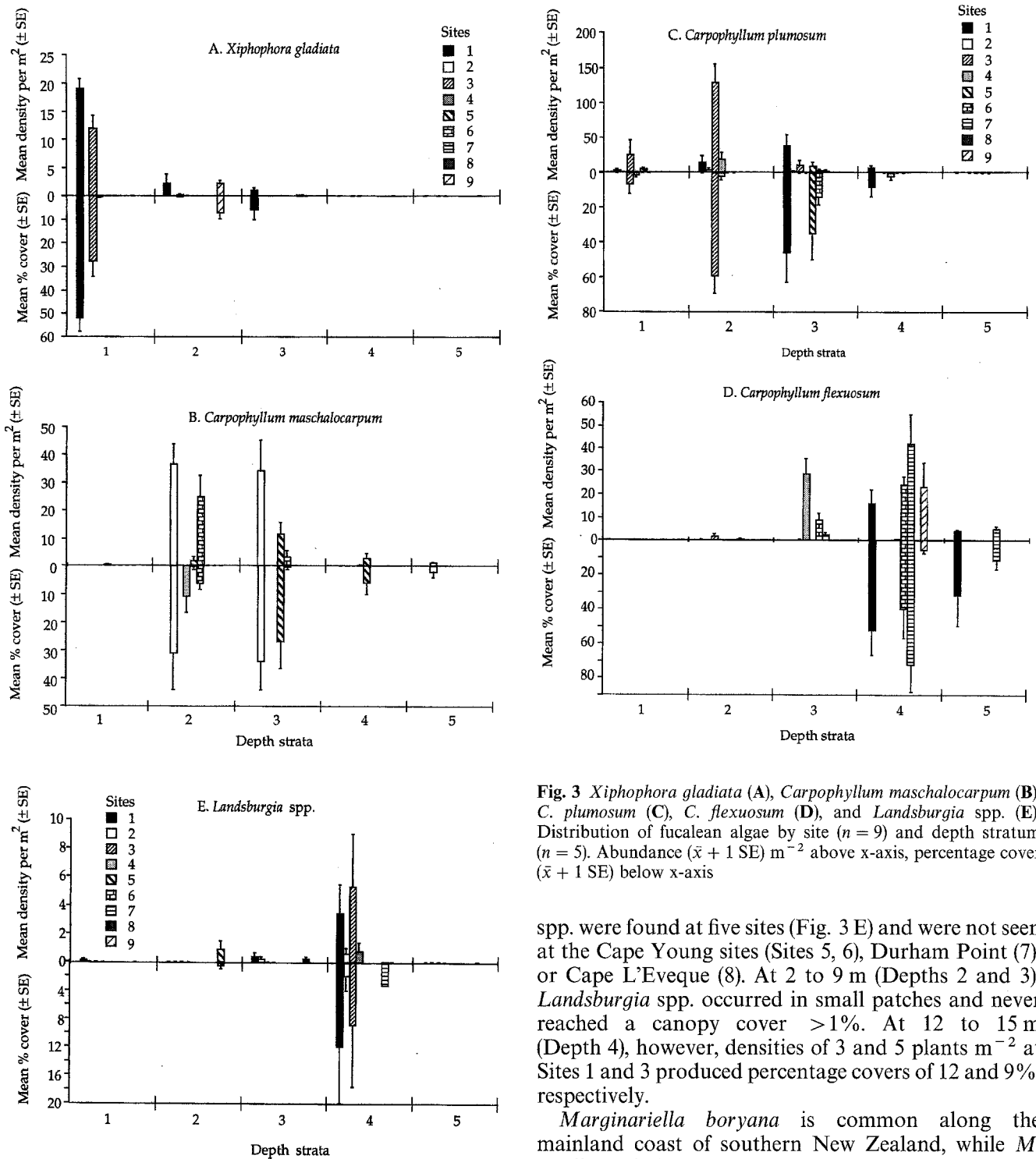


Fig. 3 *Xiphophora gladiata* (A), *Carpophyllum maschalocarpum* (B), *C. plumosum* (C), *C. flexuosum* (D), and *Landsburgia* spp. (E). Distribution of fuclean algae by site ($n = 9$) and depth stratum ($n = 5$). Abundance ($\bar{x} + 1$ SE) m^{-2} above x-axis, percentage cover ($\bar{x} + 1$ SE) below x-axis

cover ranging from 40 to 72%. The relatively small numbers of *C. flexuosum* in Depth 5 (≥ 16 m) at Sites 1 and 7 produced percentage covers of 32 and 12%, respectively, because plants were large.

Two species of *Landsburgia* occur at the Chatham Islands. *L. quercifolia* was the commoner species, but the endemic *L. myricifolia* was also found at most sites. Data for these two species were combined. *Landsburgia*

spp. were found at five sites (Fig. 3 E) and were not seen at the Cape Young sites (Sites 5, 6), Durham Point (7), or Cape L'Eveque (8). At 2 to 9 m (Depths 2 and 3), *Landsburgia* spp. occurred in small patches and never reached a canopy cover $>1\%$. At 12 to 15 m (Depth 4), however, densities of 3 and 5 plants m^{-2} at Sites 1 and 3 produced percentage covers of 12 and 9%, respectively.

Marginariella boryana is common along the mainland coast of southern New Zealand, while *M. urvilleana* is less common. Both species were encountered at the Chatham Islands, but were found only at Ocean Bay (Site 1) in 6 to 15 m (Depths 3 and 4), where they reached combined densities of $3.0 (\pm 3.00)$ and $1.5 (\pm 1.17)$ per m^2 and percentage covers of 12 and 6%, respectively. *Cystophora* spp. (*C. distenta*, *C. scalaris*, *C. torulosa*) occurred in small numbers at Sites 1, 3 and 5. The greatest average density was $0.4 (\pm 0.40)$ at Site 1, Depth 4 (12 to 15 m), with a percentage cover of $<5\%$.

There were numerous species of understory algae. The most abundant of these in terms of percentage cover were the brown algae *Halopteris* spp., *Glossophora kunthii*, and *Zonaria turneriana*. *Halopteris* spp. reached its greatest percentage cover of 8% at Site 8, Depth 2 (2 to 5 m), while *G. kunthii* had its greatest cover of 13% at Site 8, Depth 4 (12 to 15 m). Understory brown algae were more abundant in shallow water. Understory red algae (excluding corallines) were patchy in their distribution among sites. Generally, they were more abundant in the intermediate depths (2 to 15 m). No species were particularly prominent; many were combined during the survey into either filamentous or foliose forms. Green algae occurred at all sites, but were never a prominent component of the understory. The most common taxa were *Codium* spp. and *Ulva* spp.

The commonest understory algae were the corallines, which were abundant at all sites and all depths. In most cases they displayed >40% coverage of the substratum. The most common forms were thin crusts in shallow water, thin multi-layered crusts in deeper water, and small patches of geniculate turfs in all depths. The endemic, multi-layered, non-geniculate *Synarthrophyton schielianum* was particularly common on steep slopes in deep water at all sites (Woelkerling and Foster 1989). The cover of coralline algae was reduced in Depths 1 and 5 (≤ 1.5 and ≥ 16 m) at some sites. The reduction was usually associated with a high cover of fleshy algae in Depth 1 and a high coverage of sessile invertebrates at ≥ 16 m in Depth 5.

Invertebrates

The most abundant of the large, mobile invertebrates was the abalone *Haliotis iris* (Fig. 4A). This was found in all sites except Ocean Bay (Site 1) and Mangere Island (Site 9). *H. iris* is a shallow-water species and occurred deeper than 9 m only at Site 8. Juveniles (<70 mm shell length) were found exclusively on the undersides of boulders. They were abundant at Durham Point (Site 7), Cape L'Veque (Site 8), and Waitangi West (Site 2), reaching average densities up to 5.5 m^{-2} . Juveniles were not found at Ocean Bay, the two Cape Young sites (6 and 7), and Mangere Island (Site 9). This was probably due to the shortage of appropriate-sized boulders to serve as habitat. Adult *H. iris* were abundant at most sites, reaching average densities as high as 15 m^{-2} in Depth 2 (2 to 5 m). It is noteworthy that several sites with relatively dense adult populations had few or no juveniles.

Haliotis australis was much less common, and was found mostly in Depth 2 (2 to 5 m). Although it was found at six sites, it never reached densities of 3 m^{-2} . The small abalone *H. virginea* was encountered at Durham Point (Site 7), where it occurred at 0.8 m^{-2} in Depth 4.

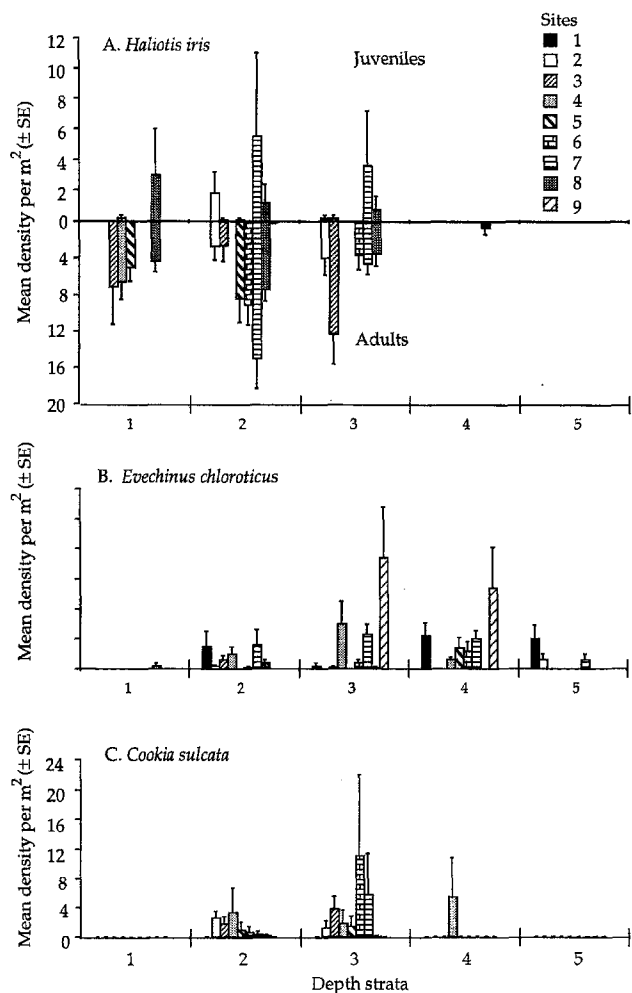


Fig. 4 *Haliotis iris* [A, juveniles (<70 mm shell length) above x-axis, adults below x-axis], *Evechinus chloroticus* (B), and *Cookia sulcata* (C). Distribution of invertebrate herbivores by site ($n = 9$) and depth stratum ($n = 5$) ($\bar{x} + 1 \text{ SE m}^{-2}$)

The other large and common invertebrate was the sea urchin *Evechinus chloroticus*. It is an ubiquitous echinoid of New Zealand kelp beds and is found throughout the coastal waters of New Zealand (Choat and Schiel 1982; Schiel 1990). *E. chloroticus* was found at all sites, with greatest densities at 6 to 15 m (Depths 3 and 4; Fig. 4B). *E. chloroticus* was most abundant at Mangere Island (Site 9), at average densities of 5 to 7 m^{-2} . Despite these relatively high average densities, *E. chloroticus* was not seen in the characteristically extensive deforested areas reported in northern New Zealand and in most kelp habitats of the world (Choat and Schiel 1982; Harrold and Pearse 1987). The abundance of *E. chloroticus* at the Chatham Islands was characterized by a high variance within sites and depths. Dense aggregations of up to 40 large echinoids per m² were encountered, but deforested patches were never seen larger than $\sim 25 \text{ m}^2$.

The turbinid gastropod *Cookia sulcata* was abundant in the three middle depths at most sites, reaching

average densities of 11 m^{-2} at 6 to 9 m (Depth 3; Fig. 4C). Other gastropods were patchy in occurrence with respect to sites and depths (not presented graphically). Trochid gastropods were found in small numbers at most sites and never reached densities $> 3 \text{ m}^{-2}$ except at Cape L'Eveque (Site 8), Depth 1 ($\leq 1.5 \text{ m}$), where the average density was 48 m^{-2} . Limpets were also very patchy, being recorded at most sites but reaching densities of $126 (\pm 46.0) \text{ m}^{-2}$ at 6 to 9 m (Depth 3) at Point Gap (Site 3) and $107 (\pm 24.9) \text{ m}^{-2}$ at Durham Point (Site 7), where they were associated with abalone, sea urchins, and encrusting coralline algae beneath a sparse canopy of *Lessonia tholiformis*.

Large, sessile invertebrates were relatively uncommon. The exception was in $\geq 16 \text{ m}$ (Depth 5) at Cape Young West (Site 5). This area had a canopy cover of *Macrocystis pyrifera* and an extensive reef that rose 2 m above the sand floor. Unlike some other deep areas where the reef was composed of low-lying boulders, it appeared that sand scour did not affect the understory here. Small sponges, tunicates, and bryozoans were common beneath layers of non-geniculate corallines. This algae-invertebrate matrix was usually 1 to 4 cm thick.

Overall associations

There were clearly site \times depth interactions in the abundances of all species. Overlaying this patchiness were broader trends in species associations. A correlation analysis of the abundance data matrix showed significant correlations at three spatial scales (Table 2). At the scale of sites, there were positive correlations among many of the fucal algae, indicating a broad overlap in the abundances of these species. Among invertebrates, *Evechinus chloroticus* tended to be abundant in sites where the deep-water fucal *Carpophyllum flexuosum* was abundant. Juvenile *Haliotis iris* covaried with limpets, *H. australis* and *H. virginea*, which shared common habitat requirements.

At the scale of depths, there were few correlations among algal species. *Durvillaea* spp. shared the shallow depth with *Xiphophora gladiata*, but there was a broad overlap of species with depth. *Haliotis iris* juveniles and adults, both of which were most abundant in shallow water, were negatively correlated with *Macrocystis pyrifera*, which is a deeper-water species. At the finer spatial scale of quadrats, the only significant algal correlation was *Landsburgia* spp. with *Marginariella* spp.. *H. iris* adults were negatively correlated with *Lessonia tholiformis* and *Carpophyllum flexuosum*, the holdfasts of which could cover much of the substratum, and were positively associated with *Durvillaea* spp., which formed a canopy over parts of the shallow rocky areas where abalone were most abundant. The sea urchin *Evechinus chloroticus* was again positively associated with *C. flexuosum*. Interestingly, at no spatial scale was

Table 2 Correlations between species at three spatial scales: by site ($n = 9$), by depth stratum ($n = 5$), and by quadrat ($n = 259$). In all cases $P < 0.05$

By site		
<i>Durvillaea</i> spp.	with	<i>Carpophyllum plumosum</i> (0.97)
<i>Landsburgia</i> spp.	with	<i>Carpophyllum plumosum</i> (0.68)
		<i>Xiphophora gladiata</i> (0.83)
<i>Carpophyllum flexuosum</i>	with	<i>Cookia sulcata</i> (0.68)
		<i>Evechinus chloroticus</i> (0.63)
<i>Marginariella</i> spp.	with	<i>Cystophora</i> spp. (0.96)
		<i>Xiphophora gladiata</i> (0.85)
<i>Haliotis iris</i> juveniles	with	Limpets (0.68)
		<i>Haliotis australis</i> (0.74)
		<i>Haliotis virginea</i> (0.79)
By depth		
<i>Durvillaea</i> spp.	with	<i>Xiphophora gladiata</i> (0.99)
		Trochids (0.99)
<i>Xiphophora gladiata</i>	with	Trochids (0.99)
<i>Haliotis iris</i> adults	with	<i>Macrocystis pyrifera</i> (−0.97)
		<i>Carpophyllum plumosum</i> (0.88)
<i>Haliotis iris</i> juveniles	with	<i>Macrocystis pyrifera</i> (−0.87)
		<i>Carpophyllum plumosum</i> (0.93)
<i>Haliotis australis</i>	with	<i>Carpophyllum plumosum</i> (0.96)
Limpets	with	<i>Cookia sulcata</i> (0.98)
By quadrat		
<i>Landsburgia</i> spp.	with	<i>Marginariella</i> spp. (0.20)
<i>Haliotis iris</i> adults	with	<i>Lessonia tholiformis</i> (−0.12)
		<i>Durvillaea</i> spp. (0.13)
		<i>Carpophyllum flexuosum</i> (−0.13)
		<i>Haliotis australis</i> (0.14)
<i>Haliotis iris</i> juveniles	with	<i>Haliotis iris</i> adults (0.23)
		<i>Haliotis australis</i> (0.38)
<i>Evechinus chloroticus</i>	with	<i>Carpophyllum flexuosum</i> (0.17)

there a correlation between *E. chloroticus* and any of the gastropod species, even though this association was found at particular sites and depths. This result is quite different from that reported for northern New Zealand (Ayling 1981; Choat and Andrew 1986).

The cluster analysis showed that sites were grouped largely by differences in exposure (Fig. 5). Sites 1 (Ocean Bay), 4 (Waihere Bay) and 9 (Mangere Island) were relatively protected within bays. Sites 3 and 7 were near each other along the coast around Durham Point and had similar protection. Site 8, along the southern coast, was the most exposed of all the sites. The three northern sites (2, 5, and 6) were similar in exposure, species composition and species abundance, except for the presence of *Macrocystis pyrifera* forests at Sites 2 and 5. At these sites, there were relatively few giant-kelp plants compared to other species, but they formed a dominant habitat because of their great percentage cover. Overall, however, most species occurred at most sites.

General patterns with depth

Superimposed on site differences, however, were differences among depths in the distributions of species. *Durvillaea* is clearly a shallow-water genus and there

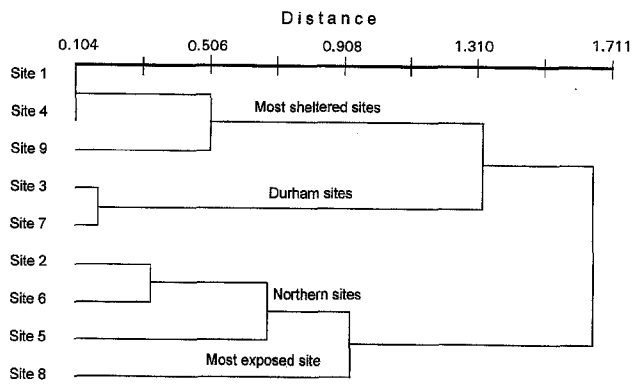


Fig. 5 Cluster analysis of abundance data for nine sites. Site numbers as in Fig. 1. Major characteristics of clusters are indicated

were no exceptions to its occurrence in the immediate subtidal zone. Its average abundance and percentage cover was considerably underestimated because we were not able to assess it quantitatively in all sites. *Lessonia tholiformis* had its peak abundances in Depths 2 (2 to 5 m) and 4 (12 to 15 m), and did not occur in Depth 5 (Fig. 6 A). *Macrocystis pyrifera* forests occurred only in Depths 4 and 5. *Carpophyllum maschalocarpum* and *C. plumosum* shared the middle depths with other fucaleans and *L. tholiformis*, although *C. plumosum* also occurred in Depth 1 (Fig. 6 B). All fucaleans except *C. flexuosum* were scarce beyond Depth 3 (>9 m). *Landsburgia* spp. were most abundant in Depth 4 (12 to 15 m) but their overall abundance was not great. *C. flexuosum* was the dominant fucalean species in deeper water, with an average abundance over all sites of $12 (\pm 2.8) \text{ m}^{-2}$ in Depth 4 and $3 \text{ m}^{-2} (\pm 0.7)$ in Depth 5, with a canopy cover of 15 to 20%.

Understory species also showed clear depth-related patterns of distribution (Fig. 6 C). Brown algae were most common in shallow water, having a cover of 5 to 6% in < 5 m (Depths 1 and 2). Red algae (other than corallines) showed the opposite pattern, with increasing cover to Depth 4 (15 m). The reduced cover of red algae in the deepest areas was at least partially due to the abundance of sponges and other encrusting invertebrates in Depth 5. Green algae had only a small coverage at most depths and were not seen beyond Depth 4.

Haliotis iris was abundant to Depth 3 (9 m) with overall densities $> 5 \text{ m}^{-2}$ (Fig. 6 D). Only a few individuals were found in deeper water and none beyond 15 m depth. The sea urchin *Evechinus chloroticus* was most abundant in deeper water from depths of 6 to 16 m, with an overall abundance of 1 to 2 m^{-2} . Gastropods other than *H. iris* reached peak abundances in Depth 3 and were uncommon in deeper water (Fig. 6 E). These were mostly limpets that occurred in great abundances at two sites.

The size-frequency distributions of the major herbivorous invertebrates also showed clear patterns with

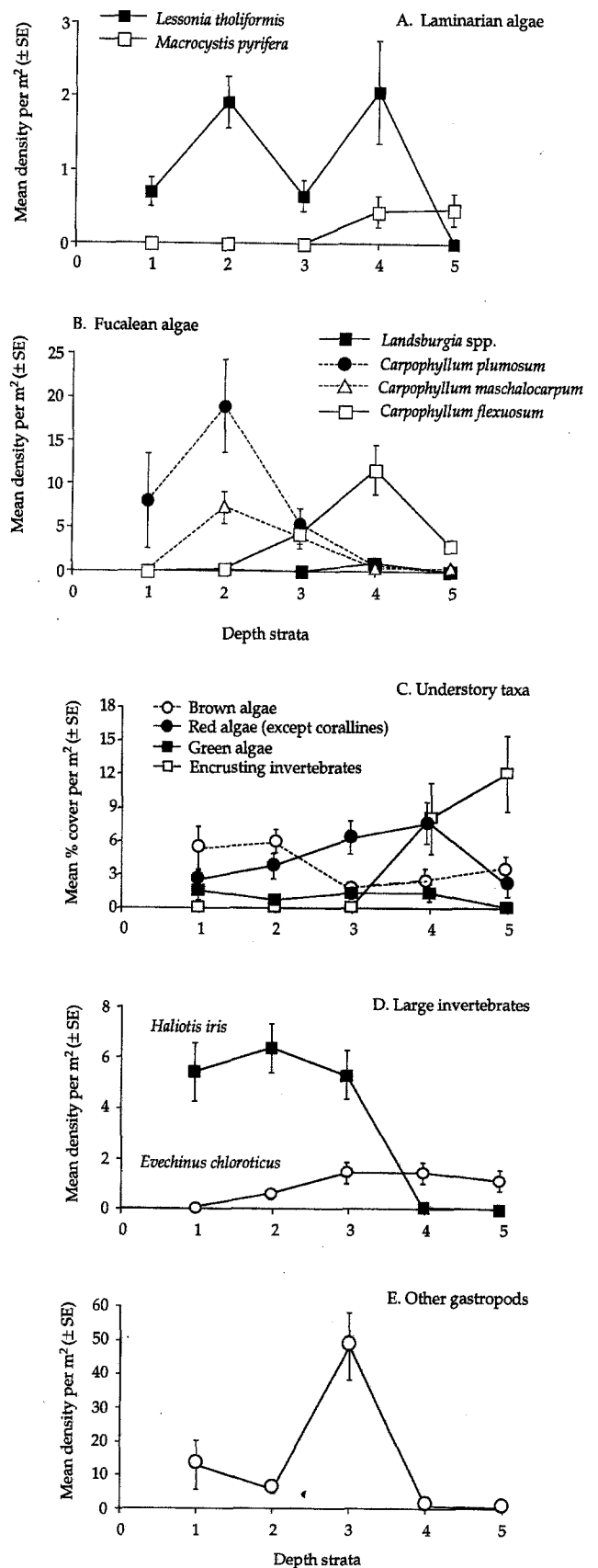


Fig. 6 Summary of taxa distributions by depth, combining data from all sites

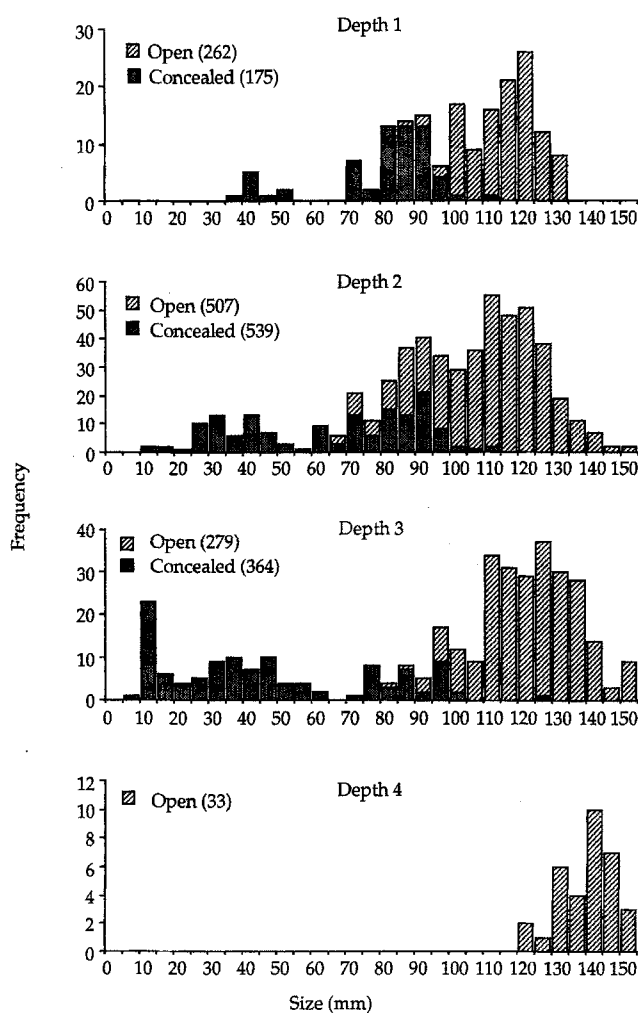


Fig. 7 *Haliotis iris*. Size-frequency (number) distributions by depth stratum. None were found in Depth 5 (*Open* individuals found exposed on rock surfaces; *Concealed* individuals on underside of rocks and boulders) Sample sizes (*N*) are given in parentheses

depth. A wide range of sizes of the abalone *Haliotis iris* occurred in Depths 1 to 3 (≤ 9 m; Fig. 7). Only large individuals, however, were found in Depth 4 and none were seen in Depth 5. All *H. iris* < 60 mm were concealed in under-boulder habitat. There was a transition of sizes as abalone emerged into open-reef habitats, and virtually all individuals beyond 100 mm were exposed on reefs. Juvenile sea urchins (< 70 mm) were seen only in Depths 2 and 3 (≤ 5 m; Fig. 8). Large individuals were found in all depths beyond 2 m. Only urchins > 100 mm were seen in deep water (> 15 m).

Discussion

Biogeography

The Chatham Islands are remote from a land mass and lie directly on the Subtropical Convergence. They are

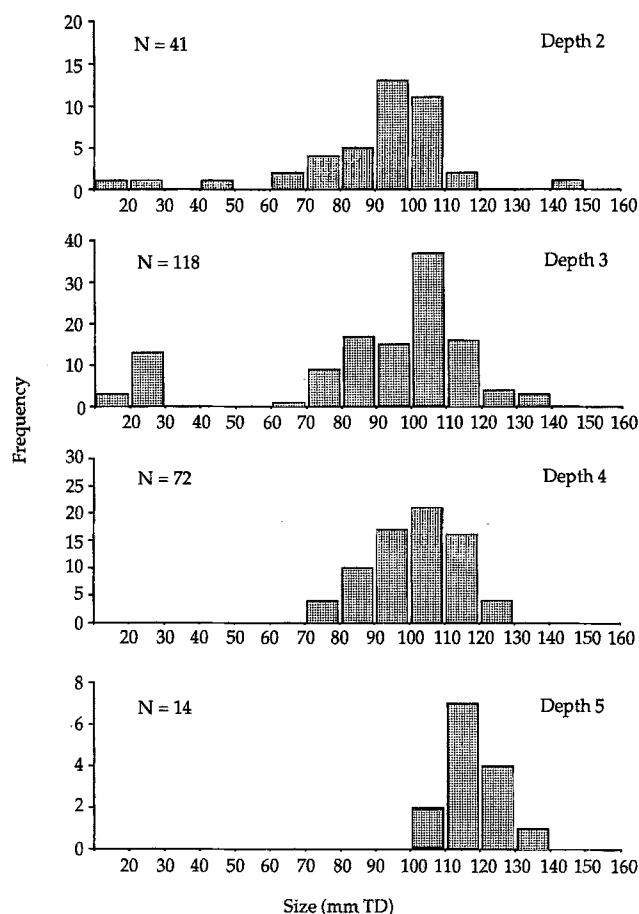


Fig. 8 *Evechinus chloroticus*. Size-frequency (number) distributions by depth stratum. None were found in Depth 1 (*TD* test diameter)

isolated from mainland New Zealand by oceanic currents and deep-sea trenches. This geographic position has important influences on the submarine flora, and provides a unique mixture of endemics and species also found on the mainland (Nelson et al. 1991). During our survey, many species were identified that are common in northern New Zealand while others are considered southern species (Nelson et al. 1991). Most notable, however, was the absence of the stipitate laminarian alga *Ecklonia radiata*, which is found extensively along mainland New Zealand and provides the dominant kelp habitat at many locations (Choat and Schiel 1982; Schiel 1988, 1990).

The flora of the Chatham Islands has clear affinities to the southern half of New Zealand, including the islands south of the mainland (Moore 1949; Knox 1963). Large algae of the genera *Macrocystis*, *Lessonia* and *Durvillaea* are abundant from Cook Strait south as far as the sub-antarctic Auckland Islands (250 km south of mainland New Zealand). In this respect there are striking similarities between the southern offshore islands of New Zealand, southern Australia, and Chile. The genera *Macrocystis*, *Lessonia* and *Durvillaea* are distributed widely along latitudes south of $\sim 42^\circ$.

Durvillaea species form the major component of the intertidal–subtidal boundary in much of Tasmania and southeastern Australia (Womersley 1981; Cheshire and Hallam 1988, 1989), Chile (Santelices et al. 1980; Bustamante and Castilla 1990), Tierra del Fuego, and the islands of the Southern Ocean (Hay 1994). *M. pyrifer* is the dominant canopy species in many sheltered areas of southern Australia (Womersley 1981), and occurs extensively along the coasts of Chile and Argentina (Santelices and Ojeda 1984a, b; Dayton 1985a, b) and many of the sub-antarctic islands (Womersley 1954). The genus *Lessonia* has a peculiar geographic distribution and the taxonomy of many species is unclear (Hay personal communication). *L. vadosa* occurs extensively in Chile and may set the upper depth limit of *M. pyrifer* (Santelices and Ojeda 1984a). *L. nigrescens* occupies the shallowest subtidal regions and competes with *D. antarctica* in central Chile (Castilla and Bustamante 1989). At the Auckland Islands, south of mainland New Zealand, *L. brevifolia* is the dominant alga at a depth of ~5 m, while *M. pyrifer* dominates in deeper water (Hay et al. 1985; Schiel 1990). *L. tholiformis* is very similar in appearance to *L. vadosa*.

At the Chatham Islands, the endemic species of large brown algae were *Lessonia tholiformis*, *Landsburgia myricifolia*, and *Durvillaea chathamensis*. Both *Lessonia tholiformis* and *D. chathamensis* occur extensively around the islands.

Site × depth interactions

There was considerable variation in the abundances of algae and invertebrates with respect to depth and sites. This patchiness was exemplified by the deep *Macrocystis pyrifer* forests that occurred at only two relatively sheltered sites, the occurrence of *Marginariella boryana* at only one site, *Cystophora* spp. as isolated plants at two sites, the extreme abundances of limpets at 6 to 9 m depth at two sites, and the large variation in abundances and depth distribution of abalone and sea urchins. This patchiness provides clues to the underlying processes that may account for the structure of assemblages at the Chatham Islands. There is no distributional evidence for the types of strong organizing processes described for northern New Zealand and for other temperate areas of the world (Dayton 1985a; Schiel and Foster 1986; Harrold and Pearse 1987; Andrew 1988; Schiel 1988; Elner and Vadas 1990). For example, the much documented sea urchin-dominated habitat of mid and deep water (Harrold and Pearse 1987) is missing from the Chatham Islands. In only one site, Durham Point, were sea urchins locally abundant in an area where there were few kelp. Interestingly, sea urchins at this site were associated with large numbers of gastropods, including the abalone *Haliotis iris*, despite the overall lack of correlation between *H. iris* and *Evechinus chloroticus*.

In the absence of a dominant herbivore such as sea urchins, interactions among algae may assume greater importance in determining habitat structure (Dayton 1985a; Schiel and Foster 1986). Further evidence for this is the complexity of algal assemblages at most sites and the lack of clear dominance of single species within depths at each site. In these circumstances, the life-history characteristics of individual species, the timing and intensity of physical disturbances, and the abilities of species to persist in different physical regimes may have the major influences on the local array of species.

Hypotheses concerning habitat structure

At larger spatial and taxonomic scales, several patterns become apparent (Fig. 9). The bull kelps, *Durvillaea* spp., are restricted to the immediate subtidal region, an area that experiences severe water motion (South and Hay 1979). Other large brown algae seem incapable of persisting at a similar depth, either because of the physical regime or else through competition with *Durvillaea* spp. Beneath the canopy of *Durvillaea* spp. is usually an area with few large brown algae. This is possibly due to the whiplash effect of *Durvillaea* spp. (cf. Santelices et al. 1980; Santelices and Ojeda 1984 b), reduced light beneath the canopy, and the inability of other algae to recruit into these areas. In this depth there are large numbers of abalone, particularly juveniles on the undersides of the tumbled boulders that are common inshore. The shallow depth zone is usually partitioned finely. Fucal species can survive well in 1.5 m depth, but were not seen in large numbers in areas of great water motion where *Durvillaea* flourished. In northern New Zealand, where *Durvillaea* spp. are rare, this shallow depth is normally occupied by a dense cover of fucal species, particularly *Carpophyllum angustifolium* (Choat and Schiel 1982), a species not found at Chatham Island (Nelson et al. 1991).

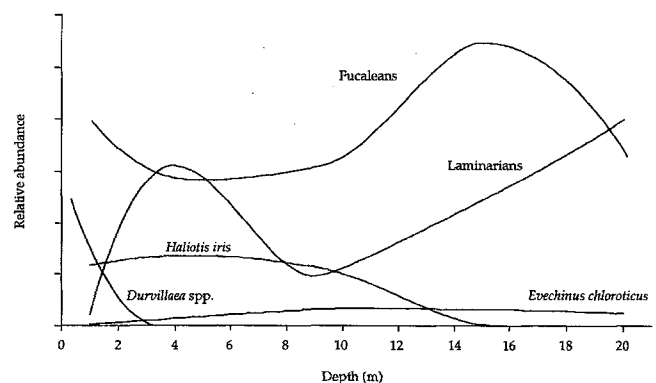


Fig. 9 Stylized graph of depth distribution of major taxa at Chatham Islands

Fucalean algae are found in all depths, with *C. Carpophyllum flexuosum* being the dominant species, both in numbers and percentage cover, in deep water. Between 6 and 15 m, fucalean algae are more abundant and have a greater cover than laminarian algae. At 2 to 5 m depth, however, laminarian and fucalean algae have approximately equal cover, but are assorted on a fine spatial scale. The species-mix of these areas may well be the result of competitive interactions among algal species based on their differential abilities to recruit and grow when free space becomes available (Schiel and Foster 1986). In the deepest areas, the only dominant large brown algae were either *Macrocystis pyrifera* or *C. flexuosum* and they tended to be mutually exclusive. Because of its large size, *M. pyrifera* required few plants to produce a dominant canopy (Fig. 2).

Lessonia spp. are capable of persisting in shallow areas of intense water motion and can be abundant to 15 m depth (Choat and Schiel 1982; Schiel 1990). In parts of northern New Zealand, especially some off-shore islands, *L. variegata* may form dense stands immediately below a zone occupied by *Carpophyllum angustifolium* (Choat and Schiel 1982). In Chile, *L. nigrescens* competes with *Durvillaea antarctica* in the intertidal-subtidal boundary (Santelices et al. 1980). Another species, *L. vadosa*, competes with *Macrocystis pyrifera* in middle depths (Santelices and Ojeda 1984 a, b). There is evidence at the Chatham Islands that fucalean species and *L. tholiformis* compete at a depth of 2 to 5 m. *L. tholiformis* increases in abundance as the fucaleans decrease (Figs. 6 and 9). However, there are few correlations, either positive or negative, among the major algal species at any spatial scale. This supports the observation that all these species are patchy in occurrence along a reef and do not generally occur in large, monospecific stands as is common in northern New Zealand (Choat and Schiel 1982). The degree of exposure may play a role in determining the abundance of species. For example, *M. pyrifera* and *C. maschalocarpum* occupy sites on the north and west sides of Chatham Island which are somewhat protected from the full force of easterly and southwesterly storms. *L. tholiformis* is found at most sites, but is particularly abundant at Site 8, which is exposed to southwesterly swells. In waters beyond 15 m depth, however, it seems unlikely that competition affects the abundance of *Lessonia*. In northern New Zealand, the Cook Strait region, the Auckland Islands, and the Chatham Islands, its abundance declines in deep water whether or not other species are present at particular sites (Schiel 1990). Virtually nothing is known about the growth rate, recruitment processes, dispersal abilities, and longevity of *Lessonia* species in New Zealand. All have a tough, fibrous stipe and leathery laminae, characteristics associated with long-lived perennials.

The absence of the stipitate kelp *Ecklonia radiata* results in major differences in the subtidal habitats of the Chatham Islands, relative to most of New Zealand.

Wherever it occurs, *E. radiata* shares dominance at depths of 2 to 8 m with fucalean species. On deeper reefs, however, it is almost invariably dominant, except in sheltered waters where *Carpophyllum flexuosum* may be abundant (Choat and Schiel 1982; Schiel 1990). *E. radiata* grows quickly, disperses well, particularly when reproductive plants are nearby, and lives for up to 10 yr (Novaczek 1984; Schiel 1988). The southern limit of *E. radiata* is the Snares Islands, just south of mainland New Zealand. If this species occurred at the Chatham Islands, it seems likely that it would extensively occupy middle and deeper portions of reef that currently have a sparse cover of *Lessonia tholiformis* and some fucalean species. In areas where it co-occurs with *C. flexuosum*, such as Fiordland (on the south-west mainland coast), *E. radiata* is the dominant species in 10 to 20 m depth, and *C. flexuosum* is reduced to occupying small patches (Schiel 1990).

The absence of *Ecklonia radiata* may also affect the large herbivorous invertebrates. The extensive sea urchin-dominated areas of northern New Zealand are invariably associated with the boundary, at ~8 m depth, between shallow fucalean species and deeper *E. radiata* beds (Choat and Schiel 1982). This border does not exist in southern New Zealand and the Chatham Islands, and instead this zone is usually occupied by several fucalean species and *Lessonia tholiformis* (Schiel 1990). These species are much less susceptible to damage and removal by sea urchins than is *E. radiata* (Schiel 1982), which may affect the ability of sea urchins to dominate the zone. In northern New Zealand, the ability of sea urchins to dominate a cleared area is enhanced by a positive association with herbivorous gastropods (Ayling 1981; Choat and Andrew 1986). This relationship was not seen at the Chatham Islands, although high densities of limpets were associated with sea urchins at two sites.

The relationship between sea urchins and abalone at the Chatham Islands is not clear. Adult abalone are found almost exclusively on encrusting coralline algae in areas where there are few large algae. Sea urchins may contribute to the provision of this sort of habitat inshore, so some form of facilitation may occur (cf. Duggins 1981). However, abalone and sea urchins have common requirements of space and algal food, and it is possible that they compete (Lowry and Pearse 1973). This seems unlikely at the Chatham Islands, because both *Haliotis iris* and *Evechinus chloroticus* feed primarily on drift algae, which seem to be abundant inshore. Moreover, *H. iris* generally occurs in shallower water than *E. chloroticus* (Figs. 7 and 8), and may be more resistant to wave action.

One of the more noteworthy results from a fisheries perspective was the poor correlation between juvenile and adult abalone, *Haliotis iris*. Juveniles occurred exclusively on the undersides of rocks and boulders inshore, while adults occurred throughout rocky substrata, mostly in < 9 m depth. Many sites that had

high densities of adults had few or no juveniles (Fig. 4). In all cases, such sites had few or no boulders inshore to provide suitable habitat for juveniles. It appears that recruitment of this important commercial species may be habitat-limited.

A major problem in deciphering the processes determining the structure of subtidal habitats in remote areas is the logistic difficulty in conducting experimental studies. Can the processes that affect more accessible areas be extrapolated to other places, particularly when the mixture of species is different? The only reasonable clues seem to lie in the distribution and demography of the prominent component species. In unique offshore areas such as the Chatham Islands, which support large inshore fisheries, these questions become important to the management of fisheries of abalone and sea urchins. If biotic processes of grazing interactions are important to the structure of nearshore areas, the commercial removal of large numbers of abalone and sea urchins may affect habitat structure and reduce the abilities of these invertebrates to recruit back into specialised habitats. If physical processes and their interplay with the life histories of species have the major effects, then offshore areas should be amenable to comparisons with more accessible places. In the absence of strong structuring interactions, the demography and life histories of individual species assume more importance. Our data support the hypotheses that physical factors, demography and life histories are the most important structuring processes in the algal and invertebrate assemblages at the Chatham Islands. Unfortunately, for remote areas such as the Chatham Islands it is unlikely that an understanding of community organisation will be derived from in situ experimental studies. In any case, changes due to species removals are likely to occur over a long time span, and the gradual reduction in numbers of commercially valuable species such as abalone, sea urchins, and lobsters may well produce only subtle effects on the rest of the community structure.

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