Biological structure of nearshore rocky subtidal habitats in southern New Zealand

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ABSTRACT

Subtidal surveys were done on rocky reefs in three regions of southern New Zealand: the east coast of the central South Island (Kaikoura and Banks Peninsula), Fiordland, and the Chatham Islands. The abundance and percentage cover of large brown algae and understorey species were assessed, and herbivorous invertebrates were counted in several depth strata within each site. Reef fish were counted in transects in shallow (3-8 m depth) and deep (12-15 m) areas within sites. Fucalean algae dominated shallow areas in all regions, but the species composition varied among regions. *Carpophyllum maschalocarpum* dominated inshore areas in some sites around Banks Peninsula, whereas *Marginariella boryana* dominated exposed sites around Kaikoura. While both species were common in outer coast sites in Fiordland and the Chatham Islands, the shallow depths in these locations were dominated by *Xiphophora gladiata*. *Carpophyllum flexuosum* was the dominant fucalean alga in all regions. *Ecklonia radiata*, the ubiquitous kelp of mainland New Zealand, dominated depths beyond 10 m in east coast sites and Fiordland, but was absent from the Chatham Is. An endemic laminarian, *Lessonia tholiformis*, dominated most shallow and mid depths at the Chatham Is. Major differences among regions were the great cover of encrusting invertebrates in the understorey around Banks Peninsula, and the large numbers of black coral, brachiopods and sea pens in the inner areas of Fiordland. The most striking differences in the mobile reef fish fauna among regions were: the large number of spotties, *Notolabrus celidotus*, around Banks Peninsula; the dominance of the fish fauna by scarlet wrasses, *Pseudolabrus miles*, in Fiordland; and the great abundance of blue cod, *Parapercis colias,* at the Chatham Is. The three regions are affected by different oceanic currents and the assemblages are strongly influenced by these and the life history features of the dominant organisms.

Keywords: subtidal species habitats, rocky reefs, brown algae, sessile invertebrates, reef fishes, Kaikoura coast, Banks Peninsula, Chatham Islands

1. Introduction

Descriptions of the distribution and abundance patterns of organisms in subtidal communities play an important role in understanding the organisation of nearshore marine ecosystems. As more hard shore communities are described from different areas of the world, few general patterns of community structure hold 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, including dispersal abilities, recruitment episodes and competition (Reed et al. 1988; Reed 1990), grazing by invertebrates, especially echinoids, and the local regimes of physical disturbance have the major impacts on algal assemblages (Dayton 1985a; Schiel & 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 & Ayling 1987; Carr 1989; Andrew & Jones 1990), and their competitive effects within and between species (Reed & Foster 1984; Santelices & Ojeda 1984a; Johnson & Mann 1988). Without knowledge of 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 & Schiel 1985, 1988). If the within-region variability is large, it has important consequences for interpreting biogeographic patterns and their putative causative processes.

One of the broadest patterns in temperate subtidal algal assemblages is the dominance of laminarian species in the Northern Hemisphere. A rich assemblage of float-bearing kelps (that form sea-surface canopies) and stipitate kelps dominate the west coast of North America from warm temperate to boreal latitudes (Dayton 1975; Duggins 1980; Foster & Schiel 1985). There are few fucalean species, although some of these may be locally abundant (Schiel 1985; Foster & Schiel 1985). Where surface-canopy kelps do not occur, stipitate laminarians form characteristically dense stands, such as along the coast of Nova Scotia (Chapman 1984; Johnson & Mann 1988), Japan and Britain (Kain 1979). Southern Hemisphere kelp beds show considerable variation in the dominance of large brown algal taxa among regions. The giant kelp *Macrocystis pyrifera* can dominate semi-protected and sheltered shores in Chile (Santelices & Ojeda 1984a, b), Argentina (Barrales & Lobban 1975), Australia (Womersley 1954) and New Zealand (Schiel 1990). Most of the coast of Chile is exposed, however, and is dominated by kelps of the genus *Lessonia* from the intertidal zone through the shallow subtidal regions to around 20 m depth (Villouta & Santelices 1984, 1986), although the southern bull kelp *Durvillaea antarctica*

is present in the immediate subtidal zone in some places (Santelices 1989). The exposed south-west coast of South Africa is dominated by a floating canopy of the kelp *Ecklonia maxima* and an understorey of *Laminaria pallida* (Field et al. 1980). In both of these regions, fucalean algae are rare.

The nearshore subtidal reef assemblages in temperate Australia and New Zealand, however, differ from those in other parts of the world because of the high diversity of fucalean algae. Dense beds of fucaleans dominate the shallow subtidal zone and usually a single species of stipitate kelp, *Ecklonia radiata*, forms dense stands at middle depths (Womersley 1981; Choat & 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 & Womersley 1971; Kingsford et al. 1989; Schiel 1990).

Another broad pattern in kelp beds worldwide is that deforested patches, resulting from grazing by echinoids, occur in most temperate kelp forests. These urchin-dominated 'barrens' may persist for long periods and form distinct habitats in many areas (Chapman 1981; Dayton 1985a; Harrold & Pearse 1987).

In New Zealand, it is difficult to attain a comprehensive view of nearshore community structure because only a few regions have been described. Choat & Schiel (1982), for example, described the patterns of distribution and abundance of algae and invertebrates in north-eastern 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 were different in many areas of southern New Zealand, where other species of laminarian and fucalean algae dominate reefs. Furthermore, the characteristically large echinoid-dominated areas common in northern New Zealand were rare in the southern sites he examined. Many southern areas, however, have yet to be described quantitatively.

Here we describe abundance patterns of algae, invertebrates and fish along depth gradients at several sites within three geographic regions: the east coast of the central South Island, Fiordland, and the Chatham Islands. Patterns are discussed in the broader context of New Zealand inshore waters and other kelp forests of the world.

2. Materials and methods

The purpose of these surveys was to describe habitats, and abundance patterns of the major algae, invertebrates, and fishes. A variety of survey techniques were used, some of which were modifications of standard methods necessary to suit the prevailing conditions at particular sites. The surveys were done, often in conjunction with other research programmes, over several years in the late 1980s and early 1990s.

2.1   STUDY SITES

Surveys were done in three geographic regions: the east coast of the central South Island (Kaikoura and Banks Peninsula), Fiordland, and the Chatham Islands. These represent major regions of southern New Zealand, and considerable logistic support was available to survey within them. Seven sites were surveyed around Kaikoura, two at Banks Peninsula, 13 at Fiordland, and nine at the Chatham Islands. In each region, we attempted to sample sites over as wide a range of rocky habitats as possible, but our choice of sites was influenced and sometimes restricted by sea conditions during the survey periods. Each of the regions presented a range of oceanic conditions. Kaikoura and Banks Peninsula are generally exposed to a prevailing oceanic swell. This region marks the northernmost position of the Subtropical Convergence, also known as the Southland Front (Heath 1985), and is frequently exposed to high-energy oceanic swells and storm waves. Annual water temperatures range from 8.5°C to 19°C (Ottaway 1976). The unusually steep longitudinal profile of rivers and streams feeding into coastal waters around the Kaikoura Peninsula produces frequent flooding (Chandra 1969). This flooding, together with the softer rock types, such as limestone and siltstone, that dominate much of the coastline (Chandra 1969) and agricultural run-off often produce a heavy sediment load in the inshore waters of the eastern South Island, making underwater clarity poor. The seven sites at Kaikoura encompassed the entire peninsula (Fig. 1). Quantitative surveys were done for fish at all sites and for all organisms at one site (Shark's Tooth reef). Underwater visibility tended to be better at Banks Peninsula than at Kaikoura. The two Banks Peninsula sites were at Godley Head and Taylor's Mistake (Fig. 2). These were on the northern side of
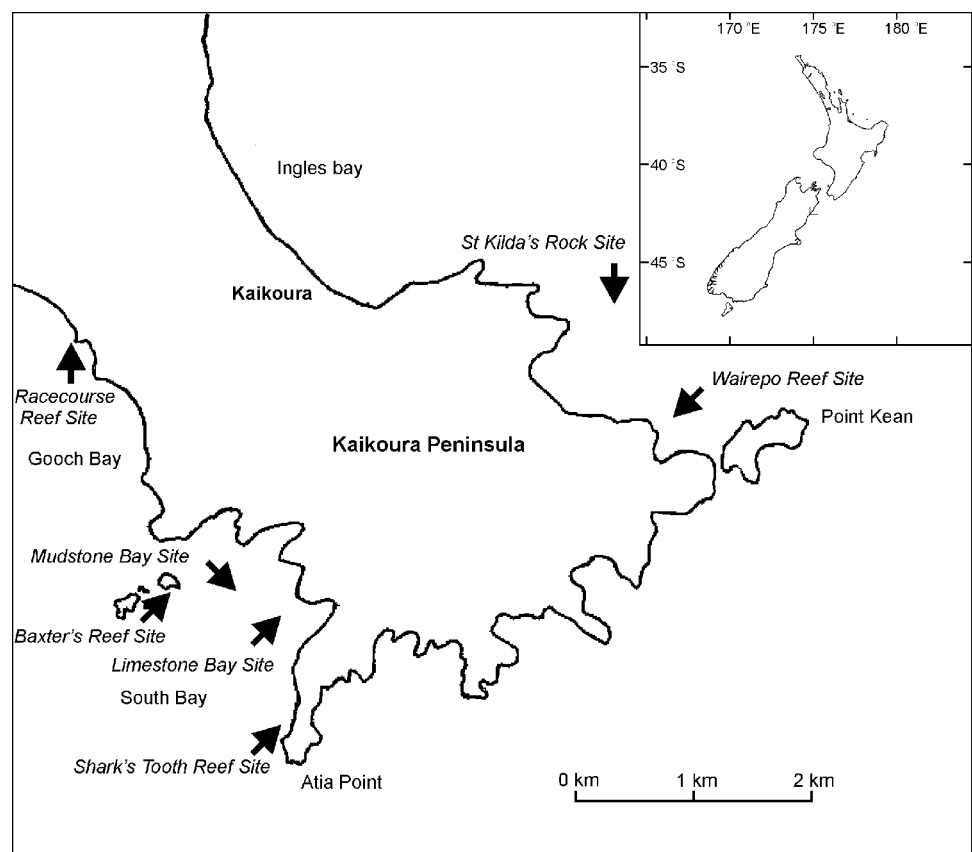

Figure 1. Study sites around Kaikoura Peninsula on the east coast of the South Island.

the peninsula and therefore protected from southerly swells. Algae, invertebrates and fish were counted at these sites.
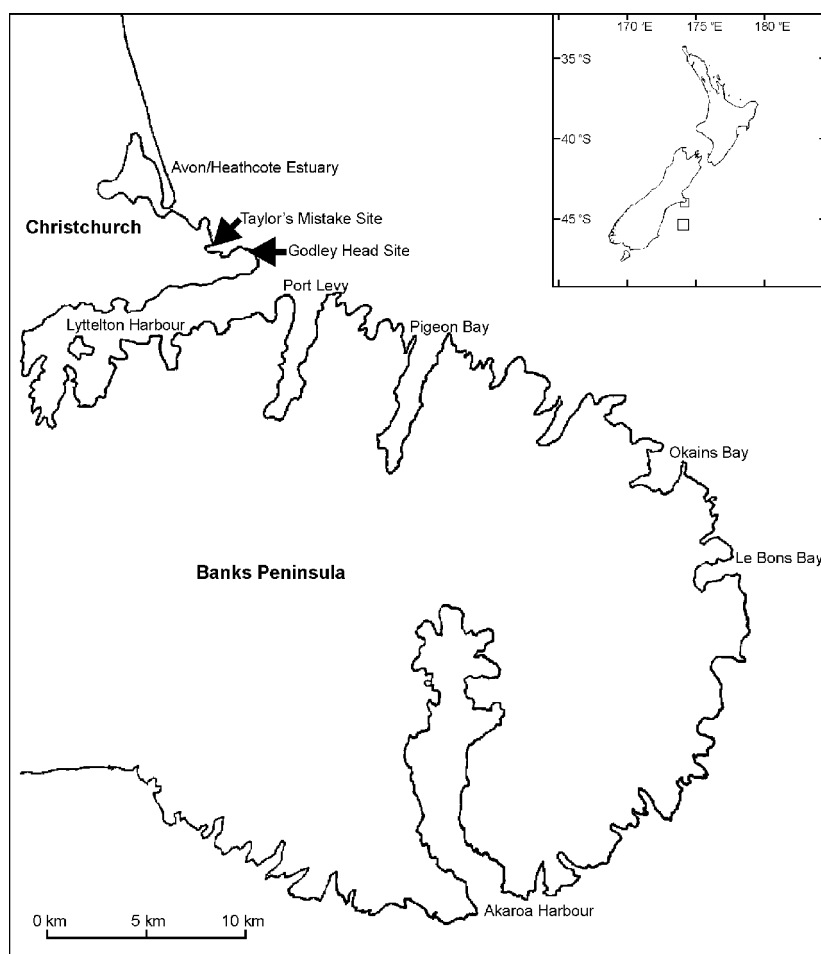

Figure 2. Study sites around Banks Peninsula on the east coast of the South Island.

The outer coast of Fiordland is exposed most of the time to extreme swells, which can limit sampling in the shallowest depths. Oceanic swells do not penetrate far into the Sounds, but underwater visibility can be poor, especially in the inner Sounds where there is a freshwater lens on the sea surface and a high organic loading. The 13 sites were distributed from Poison Bay in the north to Driftwood Cove in the south (Fig. 3). These were categorised into the inner Sounds sites (Grono Bay, 2nd Cove and 3rd Cove), mid Sounds sites (Poison Bay, Disappointment Cove and Driftwood Cove) and outer Sounds and coastal sites (Little Bay in Sutherland Sound, McKerr Point in Caswell Sound, Thompson Sound, Secretary I. in Doubtful Sound, Febrero Point, Five Fingers Peninsula and Anchor I.). Quantitative surveys for algae, invertebrates and fish were done at all sites.

Extreme weather and sea conditions are frequent at the Chatham Is. A prevailing oceanic swell from the south-east refracts around the islands. South-westerly storms frequently occur in winter, causing swells of several metres in height. Of the nine sites sampled (Fig. 4), those in the north (Ocean Bay, Waitangi West, and Cape Young East and West) were less exposed than the southern sites (Durham Point, Point Gap, Cape L'Eveque, Waihere Bay and Mangere I.). Surface seawater temperatures range from around 9°C to 17°C annually (Heath 1985).
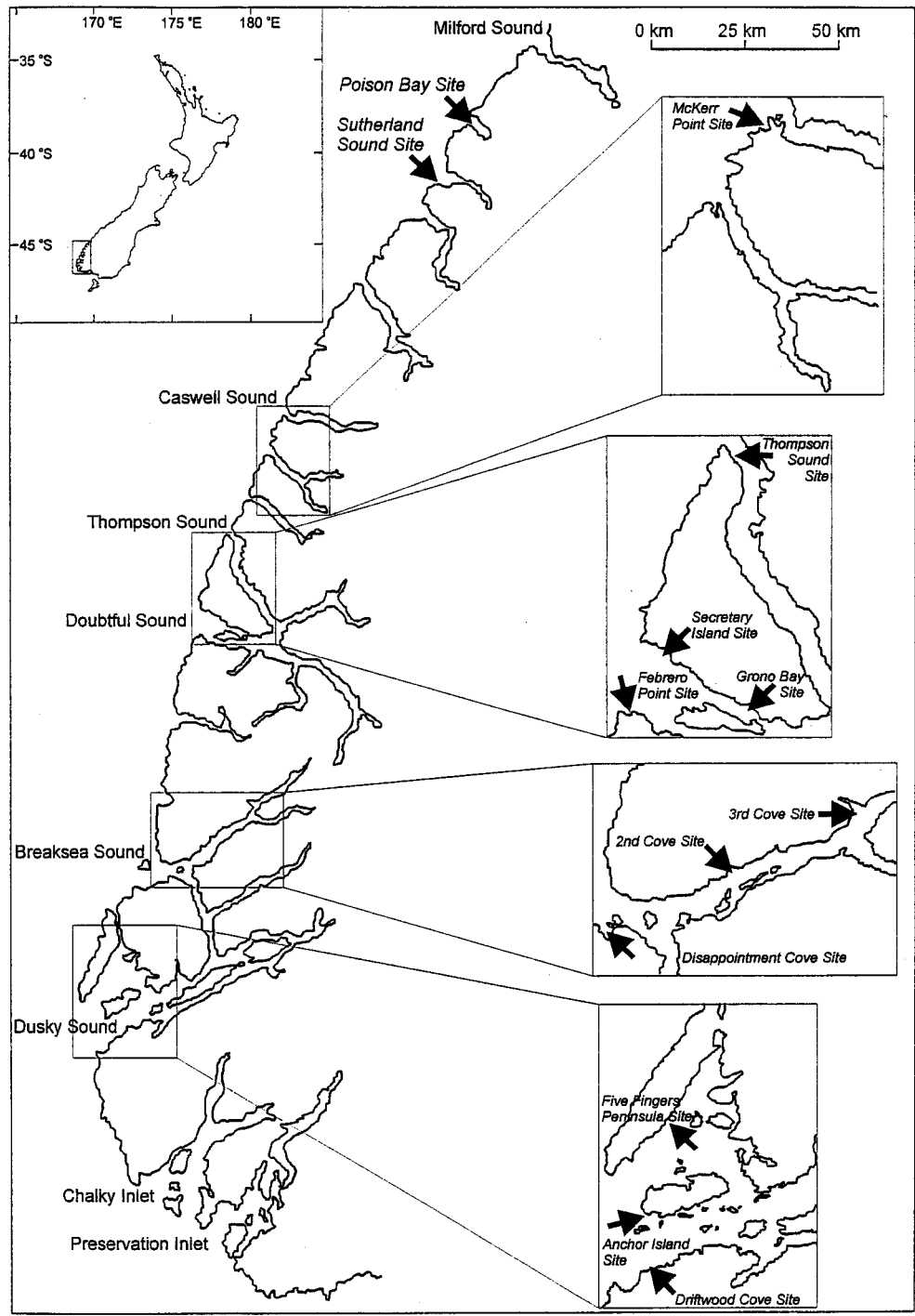
Figure 3. Study sites in Fiordland on the south-west coast of the South Island.

2.2 ALGAE AND INVERTEBRATES

Sampling varied among sites because of the differences in swell conditions and because survey methods were being developed and refined. At many sites, initial sampling efforts were to gauge the types of general habitats present so that more intensive quadrat sampling methods were sure to be placed within areas representative of the site. In these initial surveys, three transects were run at least 20 m apart perpendicular to the shore. Transects were started in as shallow a depth as possible in the prevailing conditions. The dominant habitat below each transect line was recorded in 2 m² blocks as divers swam along the
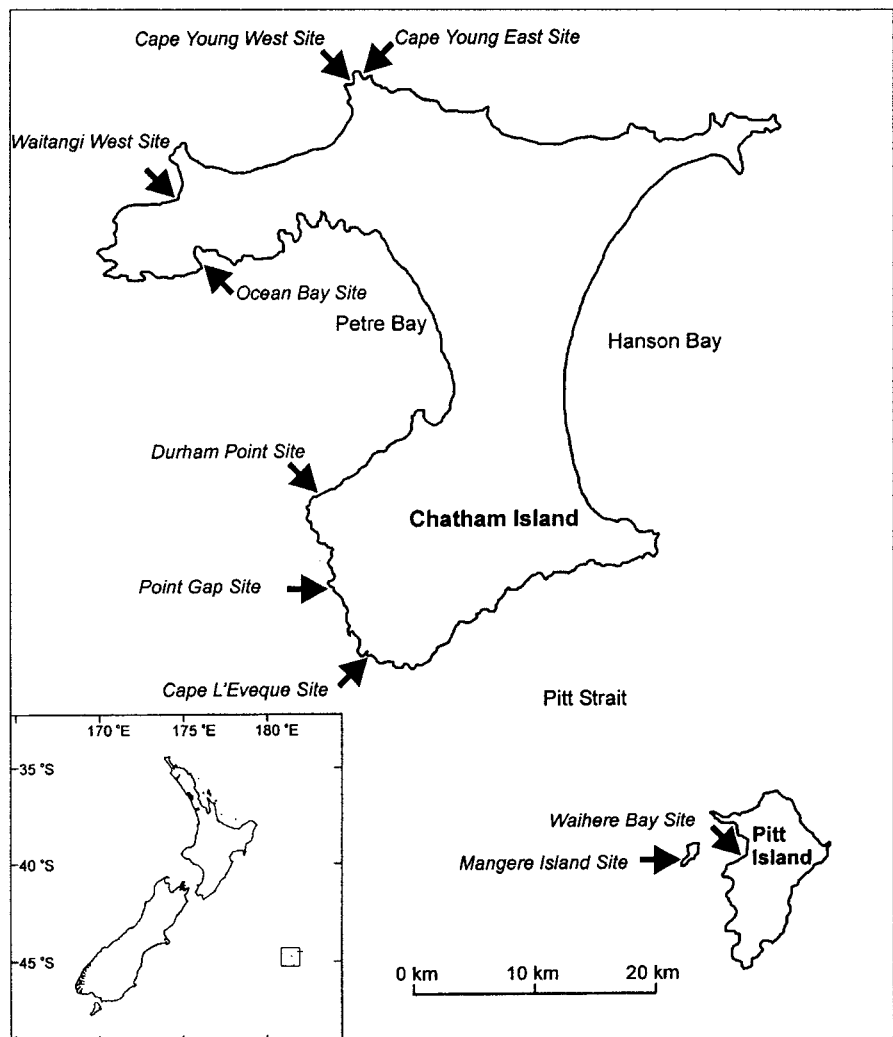
Figure 4. Study sites on Chatham and Pitt Islands.

tape. The distance along the tape and the depth of each habitat were recorded. There is necessarily a subjective element to this technique because habitats can be complex. However, it is usually possible to identify readily the dominant habitat types. Transect lengths were either 100 m or were ended where the reef went to sand. This technique was similar to that described by Underwood et al. (1991).

Stratified depth sampling was the primary method for quantitative surveys. The position of the shallowest sample depended on local swell conditions, whereas the deepest samples were usually determined by the end of rocky reef. We did not sample where reef went to sand or gravel. Quantitative estimates of the abundances of algae and invertebrates were done within each selected depth stratum. Quadrats (1 m²) 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 fucalean algae;

(2) counts of mobile invertebrates (sea urchins, abalone, limpets, sea stars, trochid and turbinid gastropods);

(3) percentage cover of algae and sessile invertebrates.

Percentage cover was estimated using the random point quadrat method of Foster (1975) using 10 points within each quadrat. Percentage cover within a quadrat could exceed 100% because of vegetational layering. The number of 1 m^2 quadrats sampled was usually 10, but only 5 were sampled in some shallow areas when swell conditions were severe. At the Chatham Is, algae were identified according to Nelson et al. (1991).

2.3 FISH SURVEYS

An optimisation procedure was used to determine the minimum transect size necessary to achieve reasonable precision in estimates of fish abundance. The ability to identify and count fish depends on local visibility conditions. This procedure was done around Kaikoura, where underwater visibility is usually poor. Furthermore, the composition of the underwater habitats, particularly rocky pinnacles with reef and gravel between them, often make it difficult to keep long transects within single habitat types. It was therefore necessary to derive a sample unit that optimised the precision of estimates of reef fish numbers in average conditions, while keeping within logistical constraints (McCormick & Choat 1987). Transect sizes were increased in areas where underwater visibility was greater, to achieve better precision in estimates of fish abundance. Transect areas are clearly designated in Section 3.

To survey fish populations, a surveyor's fibreglass tape was laid out along the substratum from randomly selected starting points and in an arbitrarily chosen direction on a reef (Leum & Choat 1980; Choat & Ayling 1987; Kingsford et al. 1989). We used an optimisation procedure to determine the precision of estimates and the effort required to survey five transect sizes (50 m × 5 m, 40 m × 5 m, 30 m × 5 m, 20 m × 5 m, and 10 m × 5 m). This was done so that we could select a transect size that was appropriate for most conditions and habitats. The goal was to choose the most precise transect length that also allowed multiple replicates to be done in a single dive. A 5 m wide transect (i.e. 2.5 m either side of the transect line) was chosen because it allowed fish to be counted in most diveable conditions. In the optimisation procedure, three replicates of each transect size were done at fifteen sites around Kaikoura, encompassing different substrata and algal types. The species and standard length of all reef fish (excluding small benthic fishes) seen in each transect were recorded. The precision, calculated as the standard error divided by the mean density estimate of the three replicate transects (Downing & Anderson 1985; McCormick & Choat 1987), was calculated at each site for each of the five transect sizes. Data were then combined to give the mean precision of each transect size across the 15 different sites. Precision was determined for total fish numbers, and individually for the two most common species, the labrids *Notolabrus celidotus* and *N. fucicola*.

At most sites, we surveyed fishes in shallow (5–10 m) and deeper (13–18 m) depth strata. All mobile reef fishes were counted and their sizes (standard length) were visually estimated.

3. Results

3.1 KAIKOURA AND BANKS PENINSULA

3.1.1 General habitats

As expected, there was considerable variation in habitat structure among sites on the east coast of the South Island. Within the Kaikoura area, five habitat types were distinguished (Table 1). These were identified during surveys of fish populations (see below). The habitats were rocky reef with mixed algal stands, rocky reefs characterised by stands of the fucalean alga *Marginariella boryana*, reefs with low-lying stands of mixed fucaleans, deeper reefs dominated by crustose coralline algae, and patch reefs in deeper water. The reef that we sampled quantitatively for all organisms at Shark's Tooth, on the southern side of Kaikoura Peninsula, was a steeply sloping reef subjected to a large prevailing swell and occasional extreme exposure. The area around this site is typified by mixed algal stands at all depths to 20 m. In terms of general habitat, the fucalean alga *Carpophyllum maschalocarpum* dominated the immediate subtidal (0-3 m), but this zone was not sampled quantitatively because of the large swell. The large fucalean *Marginariella boryana* dominated the reef from about 7 m to 10 m depth (Fig. 5A). At about 12-14 m depth, the green alga *Caulerpa brownii* and the fucalean *Landsburgia quercifolia* dominated the reef, and mixed algal stands of laminarians and fucaleans dominated depths below 14 m. The deeper parts of the reef were dominated by coralline algal habitat. The reefs in this area go to sand and shingle at about 18-20 m depth. Steep pinnacles occur commonly along the coast around Kaikoura and a range of habitats is usually encountered over short distances.

TABLE 1. HABITAT TYPES IDENTIFIED DURING SURVEYS OF FISH POPULATIONS IN THE KAIKOURA AREA.

HABITAT	DESCRIPTION
Rocky reef, mixed algae	Areas of highly broken and convoluted reef with a mixed assemblage of *M. boryana*, *C. maschalocarpum*, *L. quercifolia* and *E. radiata*. Found in depths between 0 and 20 m.
Rocky reef, *Marginariella boryana* forest	Areas of highly broken reef with a dense forest of *M. boryana*. Common in areas less than 10 m depth.
Flat reef, algal carpet	Areas of flat reef with a thick layer of low-lying algae, containing both reds and browns. *M. boryana* and *L. quercifolia* occur sporadically in small isolated patches. Common in areas less than 10 m depth.
Rocky reef, crustose coralline algae	All rock surfaces are thickly encrusted with coralline algae. Occurrence of large brown algae (*M. boryana* and *C. maschalocarpum*) is restricted to small patches of usually less than 10 plants. Sparse covering of sponges (*Halichondria* and *Tethya aurantium*). Common in areas greater than 15 m depth.
Sandy bottom, patch reefs with coralline turf	Small patch reefs encrusted with coralline turf and very low numbers of large *M. boryana*. Common in areas greater than 15 m depth.

Figure 5. Percentage cover (+SE) of the dominant habitat-formers at one Kaikoura site (A) and two Banks Peninsula sites (B & C).

3.1.2 Quadrat surveys

Algae

A wide range of organisms was encountered during the quadrat surveys (Table 2). At Kaikoura, *Marginariella* (mostly *M. boryana* with occasional *M. urvilliana*) was the dominant alga in shallow water, reaching an average of around 7 plants per m^2 in depths of 5-15 m (Fig. 6A). The average cover of *Marginariella* ranged from 20 to 60% of the substratum at these depths (Fig. 6B). Other fucoids (*Landsburgia quercifolia*, *Sargassum sinclairii* and *Carpophyllum maschalocarpum*) were common, but only to 8 m depth. The laminarian alga *Ecklonia radiata* occurred at around 3 plants per m^2 at most depths but had a cover of only about 5-10% of the substratum. The tough, leathery kelp *Lessonia variegata* occurred at only 3 plants per m^2 at 8 m depth, but these massive plants had a cover of 50%. The algal cover at Godley Head on Banks Peninsula was quite different from Kaikoura. The giant kelp *Macrocystis pyrifera* occurred at 2-4 plants per m^2 at 3-6 m depth (Fig. 6C) but the canopy covered an average of 55-85% of the substratum (Fig. 6D). The fucoids *Carpophyllum maschalocarpum* and *Landsburgia quercifolia* occurred in the understorey at 3-6 m but had only minimal cover. The most abundant plant was *Ecklonia radiata,* which occurred at 13-15 plants per m^2 at 9-12 m depth and had a canopy cover of 10-30%. At Taylor's Mistake on Banks Peninsula, *C. maschalocarpum* occurred at 12 plants per m^2 at 5 m depth (Fig. 6E) and had a cover of 15% (Fig. 6F). At middle depths, there was a mixed stand of *Marginariella, Landsburgia, C. maschalocarpum, Ecklonia and Lessonia. Lessonia* produced the largest canopy cover of 50% in the middle depth, while *Marginariella* covered 20% of the substratum in middle depths and around 50% in the deeper areas.
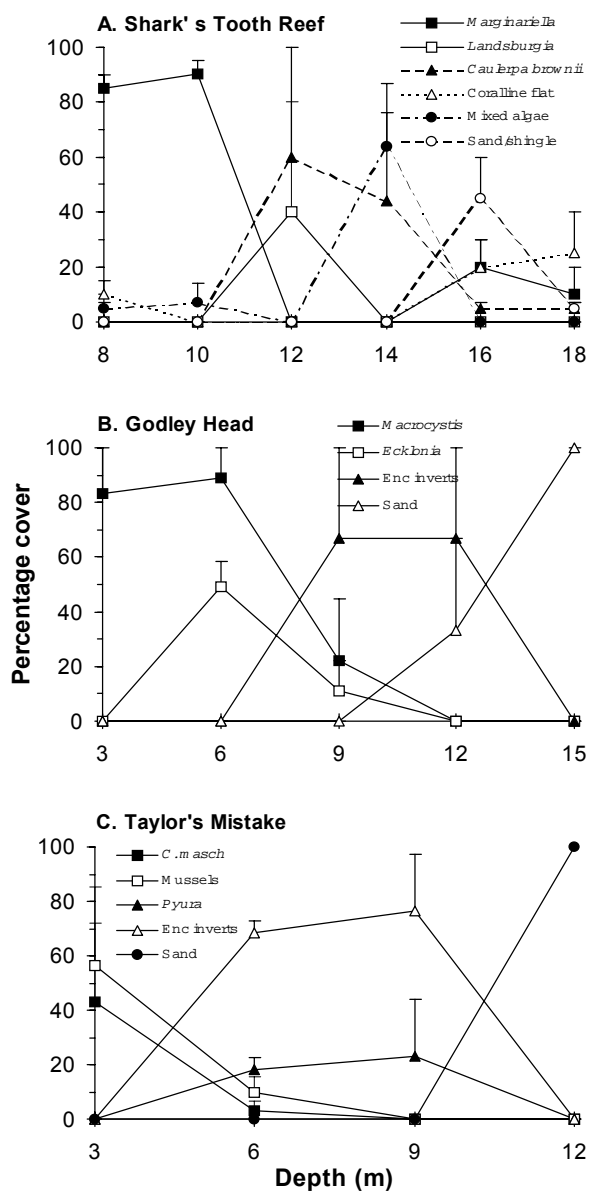
ALGAE		INVERTEBRATES	
Brown algae		**Porifera**	*Polymastia granulosa*
Laminariales	*Macrocystis pyrifera*		*P. hirsuta*
	Ecklonia radiata		*Strongylacidon novae*
	Lessonia variegata		*Chondropsis* sp. 1
Fucales	*Marginariella boryana*		*Amathia* sp.
	M. urvilliana		*Tedania connectens*
	Carpophyllum maschalocarpum	**Hydrozoans**	unidentified species
	C. flexuosum	**Molluscs**	
	Cystophora scalaris	**Bivalves**	*Perna canaliculus*
	Xiphyphora gladiata		*Mytilus edulis*
	Landsburgia quercifolia	**Gastropods**	*Haliotis iris*
	Sargassum sinclairii		*H. australis*
Durvilleales	*Durvillaea antarctica*		*Cookia sulcata*
	Durvillaea willana		*Trochus viridis*
Other	*Halopteris* spp.		*Cellana stellifera*
	Glossophora kunthii		*Radiacmea inconspicua*
	Zonaria turneriana	**Echinoderms**	
Green algae	*Codium fragile*	**Echinoids**	*Evechinus chloroticus*
	Ulva spp.	**Asteroids**	*Patiriella regularis*
	Caulerpa brownii	**Bryozoans**	*Cribricellina cribraria*
Red algae	*Polysiphonia* spp.		*Margaretta burbata*
	Plocamium spp.	**Ascidians**	*Pyura pachydermatina*
	Gigartina spp.		*Didemnum candidum*
	Corallines		*Aplidium* sp.

In terms of the major algal groups, fucalean algae dominated the canopy of the shallow depths at Kaikoura and, to a lesser extent, at Taylor's Mistake, while laminarians were dominant at Godley Head (Fig. 7A–C). Geniculate coralline algae were abundant in the understorey at all depths and at all sites. Corallines (mostly encrusting), other reds and green algae (mostly *Caulerpa brownii*) were dominant beyond 15 m depth, where large brown algae became scarce.

Invertebrates

A wide range of benthic invertebrates formed an extensive cover of the substratum at all sites. At Shark's Tooth, sponges formed a cover of 8–15% at all depths (Fig. 8A). Particularly abundant were *Polymastia granulosa*, *P. hirsuta*, *Chondropsis*, and *Strongylacidon novae*. Bryozoans formed a cover of 5–10% at all depths. Tunicates were common (23% cover) at 15 m depth and hydroids formed a small cover (2%) at the lower depths. At Godley Head, sponges formed 10–15% cover at 6–9 m depth (Fig. 8B). Tunicates and a wide range of other encrusting invertebrates formed 9–30% cover at 9–12 m. Mussels (*Perna canaliculus*) formed a 30% cover in deeper water. At Taylor's Mistake, sponges and a wide range of encrusting invertebrates dominated the understorey (Fig. 8C).

Sea tulips (*Pyura pachydermatina*) and mobile gastropods were abundant at Banks Peninsula sites (Fig. 9). At Godley Head, *P. pachydermatina* occurred at
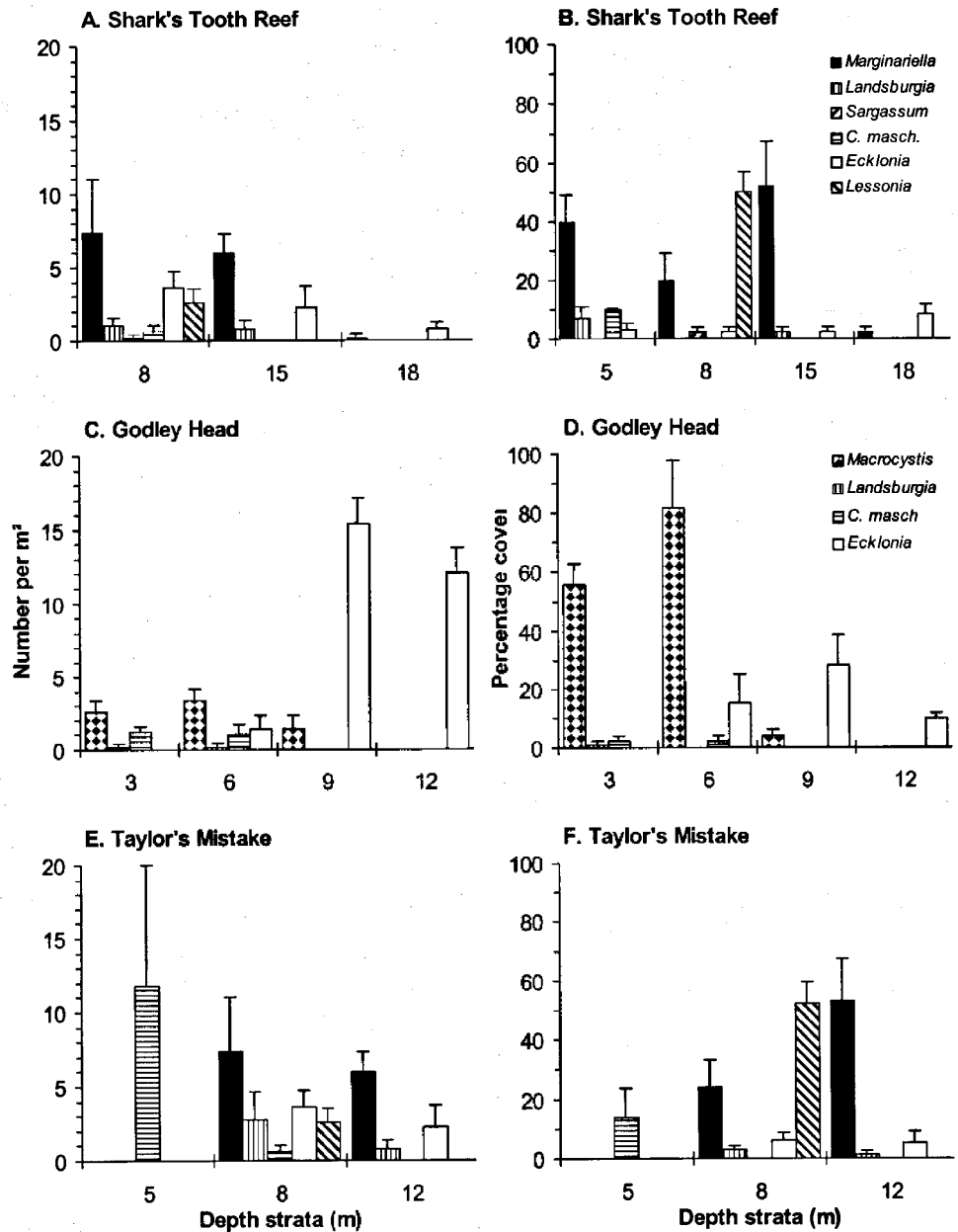
Figure 6. Mean number per m² (+SE) and the percentage cover (+SE) of the major brown algal species at the east coast, South Island sites on (A, B) Kaikoura Peninsula and (C-F) Banks Peninsula.

2-8 per m² at all the depths sampled (Fig. 9A) but at Taylor's Mistake, this species was confined to the 5 m depth stratum (Fig. 9B). The most abundant gastropods at both sites were the paua *Haliotis iris,* the topshell *Trochus viridis* and the turbinid *Cookia sulcata*.

In a separate procedure, the large mobile invertebrates were sampled in three replicate 10 × 4 m transects at all sites (Fig. 10). *H. iris* occurred at only 0.3 per 40 m² in the shallowest depth zone at Shark's Tooth (Fig. 10A), at 4 per 40 m² in 3 m depth at Godley Head (Fig. 10B), but at 70 per 40 m² at Taylor's Mistake (Fig. 10C). The sea urchin *Evechinus chloroticus* occurred at 8 per 40 m² in shallow water (5 m) at Shark's Tooth and was half as abundant in deeper water (Fig. 10A). This grazer occurred at 6-7 per 40 m² at 3-5 m depths at Godley
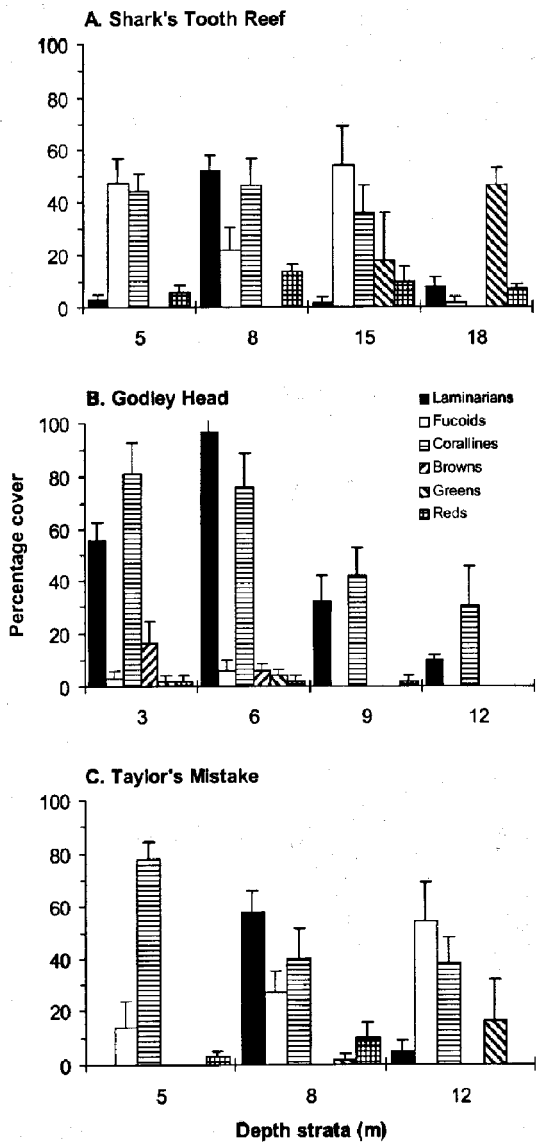
Figure 7. Percentage cover (+SE) of algal groups at one Kaikoura site (A) and two Banks Peninsula sites (B, C).
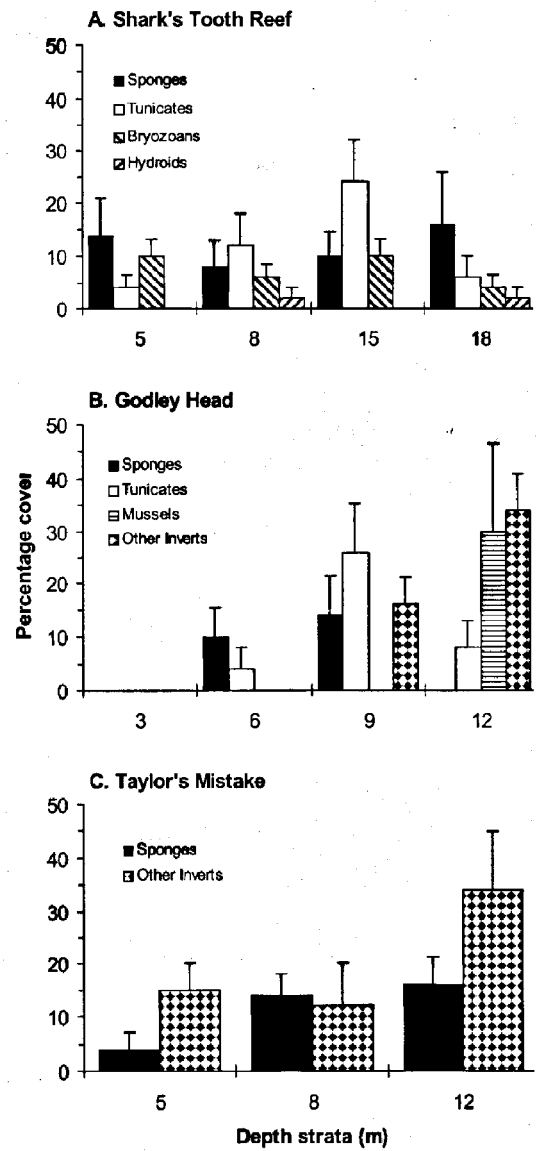
Figure 8. Percentage cover (+SE) of understorey invertebrates at one Kaikoura site (A) and two Banks Peninsula sites (B, C).

Head (Fig. 10B) and 5-15 per 40 m^2 at the two shallowest depth strata at Taylor's Mistake (Fig. 10C). *Cookia sulcata* was abundant along the transects at both Banks Peninsula sites.

3.1.3 Fish surveys

In the five transect lengths used in the optimisation procedure, the variability of fish population estimates decreased with increasing transect length (Fig. 11). For all species (Fig. 11A), and the commonest labrids, *Notolabrus celidotus* (Fig. 11B) and *N. fucicola* (Fig. 11C), the smallest transect gave a highly imprecise estimate of fish numbers. For total fish counts and both individual species, the precision stabilised at a transect area of 150 m^2, which corresponded to a 30 × 5 m transect. Therefore, this transect size was subsequently used because it provided representative samples while allowing several transects to be done per dive.
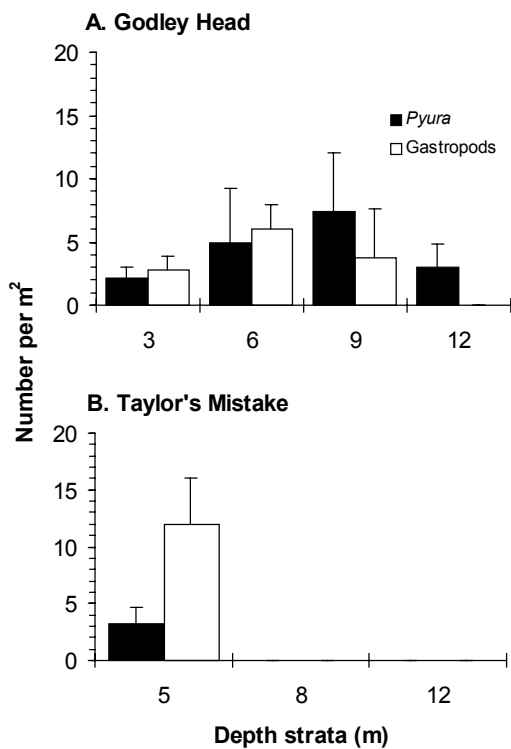
A. Godley Head

Number per m²

■ Pyura
□ Gastropods

B. Taylor's Mistake

Depth strata (m)

A. Shark's Tooth Reef

■ *H. iris*
□ *Evechinus*
▨ *Cookia*

B. Godley Head

Number per 40 m²

C. Taylor's Mistake

Depth strata (m)

Figure 9 (above). Mean number per m² (+SE) of sea tulips (*Pyura pachydermatina*) and gastropods at two Banks Peninsula sites.

Figure 10 (right). Mean number per 40 m² (+SE) of the major species of large herbivorous invertebrates at one Kaikoura site (A) and two Banks Peninsula sites (B & C).
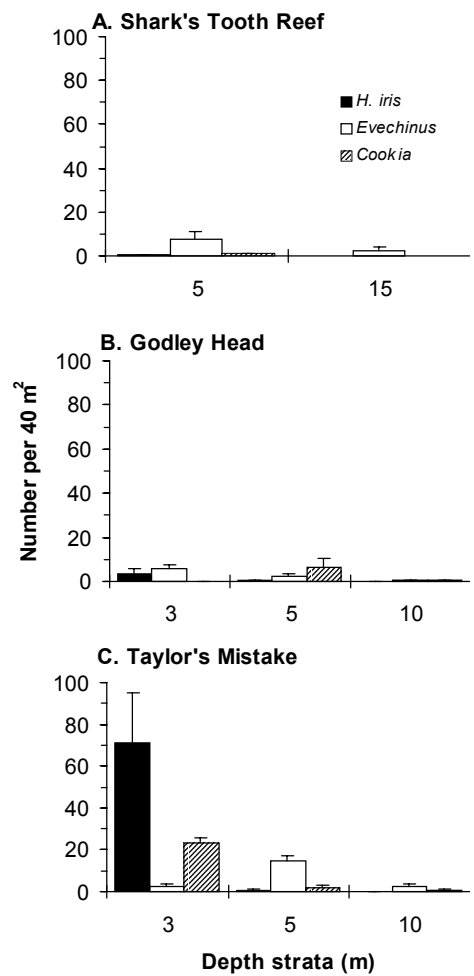
At Kaikoura, eleven species of reef fish were recorded during the visual surveys of seven sites (Table 3). Pooling sites by habitat showed that there was considerable variation in abundance of fish species across the five dominant habitats (Fig. 12). *Notolabrus celidotus* was the most abundant fish in all habitats except rocky reef with crustose coralline algae. There were significant differences in the abundance of *N. celidotus* among habitats ($F_{4,175}$ = 8.38, p < 0.001), with greatest densities of around 23 fish per 150 m² occurring in the habitat with sandy bottom and patch reefs (Fig. 12E). The two species of deep water wrasses, *Pseudolabrus miles* ($F_{4,175}$ = 73.63, p < 0.001) and *Notolabrus cinctus* ($F_{4,175}$ = 50.91, p < 0.001) were each observed in significantly higher densities in the deeper habitat (15-20 m depth) composed of rocky reef with crustose coralline algae (Fig. 12D) than in the other habitats. The three large carnivores *Nemadactylus macropterus* ($F_{4,175}$ = 4.84, p < 0.001), *Latridopsis ciliaris* ($F_{4,175}$ = 11.52, p < 0.001) and *Parapercis colias* ($F_{4,175}$ = 30.05, p < 0.001) were all observed in significantly higher numbers over habitat of sandy bottom with small patch reefs (Fig 12E). The total fish numbers per transect were also significantly different among habitats ($F_{4,175}$ = 6.48, p < 0.001) with greatest numbers on sandy bottoms with small patch reefs. *Notolabrus fucicola* was common in all habitats and showed no significant difference among them ($F_{4,175}$ = 2.17, p = 0.074).

Relatively few species were recorded in each visual transect, with the average ranging from 2.6 to 4.6 (Fig. 13). The differences were significant among the five habitats ($F_{4,175}$ = 6.84, p < 0.001), with the greatest average number of

Figure 11. Mean precision (± SE) for all species (total fish), *Notolabrus celidotus* and *N. fucicola*, in relation to the area searched in each transect size (10 X 5 m, 20 X 5 m, 30 X 5 m, 40 X 5 m, 50 X 5 m) in Kaikoura.

A. Total fish

B. *Notolabrus celidotus*

C. *Notolabrus fucicola*

species per transect occurring over sandy bottom with small patch reefs. *P. miles* and *N. cinctus* were usually found together on rocky reefs with crustose coralline algae (r_{178} = 0.590, p < 0.001), which extended into deeper water. The large carnivores *L. ciliaris* and *P. colias* were usually found together in habitats that contained open areas of sand or gravel (r_{178} = 0.305, p < 0.001). The algal grazing butterfish, *Odax pullus*, and *P. colias* were negatively correlated (r_{178} = -0.146, p < 0.05), with the former being present in algae-dominated habitats and the latter being more common in the sandy habitat.

Around Banks Peninsula, the most common fishes were the wrasses *N. fucicola* and *N. celidotus* (Fig. 14). *N. celidotus*
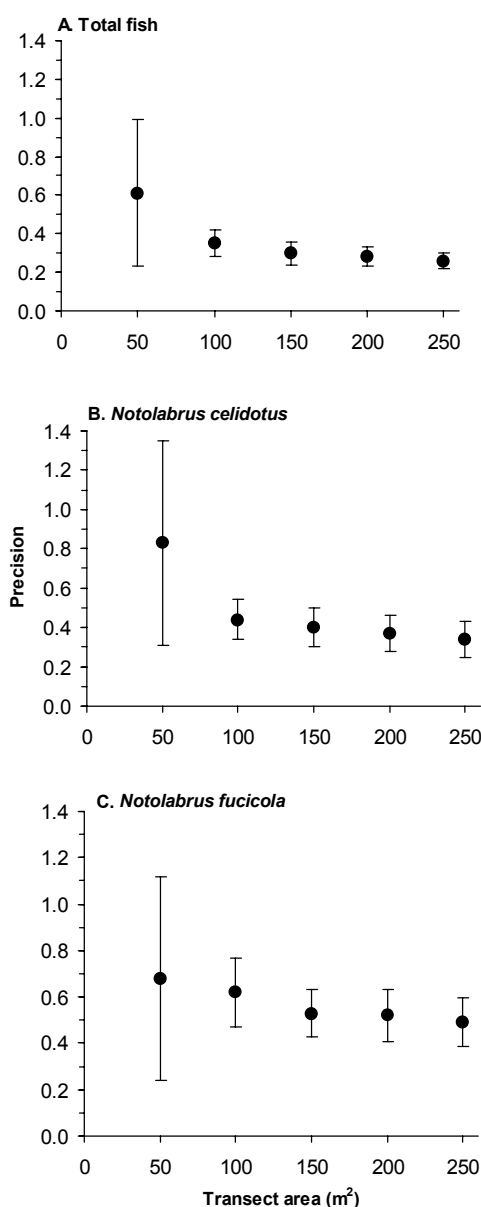
TABLE 3. THE SPECIES AND COMMON NAME OF FISH OBSERVED DURING VISUAL TRANSECTS AT SEVEN SITES AROUND KAIKOURA.

|		
Scorpaenidae	*Scorpaena papillosus* (Schneider & Forster, 1801)	Red rock cod
Aplodactylidae	*Aplodactylus arctidens* Richardson, 1839	Marblefish
Cheilodactylidae	*Nemadactylus macropterus* (Bloch & Schneider, 1801)	Tarakihi
Latrididae	*Latridopsis ciliaris* (Bloch & Schneider, 1801)	Blue moki
Labridae	*Notolabrus celidotus* (Bloch & Schneider, 1801)	Spotty
	Notolabrus cinctus (Hutton, 1877)	Girdled wrasse
	Notolabrus fucicola (Richardson, 1840)	Banded wrasse
	Pseudolabrus miles (Bloch & Schneider, 1801)	Scarlet wrasse
Odacidae	*Odax pullus* (Bloch & Schneider, 1801)	Butterfish
Pinguipedidae	*Parapercis colias* (Bloch & Schneider, 1801)	Blue cod
Monacanthidae	*Parika scaber* (Bloch & Schneider, 1801)	Leatherjacket
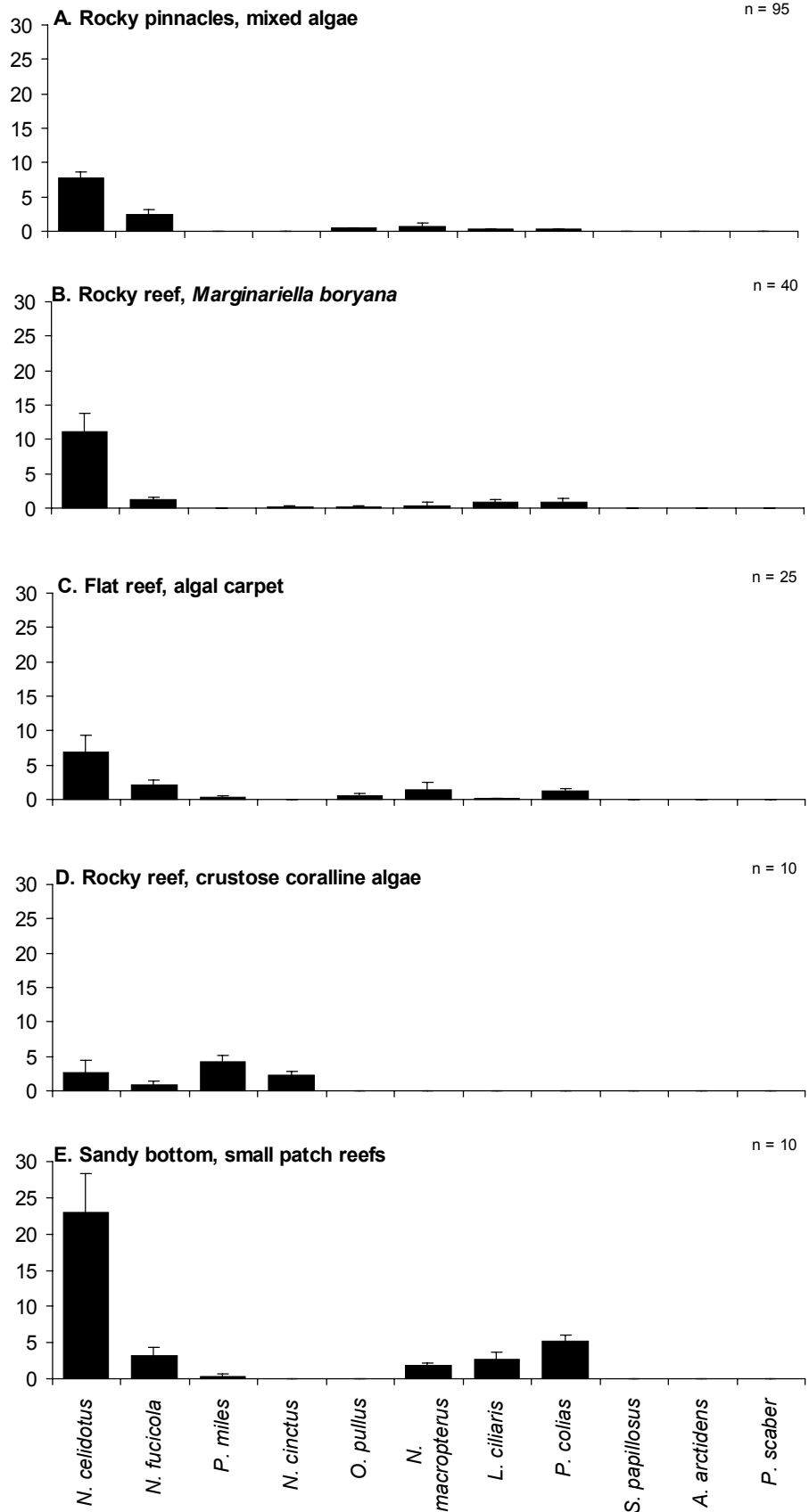
Figure 12. Mean number (+SE) per 150 m^2 transect of 11 species of reef fish in each of five different habitats (n = number of transects).
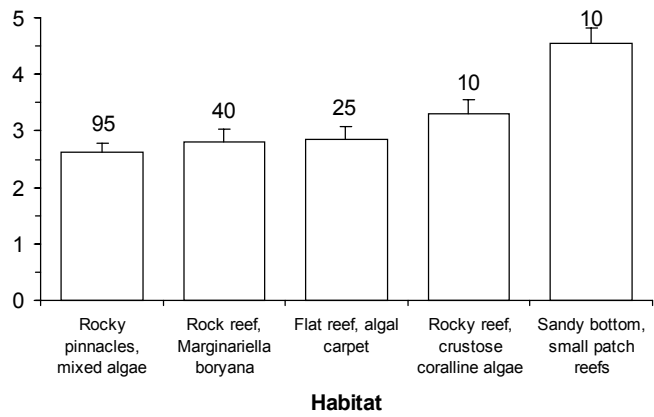
Figure 13. Mean number of species (+SE) observed per transect in each of five habitats (number of transects given above bars).

occurred mostly in deeper water at Godley Head at an average density of 6 per 150 m². At Taylor's Mistake, *N. celidotus* occurred mostly in shallow water, at a density of 5 per 150 m². This species was also particularly abundant in the shallow kelp beds inside Akaroa Harbour, such as around Wainui. Leatherjackets (*Parika scaber*) and butterfish (*Odax pullus*) were also recorded.

Figure 14. Mean number (+SE) per 150 m² of individual fish species at Banks Peninsula sites.

3.2 FIORDLAND

3.2.1 Algae and invertebrates

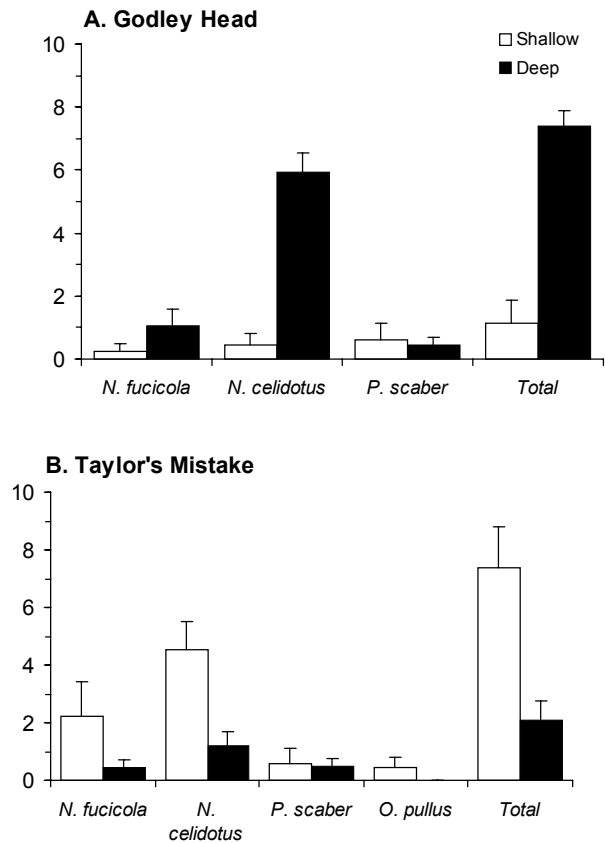Sampling for algae and invertebrates was stratified in 6 depth categories at the 13 sites. Not all depths were represented at each site because of swell conditions or the absence of rocky reef. The depth strata were 1: 1–1.5 m; 2: 2–4 m; 3: 5–6.5 m; 4: 7–9 m; 5: 10–12.5 m; 6: 14–18 m.

Suites of fucalean and laminarian algae were the characteristic habitat-formers at most sites. At around 1 m depth, *Xiphophora gladiata* was the most common alga. Its canopy cover reached 28% of the substratum at Anchor I. (Fig. 15A). It became more abundant in the southern Sounds but was found in lesser abundance at 2–4 m depth in the northern Sounds. This species occurred predominantly in rougher water in the more exposed sites. *Cystophora congesta* was found primarily in waters <4 m deep (Fig. 15B). It was most abundant in the northern sites of Poison Bay and Sutherland Sound where it reached average densities of 7 per m² and an average cover of 47%. This species
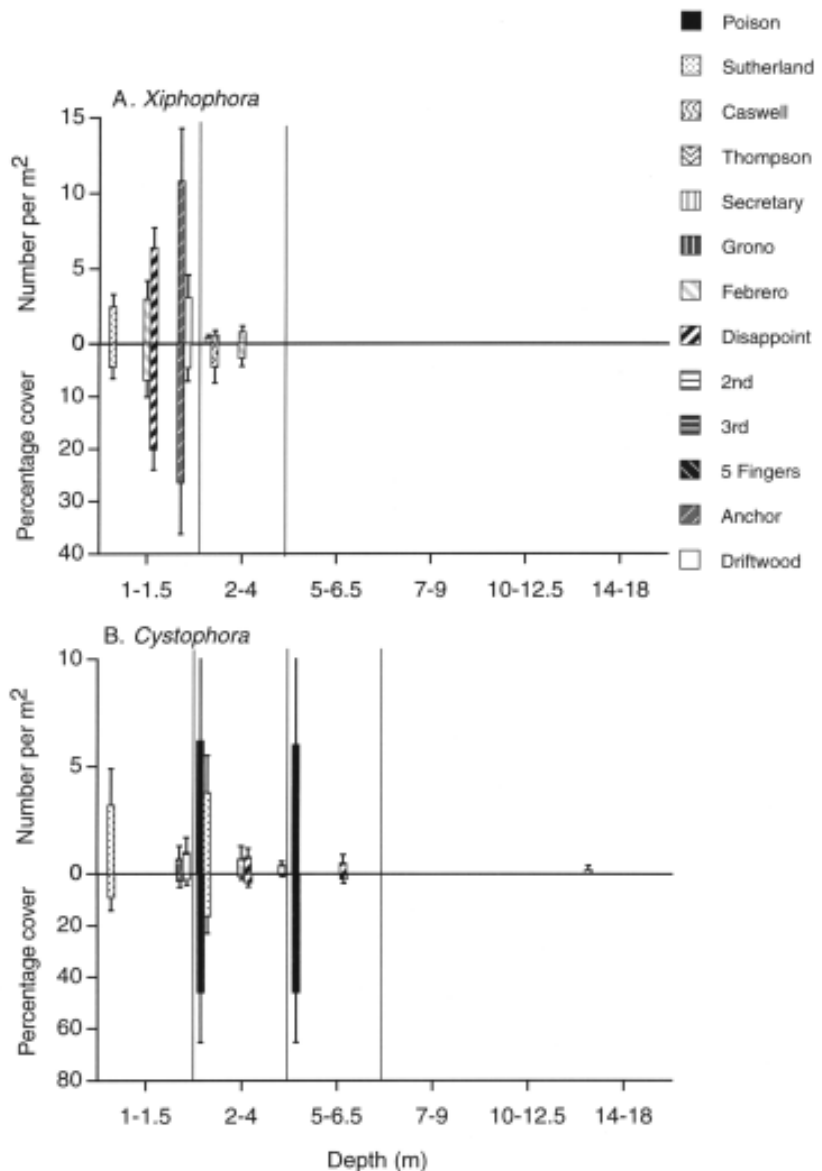

Figure 15. Mean number (+SE) per m² (above bar) and mean percentage (+SE) cover (below bar) of (A) *Xiphophora gladiata* and (B) *Cystophora congesta* at the 13 sites in Fiordland.

was rare in southern sites. *Marginariella* species (*M. boryana* and *M. urvilliana*) were commonly found in the outer coastal sites but did not achieve average densities beyond 2 per m² (no graph presented). *Marginariella* was seen more in the southern Sounds region and in shallow depths. Other fucaleans commonly encountered in low densities were *Landsburgia quercifolia* and *Sargassum sinclairii*. Neither of these species had a cover greater than a few per cent at any of the sites. By far the most common fucalean species overall was *Carpophyllum flexuosum* (Fig. 16A). It reached its greatest density of 25 plants per m² and a cover of 50% in the shallowest depth of the sheltered Second Cove, but also had relatively high densities and percentage cover at 5–9 m depths in Febrero Point and Poison Bay. It was the most abundant large alga in the middle depth strata (4–10 m depth) at all sites. There was no north-south trend in its abundance or dominance. *C. flexuosum* was a major habitat-former, commonly having a cover of 30–50%. Overall, fucalean algae dominated depth strata 1–4 (<10 m) at all sites, having a combined cover of up to 75% (Fig. 16B).
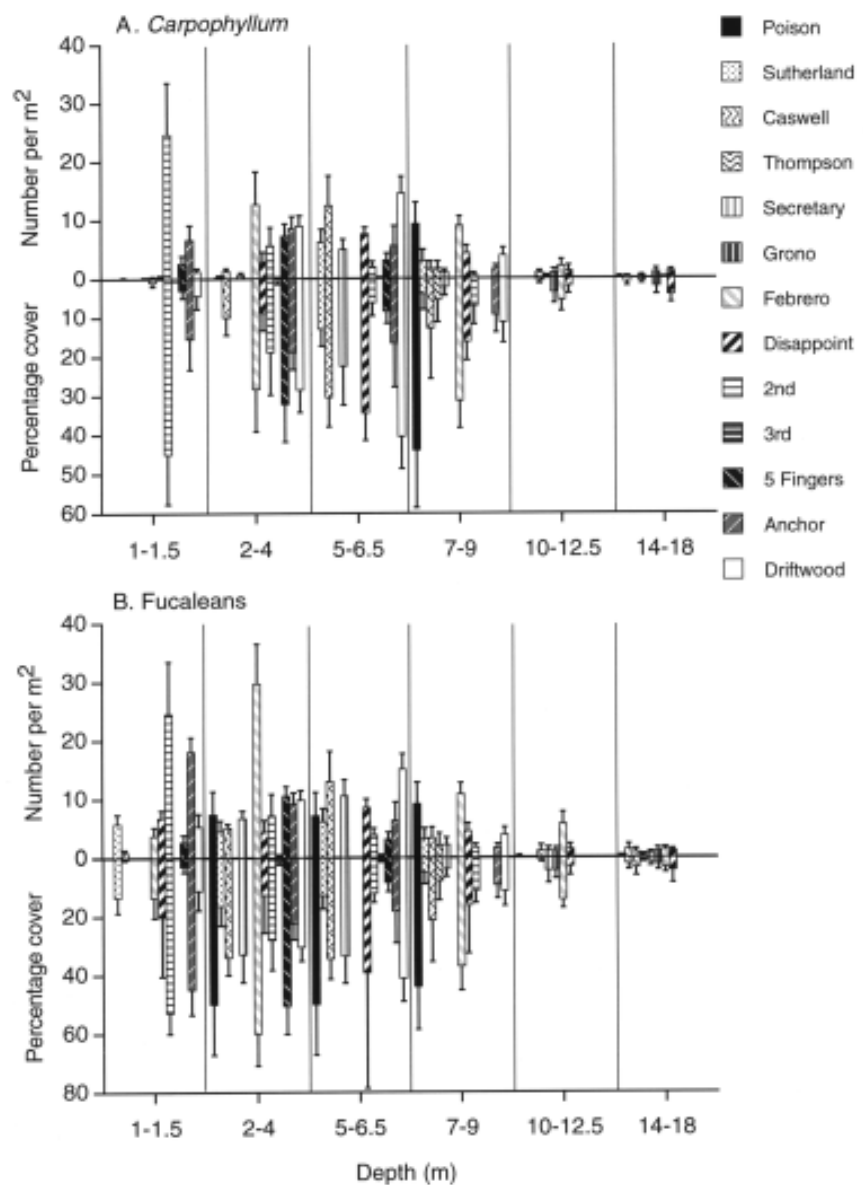

Figure 16. Mean number (+SE) per m² (above bar) and mean percentage (+SE) cover (below bar) of (A) *Carpophyllum flexuosum* and (B) all fucalean algae at the 13 sites in Fiordland.

Laminarian algae were present at all depths. *Lessonia* species were common at depths of 2–7 m, particularly in a narrow band around Five Fingers Peninsula, but had low overall densities (Fig. 17A). *L. variegata* was the most common of the *Lessonia* species but another species was seen in dense clumps around the protected inner area of Five Fingers Peninsula. This species had thick and robust stipes and may well be *L. brevifolia*, which is characteristic of the Auckland Islands (D. Schiel pers. obs.; C. Hay pers. comm.). Giant kelp, *Macrocystis pyrifera*, was seen occasionally in semi-protected southern sites but it did not occur in our surveyed areas. *Ecklonia radiata* was by far the most abundant laminarian alga and was the characteristic alga of deeper water (Fig. 17B). It was commonly found from 2–10 m depth but was the dominant alga at 10–20 m, where it reached an average cover of up to 75% in Thompson Sound, 55% at Febrero Point, and >20% at Disappointment Cove and Anchor I. It was found in both exposed and sheltered sites. The abundance patterns of laminarian algae mostly mirrored that of *Ecklonia*, both in numbers and percentage cover (Fig. 18). Only in the protected site of 2nd Cove did laminarian algae (*Ecklonia*) achieve a high cover (c. 35%) in shallow water.
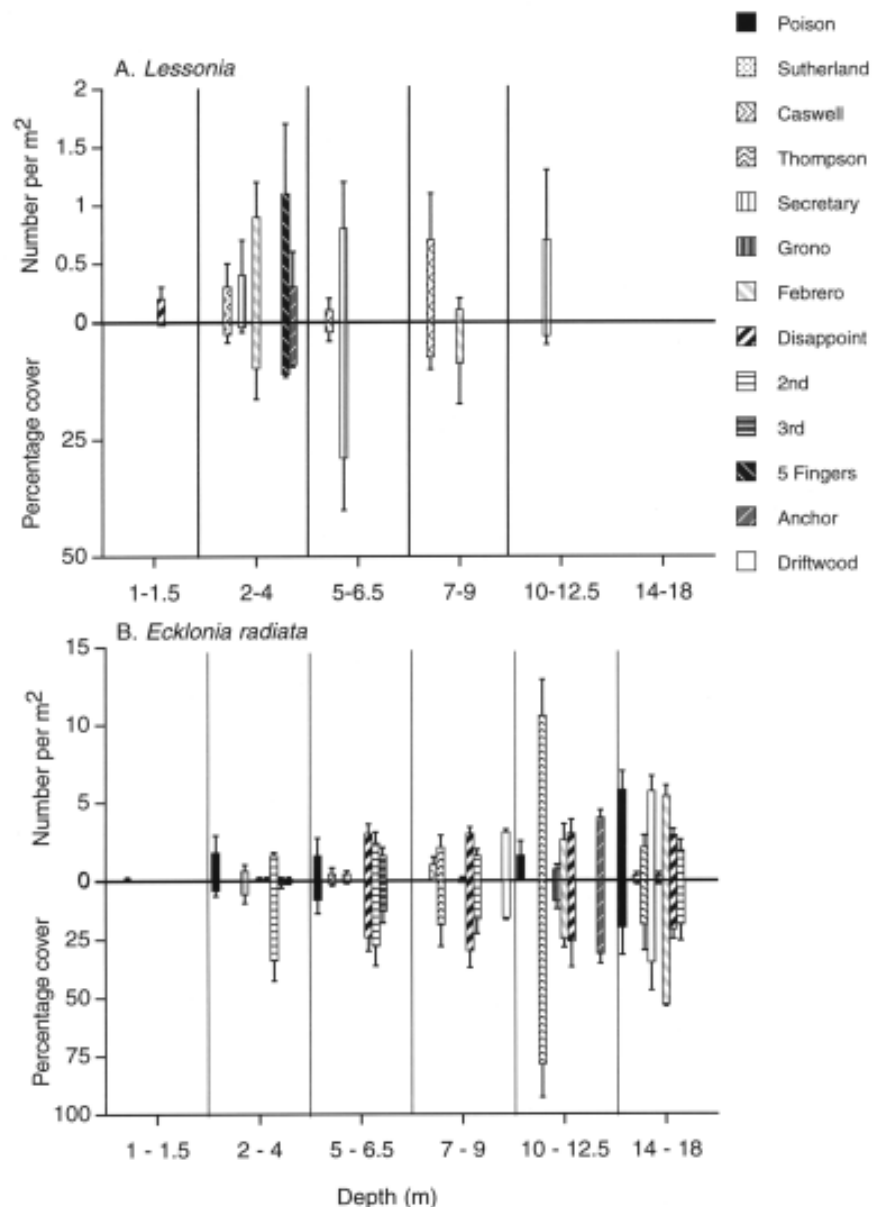

Figure 17. Mean number (+SE) per m² (above bar) and mean percentage (+SE) cover (below bar) of (A) *Lessonia* spp. and (B) *Ecklonia radiata* at the 13 sites in Fiordland.
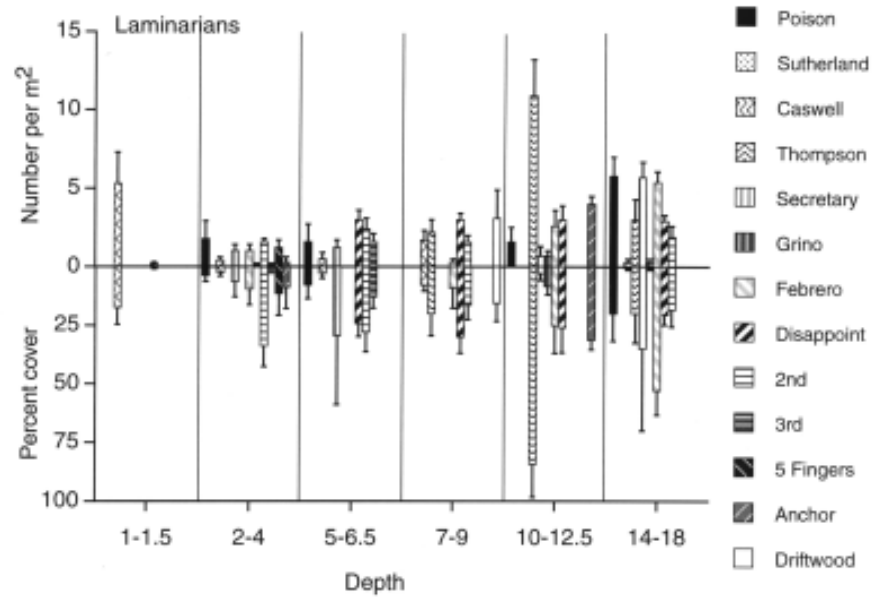
Figure 18. Mean number (+SE) per m² (above bar) and mean percentage (+SE) cover (below bar) of all laminarian algae at the 13 sites in Fiordland.

Overall patterns

There were clear patterns in the distribution and abundance of dominant organisms with respect to distance into the Sounds. Sites were categorised with respect to their position in the outer (n = 7), mid (n = 3) or inner (n = 3) Sounds regions. Although it was not recorded in this survey because of a large swell on the outer coast, the southern bull kelp *Durvillaea antarctica* dominated the immediate subtidal zone on the outer coast and barely extended into the Sounds. *Xiphophora gladiata* was found predominantly in the exposed outer coast sites and extended into the semi-protected sites in the entrances to Sounds but was not recorded in inner sites (Fig. 19A). *Cystophora* species, *Landsburgia quercifolia* and *Marginariella* species were found mostly on the outer coast. *Carpophyllum flexuosum* and *Sargassum sinclairii* were equally abundant in all three positional strata. *C. flexuosum* was the most abundant large brown alga in all types of sites. Laminarian algae were mostly found on the outer coast sites (Fig. 19B). *Lessonia variegata* was recorded in outer and mid sites and not found at all in inner sites. *Ecklonia radiata* formed stands at sites in all three positions within the Sounds. Of the understorey taxa, brown and red algae (except corallines) were less abundant at inner sites than in outer and mid sites (Fig. 19C). Green algae were least abundant in the mid sites whereas encrusting invertebrates (sponges, bryozoans, and
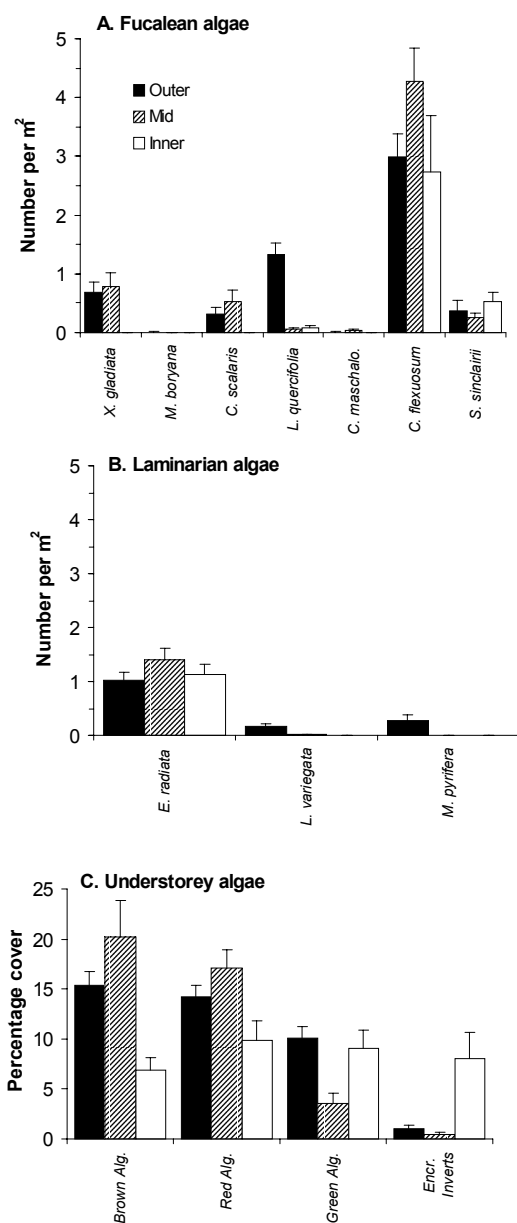

Figure 19. Mean number (+SE) per m² of (A) fucalean algae, (B) laminarian algae and (C) understorey algae at the Fiordland sites, grouped into outer, mid and inner locations.

ascidians) were most abundant in the protected inner sites, where they had a cover of around 8% of the substratum. The abundances of fucalean and laminarian species were associated with the availability of rocky substrata. Sand and silt cover of the primary substratum became much more abundant in inner areas of the Sounds, reaching a combined average cover of >30% (Fig. 20A). This coincided with a decrease in the cover of large brown algae. Large grazing invertebrates were relatively scarce at inner sites (Fig. 20B). Paua, *Haliotis iris*, were found at c. 1 per m^2 on the outer coast and mid, semi-exposed sites. They became much more patchy in occurrence at the mid sites, as evidenced by the large error bars. Sea urchins, *Evechinus chloroticus*, were present in isolated patches in all three positions, but were relatively scarce at inner sites.

Smaller gastropods, primarily limpets (*Cellana stellifera*), turban snails (*Cookia sulcata*) and top shells (*Trochus viridis*) were found in small numbers at most sites (Fig. 20C). The grazing seastar *Patiriella regularis* was found beneath algal canopies at outer and semi-exposed sites. Brachiopods were particularly common at inner sites, reaching average densities of several per m^2. Particularly striking was the abundance of black coral (*Antipathes fiordensis*) in the inner Sounds sites. These were common from a depth of 4-5 m at the inner sites, but were more abundant in deeper water, where they reached average densities c. 1 per 10 m^2 (Fig. 21).

The overall depth distribution of taxa was typical of most of the New Zealand coast. A suite of fucalean algae dominated depths to 10 m (Fig. 22A) and the laminarian alga *Ecklonia radiata* dominated the lower depths (Fig. 22B). Overall, *Xiphophora* dominated the shallowest depth sampled (1.5 m) and *C. flexuosum* dominated the middle depths of 2-10 m. *Ecklonia* was the most abundant large brown alga in deep water. Of the understorey taxa, brown algae, particularly *Halopteris*, dominated the shallowest depths and green algae (*Caulerpa brownii*) were abundant in deep water (Fig. 22C). Red algae were most abundant at the middle depths. Of the large invertebrates, *Haliotis iris* was confined almost exclusively to <5 m depth and sea
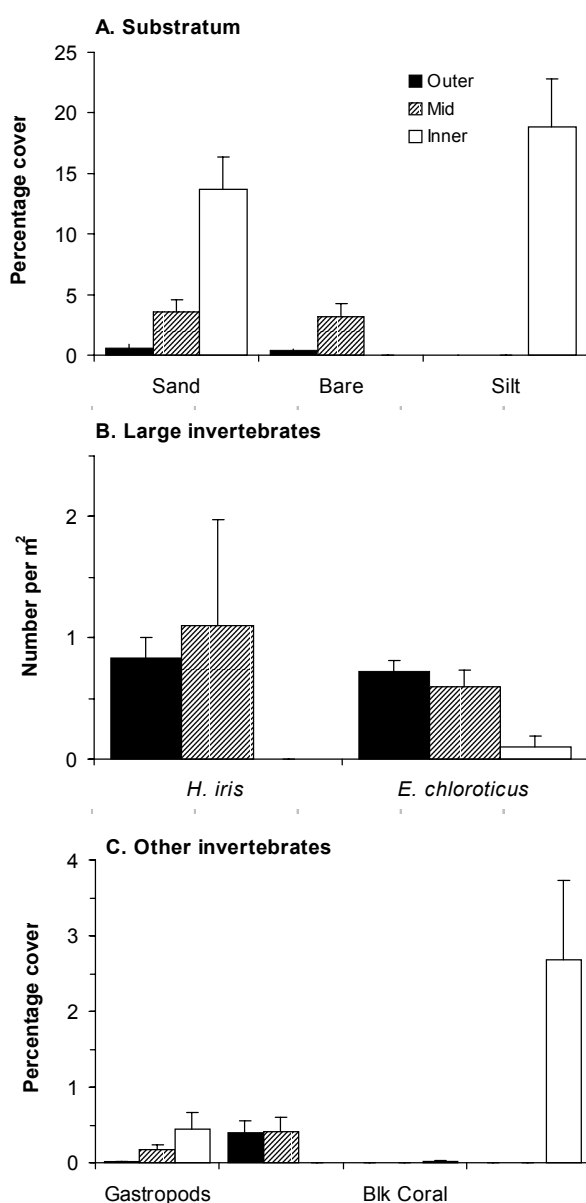

Figure 20. Mean percentage cover (+SE) of (A) substratum types, and mean number of (B) large and (C) other invertebrates in outer, mid and inner sites of Fiordland.
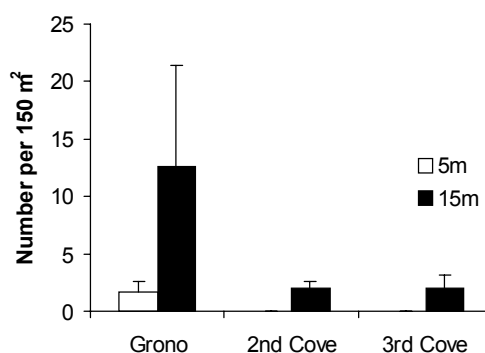
Figure 21. Mean number (+SE) per 150 m^2 of black coral at three inner sites of Fiordland.
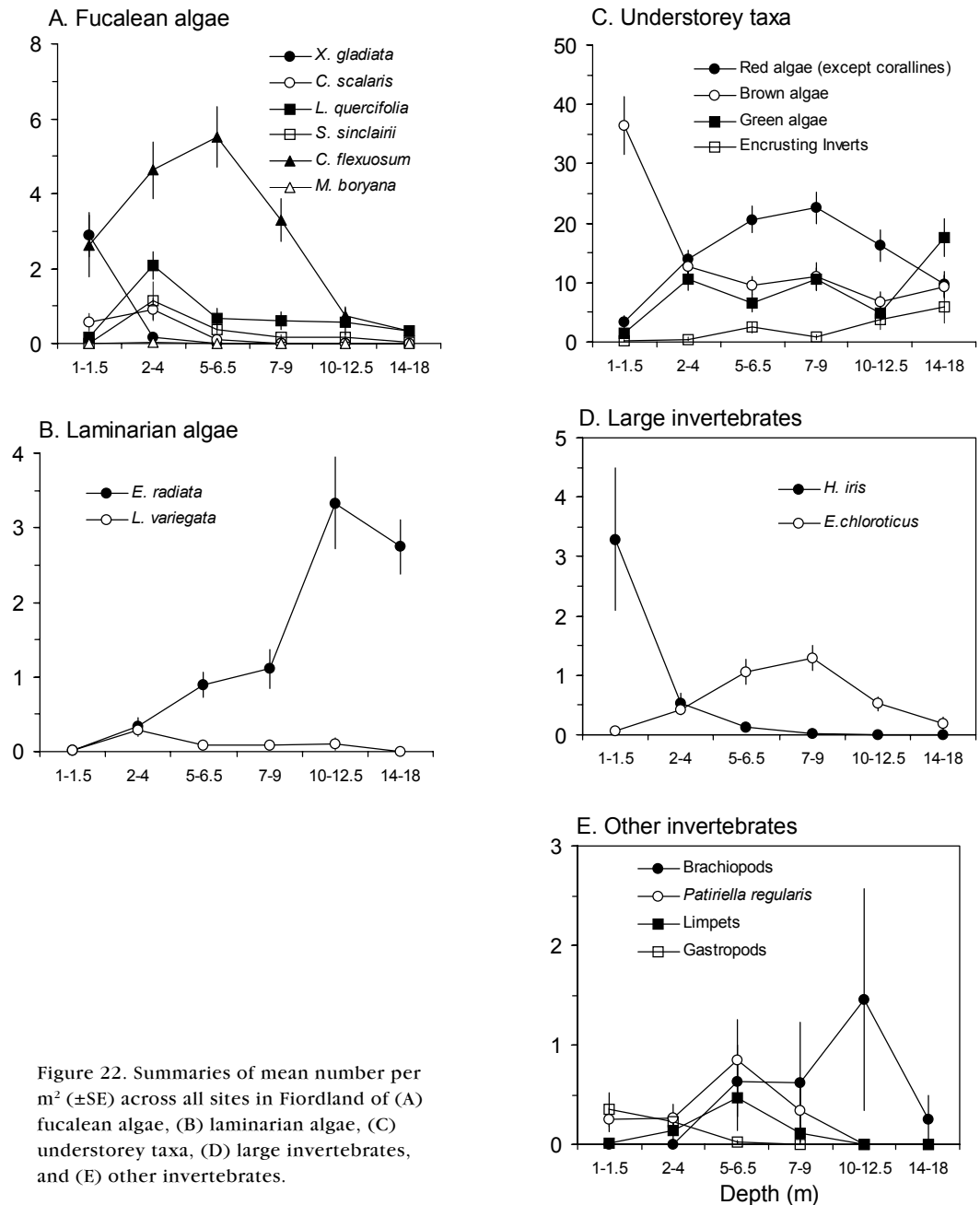
Figure 22. Summaries of mean number per m² (±SE) across all sites in Fiordland of (A) fucalean algae, (B) laminarian algae, (C) understorey taxa, (D) large invertebrates, and (E) other invertebrates.

urchins were most abundant in the middle depths of 6.5–12.5 m (Fig. 22D). Most invertebrates were more abundant in the shallow depths except for brachiopods, which reached peak abundances at around 12.5 m (Fig. 22E).

3.2.2 Fish

By far the most abundant fish recorded throughout the surveyed sites was the planktivorous serranid *Caesioperca lepidoptera*, the butterfly perch. It was found predominantly in deeper water (> 10 m) and was recorded at all sites except for Five Fingers Peninsula and Driftwood Cove (Fig. 23A). It was recorded at > 100 fish per 300 m² transect at several sites. This species normally is found in the water column a few metres above the kelp canopy. Another serranid, the red-banded perch *Ellerkeldia huntii*, was recorded as a solitary individual in deep water at Disappointment Cove.

Labrids occurred at most sites and depths. The most abundant of this family was the scarlet wrasse *Pseudolabrus miles*. It varied considerably in abundance among sites but there was no trend in abundance from north to south (Fig. 23B). However, it was more abundant in deeper water. It commonly occurred at densities of >40 per 300 m² (Sutherland Sound, Caswell Sound, Secretary I. and Febrero Point). The banded wrasse *Notolabrus fucicola* was commonly found throughout the Fiordland region (Fig. 23C). It was found in both depth zones but was usually far more abundant in shallow water (except at Anchor I.), commonly reaching densities >15 fish per 300 m². Spotties, *N. celidotus,* were
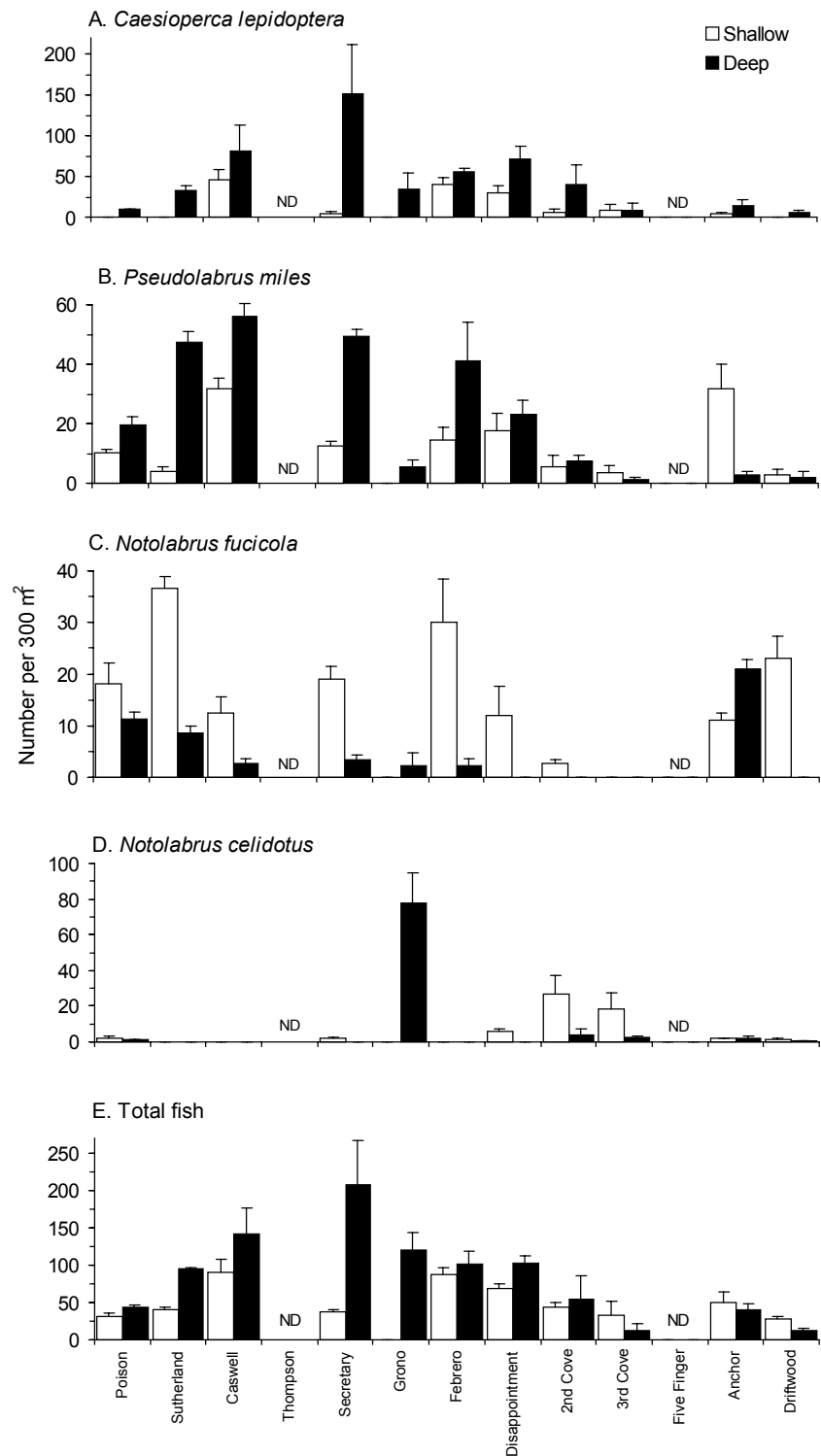

Figure 23. Mean abundance (+SE) per 300 m² of (A-D) the four most common fish species and (E) total fish in deep and shallow transects at the 13 sites of Fiordland.

abundant only in the middle Sounds region (Fig. 23D). They occurred at < 5 fish per transect at Poison Bay, Sutherland Sound, Caswell Sound, Secretary Island, Febrero Point, Anchor Island and Driftwood Cove. At Grono Bay they occurred at c. 80 per transect in the deeper transects. In other sheltered sites such as Second Cove and Third Cove they occurred at c. 20 fish per 300 m² in the shallow transects. Girdled wrasses, *N. cinctus*, were recorded at only one site (Disappointment Cove). Overall, fish were least abundant in the northern and southern sites, with peaks in the central region of the Sounds (Fig. 23E).

The abundances of the species that occurred at all sites varied significantly among sites and depths (Table 4). There was considerable topographic variety among sites, from gradually sloping reefs to steeper inclines, and considerable differences in associated biota and exposure. Site factors accounted for > 35% of the variation in all species, while depth ranged from 10 to 50%. *Caesioperca lepidoptera* and *Notolabrus celidotus* showed the most affinity to a particular depth stratum.

TABLE 4. MEAN SQUARES, F-VALUES, SIGNIFICANCE, AND % VARIANCE OF THE MODEL ACCOUNTED FOR BY EACH FACTOR FOR THE MOST ABUNDANT FISH SPECIES IN FIORDLAND.

		Caesioperca lepidoptera			*Notolabrus fucicola*			*Notolabrus miles*			*Notolabrus celidotus*		
Source	df	MS	F	%	MS	F	%	MS	F	%	MS	F	%
Site	7	39.9	10.7***	41.8	8.8	27.2***	35.6	18.6	21.9***	59.4	6.7	10.1***	50.4
Depth	1	191.8	51.5***	28.8	85.1	263.6***	49.3	26.1	30.8***	11.9	8.9	13.5***	9.6
S X D	7	10.9	2.9*	11.4	2.2	7.0***	9.1	5.1	6.0***	16.3	2.3	3.5***	17.2
Residual	32			17.9	0.3			0.8		12.4	0.7		22.8

Significance levels: *$P < 0.05$, **$P < 0.01$; ***$P < 0.001$.
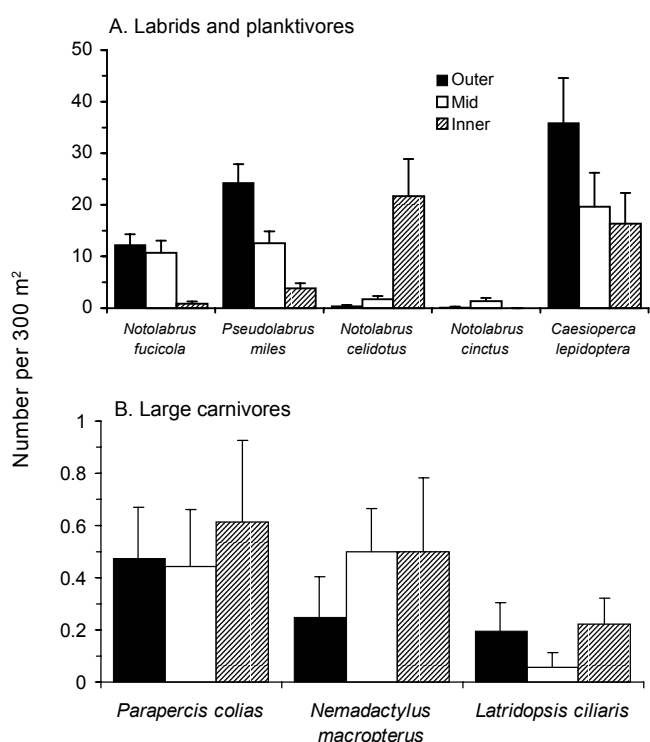
Figure 24. Mean number (+SE) per 300 m² for (A) labrids and planktivores, and (B) large carnivores in outer, mid and inner sites of Fiordland.

Overall patterns

There was an overall trend for the smaller species of reef fish to be less abundant further into the Sounds (Fig. 24A). Banded wrasses (*N. fucicola*) were equally abundant in the outer and middle areas but far less abundant in the inner Sounds. Scarlet wrasses (*Pseudolabrus miles*) showed a gradient of abundance from 25 fish per 300 m² in the outer sites, to 13 in the mid sites to 5 per 300 m² in the inner sites. Spotties (*N. celidotus*), however, were far more abundant in the protected inner sites, with an average density of c. 22 per transect. Girdled wrasses (*N. cinctus*) were not abundant in any region of the Sounds. Butterfly perch (*Caesioperca lepidoptera*) were most abundant in the outer sites but were also one of the most abundant fish species in the mid and inner sounds.

Of the large carnivorous fish species, blue cod (*Parapercis colias*) and tarakihi (*Nemadactylus macropterus*) were slightly more abundant in the inner Sounds, but their variation was high (Fig.

24B). Blue moki (*Latridopsis ciliaris*) were never abundant, but they occurred in all regions (Fig 24B). Fourteen species of reef fish were recorded in the transects throughout Fiordland, four of which (*N. fucicola, P. miles, N. celidotus* and *Caesioperca lepidoptera*) dominated the fauna overall (Fig. 25).
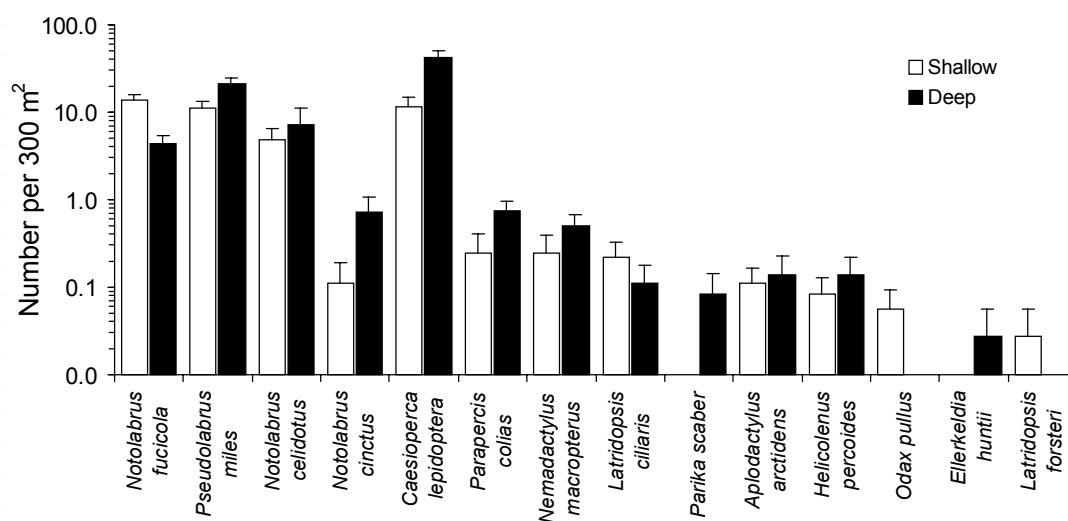

Figure 25. Mean abundance (+SE) per 300 m² across 13 sites in Fiordland of 14 fish species encountered during shallow and deep transects (note log scale).

3.3 CHATHAM ISLANDS

3.3.1 Algae and invertebrates

The nine sites we sampled were located along the eastern and northern coasts of Chatham Island and Pitt Island (Fig. 4). Some of these sites, particularly those south of Point Gap, were very exposed. We sampled in 5 depth strata: Depth 1 < 1.5 m, Depth 2 = 2-5 m, Depth 3 = 6-9 m, Depth 4 = 12-15 m, and 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.

Many more species were encountered than can be accommodated here. Species of larger algae are presented separately but smaller species of algae are grouped into browns, reds, and greens. The most commonly encountered species and taxonomic authorities are listed (Table 5).

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 Point Gap, where it averaged 2.7 plants (± 1.24) per m² and had a canopy cover of 56%. In several other sites, particularly Durham Point, Cape L'Eveque, Waihere Bay, and Mangere I., *Durvillaea* spp. formed virtually a closed canopy in the immediate subtidal zone.

Algal identifications were after Nelson et al. (1991), invertebrates after Powell (1970).

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

We found only two species of laminarian algae during the survey (Fig. 26). The giant kelp *Macrocystis pyrifera* formed forests at Waitangi West and Cape Young West, which are generally protected from the severe weather of the north-east and south-west. At 12–15 m, *M. pyrifera* occurred at average densities of 0.8 plants per m^2 at Waitangi West and 3.2 at Cape Young West (Fig. 26A). Deeper plants were found only at Waitangi West (1.4 plants per m^2). Most plants reached the sea surface but had no more than five stipes. The higher densities of *M. pyrifera* at Cape Young West produced a cover of attached holdfasts and basal fronds of only 12% of the substratum, whereas the lesser numbers at Waitangi West produced a cover of 30% at 12–15 m and 54% at > 16 m depth.

The other laminarian was *Lessonia tholiformis,* which is endemic to the Chatham Islands. It occurred to 15 m depth at most sites (Fig. 26B). Average densities within a depth stratum ranged up to 11 per m^2 but there was considerable site-to-site variation. The canopy of this species, formed about 1 m above the substratum, had a cover of >10% at 2–9 m at Ocean Bay, Cape L'Eveque and Mangere Island. *L. tholiformis* was particularly dense at Cape L'Eveque where the cover was 65% at 2–5 m and 50% at 12–15 m. Overall, the

Figure 26. Mean number (+SE) per m² (above bar) and mean percentage (+SE) cover (below bar) by depth stratum of (A) *Macrocystis pyrifera* and (B) *Lessonia tholiformis* at the nine sites of the Chatham Islands.

percentage cover largely reflected the abundance of plants except at the shallowest depth where the plants were small and provided little canopy 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.

Eleven species of fucalean algae were seen during the survey (Table 5), primarily in shallow water. *Xiphophora gladiata* was particularly common at Ocean Bay and Point Gap, primarily at < 1.5 m depth (Fig. 27A). It was also seen in low abundances between 2 and 9 m depth at these sites and also at Mangere I. Its cover reached 52% at Ocean Bay and 28% at Point Gap in < 1.5 m depth.

Carpophyllum maschalocarpum and *C. plumosum* are common fucaleans along mainland New Zealand, found primarily in shallow water. At the Chatham Is, they were most abundant between 2 and 9 m depth (Fig. 27B, C).
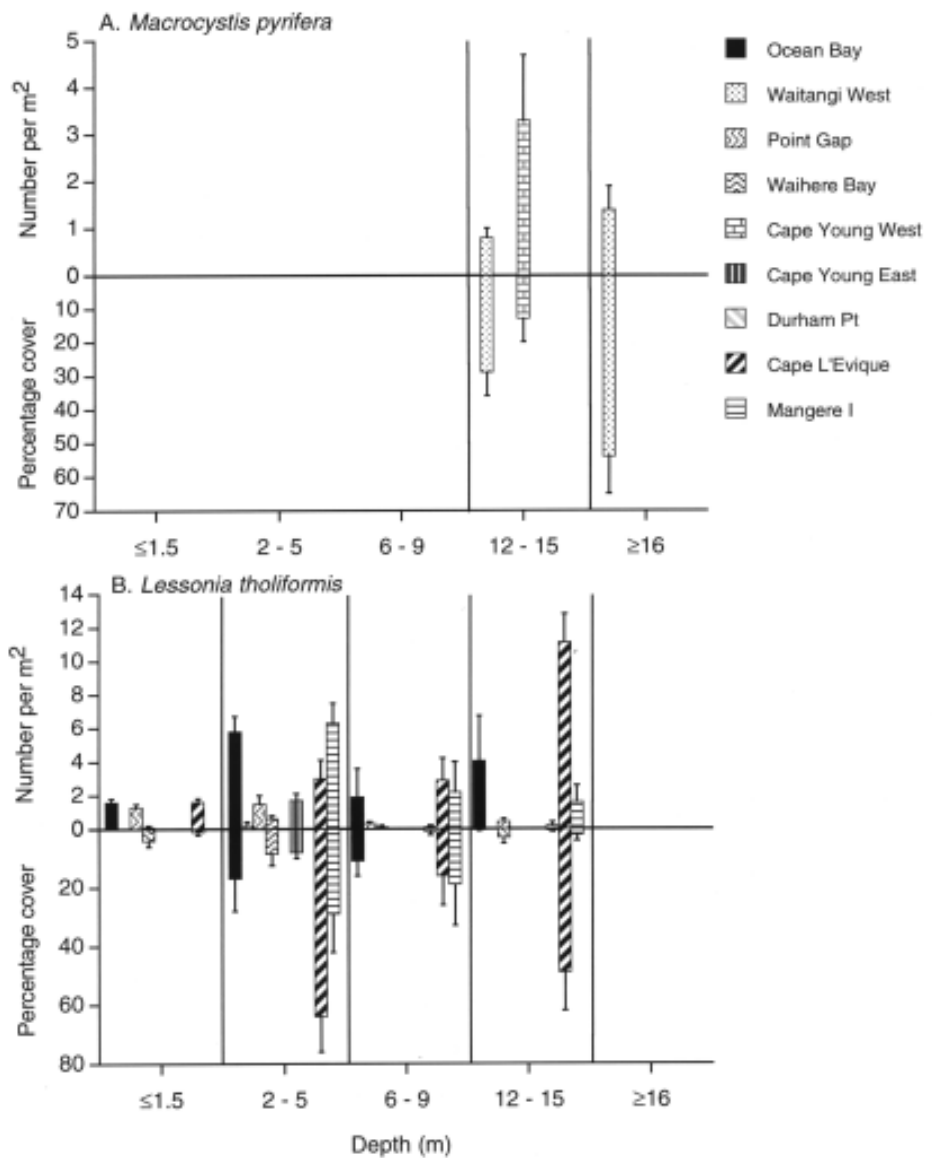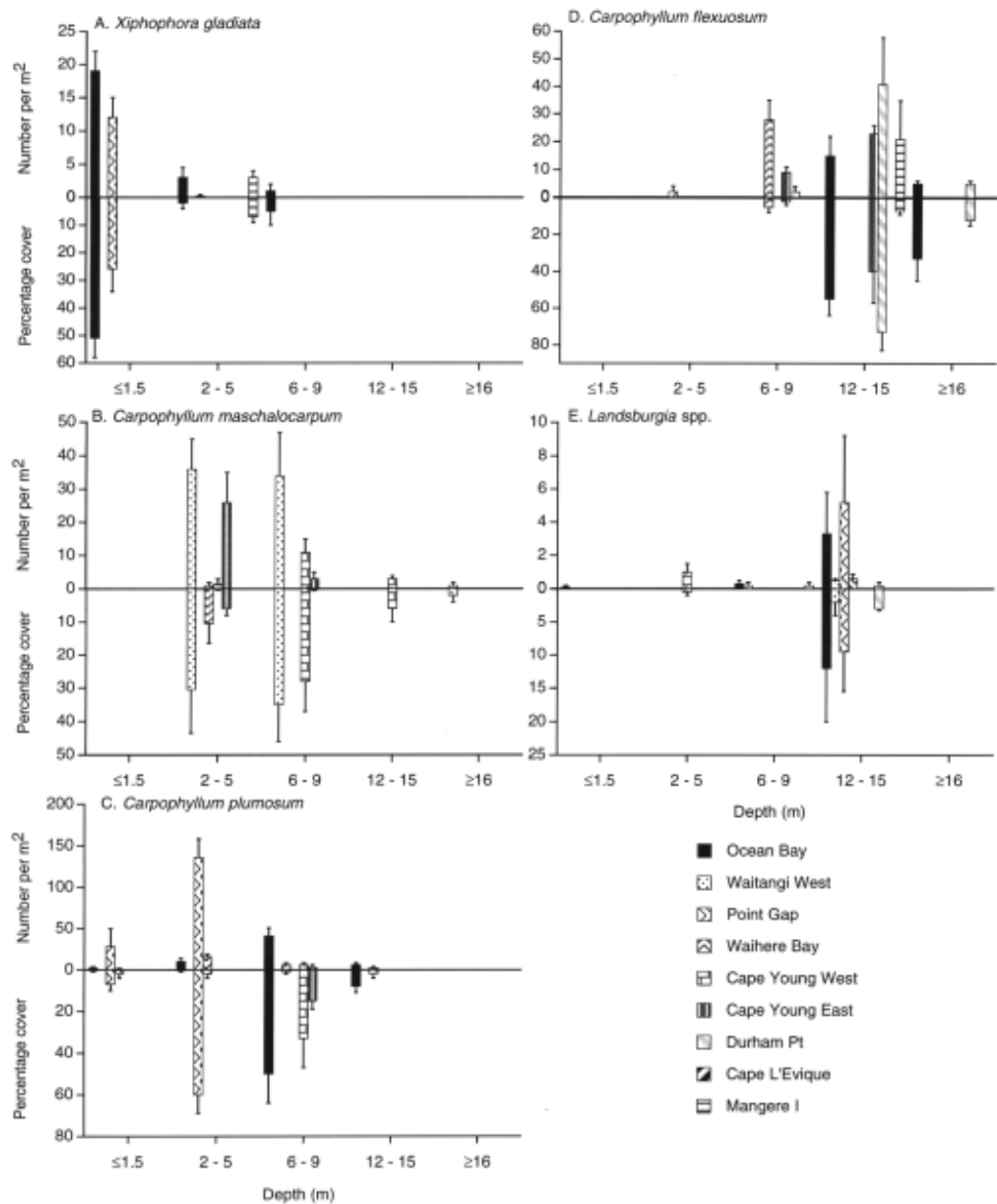
Figure 27. Mean number (+SE) per m² (above bar) and mean percentage (+SE) cover (below bar) by depth stratum of (A) *Xiphophora gladiata*, (B) *Carpophyllum maschalocarpum*, (C) *C. plumosum*, (D) *C. flexuosum,* and (E) *Landsburgia* spp. at the nine sites of the Chatham Islands.

C. maschalocarpum was particularly abundant at Waitangi West, where it reached averages of 37 plants per m² and a cover > 30% in 2-9 m depth. *C. plumosum* reached greatest densities at Point Gap and Ocean Bay (Fig. 27C). Average densities of 129 plants per m² at Ocean Bay in 2-5 m depth produced a canopy cover of 59%, while an average of 38 plants per m² at 6-9 m produced a canopy cover of 46%. *C. flexuosum* occurred in the middle depths and beyond (Fig. 27D). Some small plants were seen between 2 m and 9 m depth, reaching an average of 29 plants per m² at Waihere Bay. However, the percentage cover of these plants was virtually nil, as plants were recent recruits. Overall, the greatest numbers and cover occurred in the two deeper depth strata (12-16+ m). *C. flexuosum* was particularly abundant at Ocean Bay, Cape Young East, Durham Pt. and Mangere I. Average densities at 12-15 m depth ranged from 16

to 42 plants per m², with percentage covers ranging from 40 to 72%. The relatively small numbers of *C. flexuosum* in depths > 16 m at Ocean Bay and Durham Pt produced canopy covers of 32% and 12% 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. 27E) and were not seen at the Cape Young sites, Durham Point and Cape L'Eveque. At 2–9 m, *Landsburgia* occurred in small patches and never reached a canopy cover > 1%. At 12–15 m, however, densities of 3 and 5 plants per m² at Ocean Bay and Point Gap produced canopy covers of 12 and 9%, although these stands were patchy with considerable variation in numbers and cover.

Marginariella boryana is common along the mainland coast of southern New Zealand, and *M. urvilliana* is less common. Both species were encountered at the Chatham Islands, but found only at Ocean Bay in the 6–9 m and 12–15 m depth strata, where they reached combined densities of 3.0 (± 3.00) and 1.5 (± 1.17) plants per m² and percentage covers of 12% and 6% (no graphs presented). *Cystophora* spp. (*C. torulosa, C. distenta, C. scalaris*) occurred in small numbers at Ocean Bay, Point Gap and Cape Young West. The greatest average density was 0.4 (± 0.40) plants per m² at 12–15 m depth in Ocean Bay, with a percentage cover of < 5%.

The most abundant of the large, mobile invertebrates was the abalone *Haliotis iris* (Fig. 28A). These were found in all sites except Ocean Bay and Mangere I. *H. iris* is a shallow-water species and occurred deeper than 9 m only at Cape L'Eveque. Juveniles (< 70 mm shell length) were found exclusively on the undersides of boulders. They were abundant at Durham Point, Cape L'Eveque, and Waitangi West, reaching average densities up to 5.5 per m². Juveniles were not found at Ocean Bay, the two Cape Young sites, and Mangere I. This was probably due to the shortage of appropriately sized boulders to serve as habitat. Adult *H. iris* were abundant at most sites, reaching average densities as high as 15 per m² in 2–5 m depth. It is noteworthy that several sites with relatively dense adult populations had few or no juveniles. The major exceptions to this were Durham Point and Cape L'Eveque, where there was good correspondence between adult and juvenile numbers.

The yellow-foot paua *Haliotis australis* was much less common than *H. iris* and was found mostly in 2–5 m depth. Although it was found at six sites, it never reached densities greater than 3 per m² (no graph presented) The small abalone *H. virginea* was encountered at Durham Point, where it occurred at 0.8 per m² at 12–15 m depth.

The other large and common invertebrate was the ubiquitous sea urchin of the New Zealand coast, *Evechinus chloroticus*. This grazer was found at all sites at the Chatham Islands, with greatest densities at 6–15 m (Fig. 28B). It was most abundant at Mangere I., at average densities of 5–7 per m². 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 & Schiel 1982; Harrold & Pearse 1987). The abundance of *E. chloroticus* at the Chathams was characterised by a high variance within sites and depths. Dense aggregations of up to 40 large
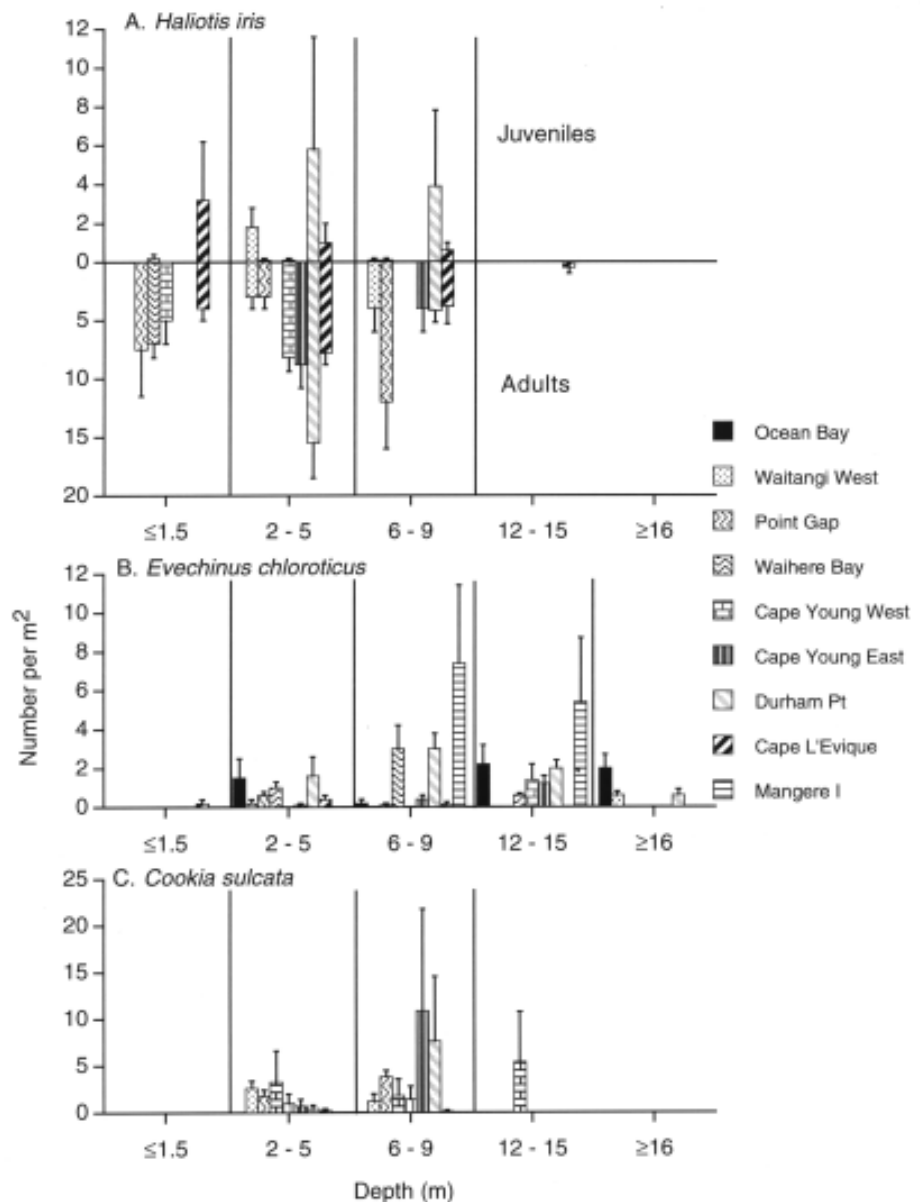
Figure 28. (A) Mean number (+SE) per m² of *Haliotis iris* juveniles (<70 mm shell length; above bar) and adults (below bar), and mean number (+SE) per m² of (B) *Evechinus chloroticus* and (C) *Cookia sulcata* at the nine sites of the Chatham Islands.

echinoids per m² were encountered, but deforested patches were never seen larger than c. 25 m².

The turbinid gastropod *Cookia sulcata* was abundant in the three middle depths at most sites reaching average densities of 11 per m² at 6–9 m (Fig. 28C). Other gastropods were patchy in occurrence with respect to sites and depths (no graph presented). Trochid gastropods were found in small numbers at most sites and never reached densities > 3 per m² except in the shallowest depth samples at Cape L'Eveque, where the average density was 48 per m². Limpets were also very patchy, being recorded at most sites but reaching densities of 126 (± 46.0) per m² at 6–9 m at Point Gap and 107 (± 24.9) per m² at Durham Pt, where they were associated with sea urchins, abalone, and encrusting coralline algae beneath a sparse canopy of *Lessonia*.

Large, sessile invertebrates were relatively uncommon. The exception was in > 16 m depth at Cape Young West. 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 understorey here. Small sponges, tunicates, and bryozoans were common beneath layers of non-geniculate corallines. This algae-invertebrate matrix was usually 1–4 cm thick.

Overall patterns

There were clearly site × 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 6). At the scale of Sites, there were positive correlations among many of the fucalean algae, indicating a broad overlap in the abundances of these species. Among invertebrates, *Evechinus* tended to be abundant in sites where the deep-water fucalean *C. flexuosum* was

TABLE 6. CORRELATIONS BETWEEN SPECIES AT THREE SPATIAL SCALES.

Correlations by site (*n* = 9), by depth stratum (*n* = 5), and by quadrat (*n* = 259);
in all cases P < 0.05.

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

abundant. Juvenile *H. 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*, but there was a broad overlap of species with depth. *H. iris* adults and juveniles, both of which were most abundant in shallow water, were negatively correlated with *Macrocystis*, which is a deeper-water species. At the finer spatial scale of 'Quadrats', the only significant algal correlation was *Landsburgia* with *Marginariella*. *H. iris* adults were negatively correlated with *Lessonia* and *C. flexuosum*, the holdfasts of which could cover much of the substratum, and 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* was again positively associated with *C. flexuosum*. Interestingly, at no spatial scale was there a correlation between *Evechinus* 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 in northern New Zealand (Ayling 1981; Choat & Andrew 1986).

Similarities of sites for all of the organisms sampled were assessed 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 summarised by depth. A correlation matrix was used to assess associations between species at different spatial scales (Sites, Depth, Quadrats). The cluster analysis showed that sites were grouped largely by differences in exposure (Fig. 29). Ocean Bay, Waihere Bay and Mangere I. were relatively protected within bays. Point Gap and Durham Point were near each other along the south-western coast and had similar protection. Cape L'Eveque, along the southern coast, was the most exposed of all the sites. The three northern sites (Waitangi West, Cape Young East, Cape Young West) were similar in exposure, species composition and species abundance, except for the presence of *Macrocystis* forests at Waitangi West and Cape Young West. At these sites, there were relatively few giant kelp plants compared to other species, but they formed a dominant habitat because of their large size. Overall, however, most species occurred at most sites.
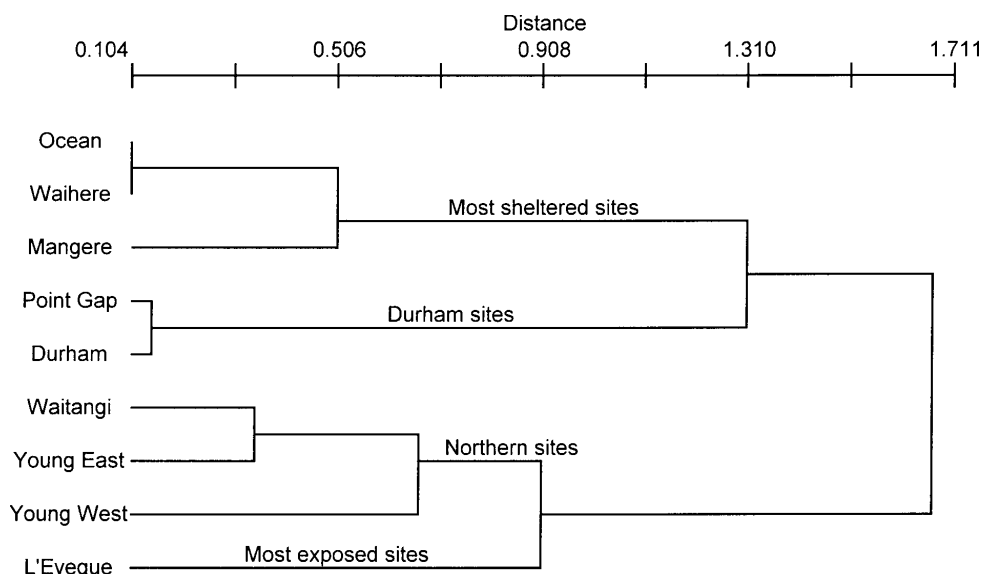

Figure 29. Cluster analysis of abundance data for nine sites of the Chatham Islands. Major characteristics of clusters are indicated.

Superimposed on site differences, however, were differences among depths in the distributions of species. *Durvillaea* is clearly a shallow-water genus and there were no exceptions to its occurrence in the immediate subtidal zone. Its average abundance and percentage cover were considerably underestimated because we were not able to assess it quantitatively in all sites. *Lessonia tholiformis* had a bimodal depth distribution with greatest numbers in 2–5 m and 12–15 m depths (Fig. 30A). *Macrocystis* forests occurred only in the two deeper strata. *Carpophyllum maschalocarpum* and *C. plumosum* shared the middle depths with other fucaleans and *Lessonia*, although *C. plumosum* also occurred in the shallowest depth zone (Fig. 30B). All fucaleans except *C. flexuosum* were scarce beyond 9 m. *Landsburgia* spp. were most abundant in 12–15 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 (± 2.8) plants per m² in 12–15 m, with an overall average canopy cover of 15–20%.

Understorey species also showed clear depth-related patterns of distribution (Fig. 30C). Brown algae were most common in shallow water, having an overall average cover of 5–6% in < 5 m. The most abundant of these in terms of percentage cover were *Halopteris* spp., *Glossophora kunthii*, and *Zonaria*
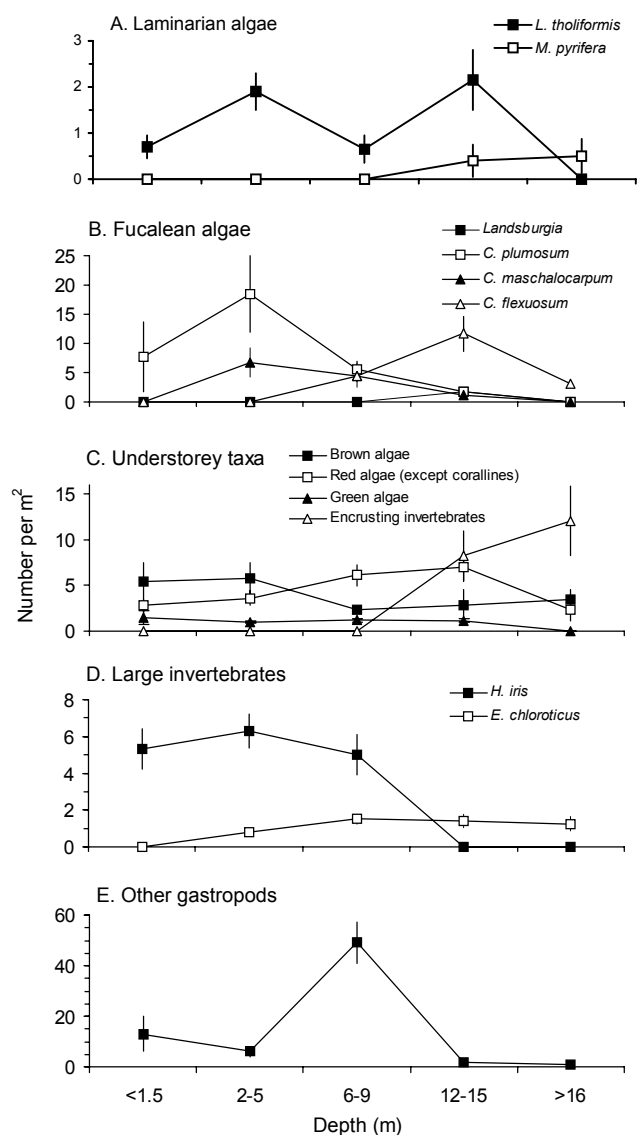

Figure 30. Summaries of mean number per m² (±SE) across all sites in the Chatham Islands of (A) laminarian algae, (B) fucalean algae, (C) understorey taxa, (D) large invertebrates, and (E) other gastropods.

turneriana. Red algae (other than corallines) showed the opposite pattern, with increasing cover to 15 m. No species was particularly prominent; many were combined during the survey into either filamentous or foliose forms. The reduced cover of red algae in the deepest areas was at least partially due to the abundance of sponges and other encrusting invertebrates. Green algae had only a small coverage at most depths and were not seen deeper than 15 m. The most common taxa were *Ulva* spp. and *Codium* spp.

Haliotis iris was abundant to 9 m depth with overall densities > 5 per m^2 (Fig. 30D). Only a few individuals were found in deeper water and none beyond 15 m depth. The sea urchin *Evechinus* was most abundant in deeper water from depths of 6–16 m, with an overall abundance of 1–2 per m^2. Gastropods other than *H. iris* reached peak abundances in 6–9 m and were uncommon in deeper water (Fig. 30E). These were mostly limpets that occurred in great abundances at two sites.

Corallines were the commonest understorey algae. They were abundant at all sites and all depths, in most cases covering > 40% 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 & Foster 1989). The cover of coralline algae was reduced in shallow and deep water (1.5 m and > 16 m depths) at most sites. The reduction was usually associated with a high cover of fleshy algae at around 1.5 m depth, and a high coverage of sessile invertebrates at > 16 m.
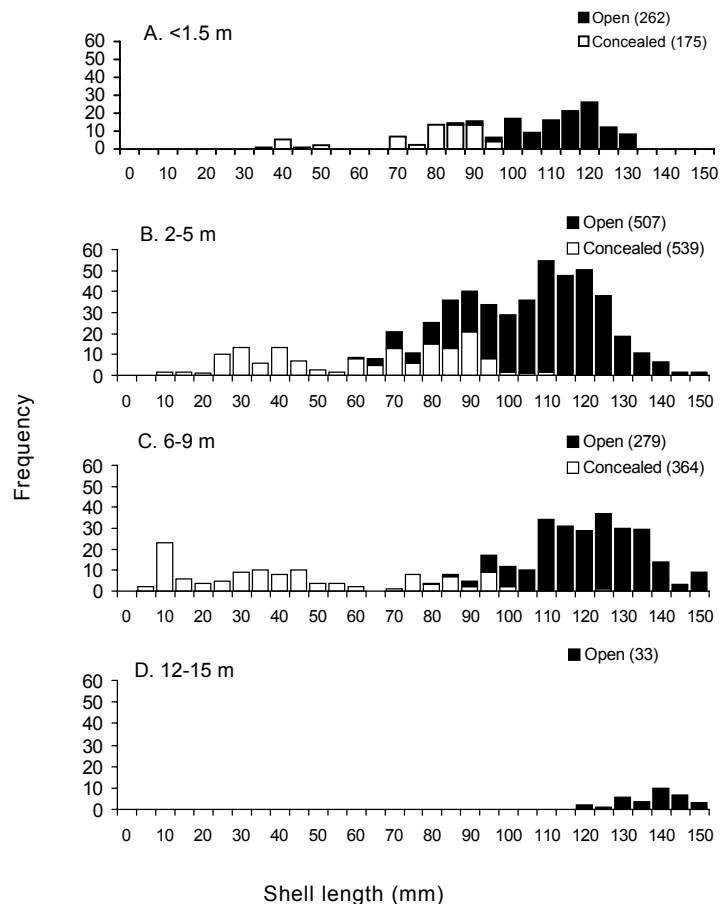

Figure 31. *Haliotis iris* size-frequency (number) distributions by four depth strata (A–D) across all sites at the Chatham Islands. None were found in Depth 5. Open bars indicate individuals found exposed on rock surfaces; black bars indicate concealed individuals on underside of rocks and boulders. Sample sizes (N) are given in brackets.

The size-frequency distributions of the major herbivorous invertebrates also showed clear patterns with depth. A wide range of sizes of the abalone *H. iris* occurred to 9 m depth (Fig. 31A–C). Only large individuals, however, were found at 12–15 m (Fig. 31D) and none were seen deeper than this. 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 animals beyond 100 mm were exposed on reefs. Juvenile sea urchins (< 70 mm) were seen only < 9 m deep (Fig. 32A, B). Large individuals were found in all depths beyond 2 m. Only urchins >100 mm were seen in deep water (>16 m; Fig. 32D).
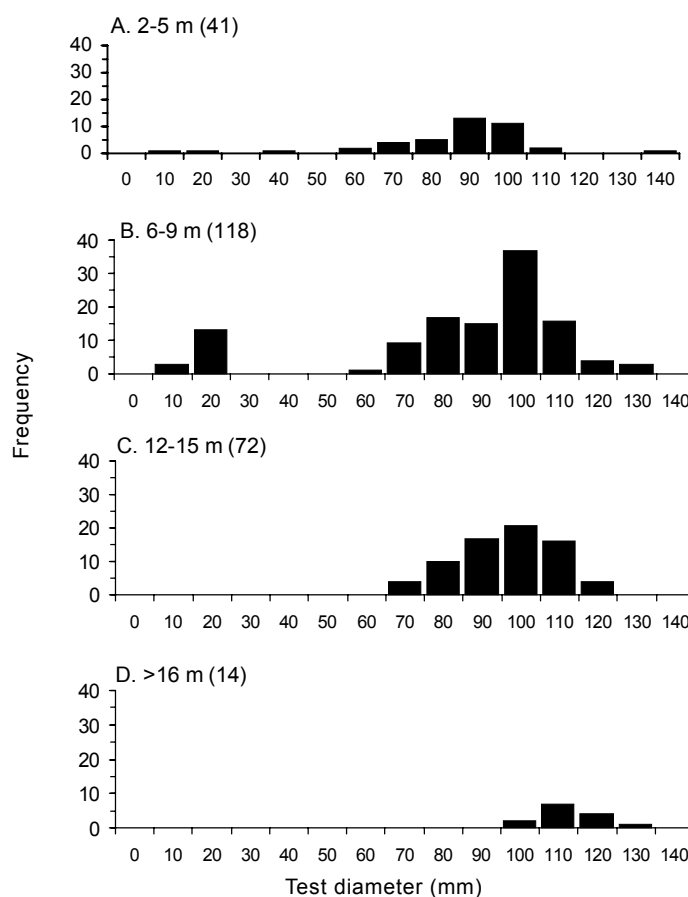

Figure 32. *Evechinus chloroticus* size-frequency (number) distributions by four depth strata (A–D) across all sites at the Chatham Islands. None were found in Depth 1.

3.3.2 Fish

Only nine species of reef fish (excluding blennioids) were encountered in the fish transects at the Chathams. Rather than using site-by-site comparisons of abundance, fish were grouped according to the site categories discerned with the Sorenson's index above. Group 1 comprised the most sheltered sites (Ocean Bay, Waihere Bay and Mangere I.); Group 2 was the Durham sites (Point Gap and Durham Pt.); Group 3 was the most exposed site (Cape L'Eveque); Group 4 was the northern sites (Waitangi West, Cape Young East and Cape Young West).

Blue cod, *Parapercis colias*, was the most abundant fish species on reefs at the Chathams. It occurred in both shallow (5–10 m) and deep (15–18 m) water at all groups of sites (Fig. 33A). In the sheltered sites, blue cod were equally abundant in shallow and deep water, at a density of c. 10 fish per 300 m². At the Durham and northern sites (Groups 2 and 4), blue cod were more abundant in deep water. They were least abundant overall at the most exposed site (Group 3).
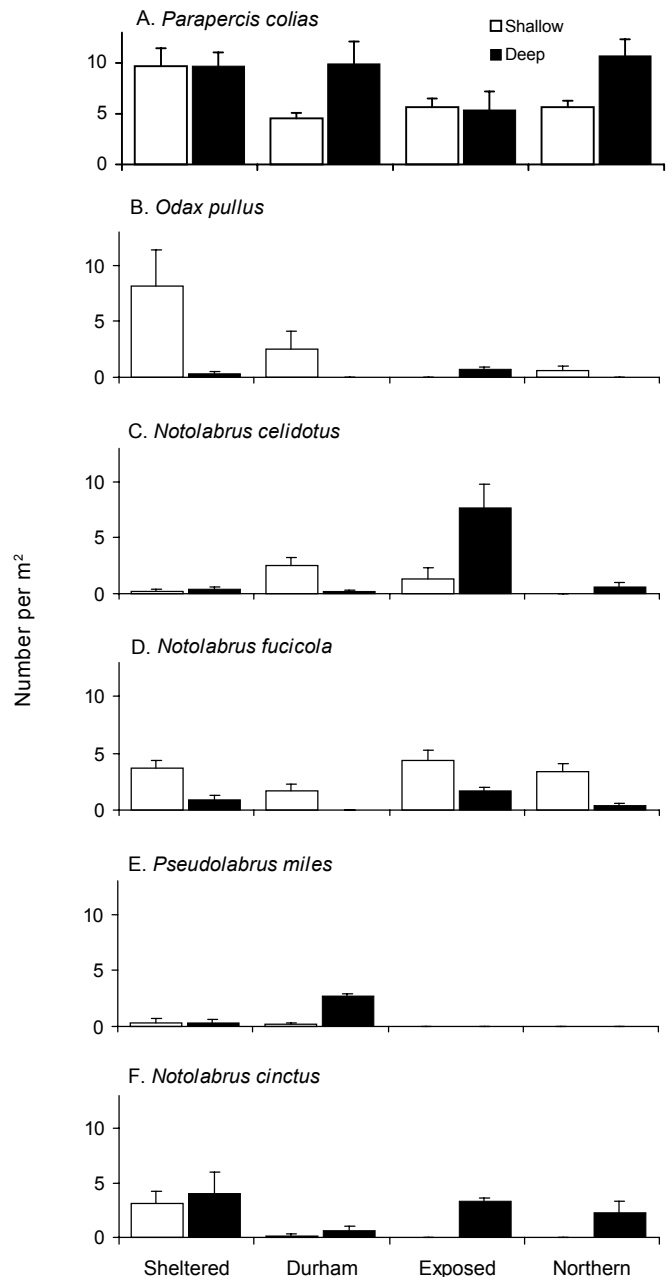
Figure 33. Mean abundance (+SE) per 300 m² in deep and shallow transects of six species of fish (A–F) at the Chatham Islands. Sites are grouped according to the cluster analysis of Figure 29.

The herbivorous *Odax pullus* was most abundant in shallow water in the sheltered sites (Group 1; Fig. 33B). Its greatest abundance was at Mangere I. where there were 22 fish per 300 m². This species co-occurred with dense beds of the laminarian alga *Lessonia tholiformis*. A suite of labrid fishes was common at all sites. The spotty *Notolabrus celidotus*, although reported as being absent from the Chatham Islands (Roberts 1991), was found in sites of all groupings (Fig. 33C). Its greatest abundance of 8 fish per 300 m² occurred in deep water at the exposed Cape L'Eveque on the southern side of Chatham Island. Banded wrasses, *N. fucicola*, were far more abundant in shallow than in deep water (Fig. 33D). They were least abundant in the sites along the Durham coast (Group 2). The scarlet wrasse *Pseudolabrus miles* had a variable distribution (Fig. 33E). It occurred at less than one fish per transect in the sheltered (Group 1) sites, but was abundant in deep water at the Durham (Group 2) sites. It was not found at all in the northern sites and at Cape L'Eveque (Groups 3 and 4). Girdled wrasses, *N. cinctus*, were found mostly in

deep water at average densities of 2-4 per 300 m² (Fig. 33F). They were least abundant along the Durham coast (Group 2). Leatherjackets, *Parika scaber*, had a similar distribution to *P. miles*, being found in small numbers at the sheltered and Durham sites (Groups 1 and 2) and not at all in Groups 3 and 4 sites (Fig. 34A).

Of the larger reef fish, blue moki (*Latridopsis ciliaris*) occurred at an average of 1-3 fish per 300 m² at most sites (Fig. 34B). It had a variable distribution with respect to depth and occurred mostly in coralline-dominated patches, regardless of depth. Tarakihi, *Nemadactylus macropterus*, were found at 3 per 300 m² in the shallow areas of sites along the Durham coast (Group 2), but occurred at less than 1 fish per transect in all other sites (Fig. 34C).

There were few trends in total fish abundance with respect to site groupings (Fig. 34D). Fish were slightly more abundant in the shallow areas of sheltered sites (Group 1), at 27 per 300 m². They were least abundant at the northern sites (Group 4), at 10–15 fish per transect. Over all sites combined, there were more fish encountered per transect in shallow water (22 per 300 m²) than in deep water (17 per transect: Fig. 35).

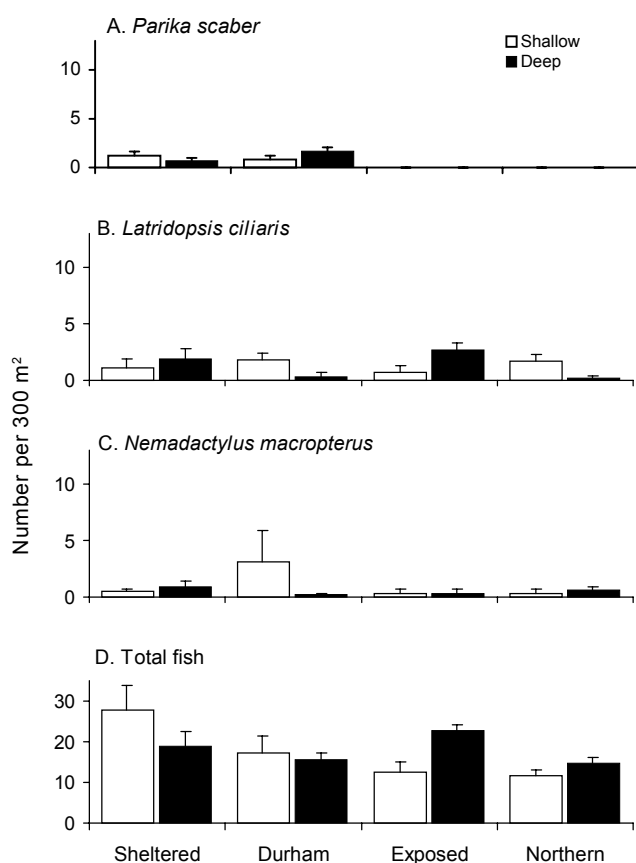Figure 34. Mean abundance (+SE) per 300 m² in deep and shallow transects of three fish species (A–C) and all species combined (D) in deep and shallow transects at the Chatham Islands. Sites are grouped according to the cluster analysis of Figure 29.
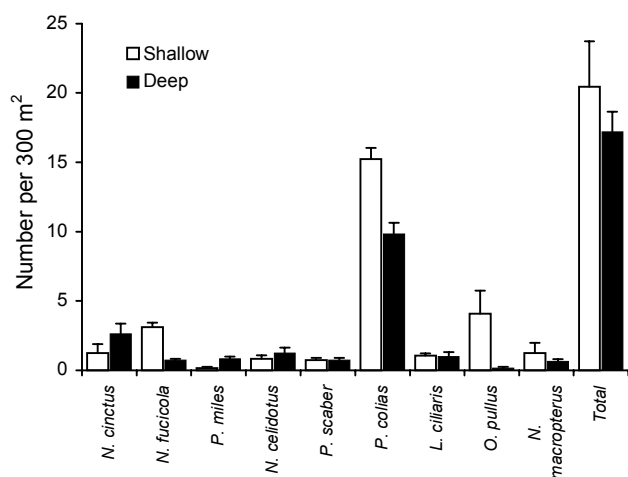

Figure 35. Mean abundance (+SE) per 300 m² of all species of fish that were found in shallow and deep transects across all sites at the Chatham Islands.

4. Geographic patterns

Despite the great variation within each region, there were clear geographic patterns to the dominant species and the habitats they characterised. Fucalean algae dominated shallow-water habitats in each region. At exposed sites in all regions, *Durvillaea* was the dominant alga. At the Chathams, the indigenous *D. chathamensis* was common. *Xiphophora gladiata* was the dominant alga in 1.5 m depth at exposed sites in Fiordland and the Chatham Islands. While *Marginariella* occurred in all regions, it was dominant only at Kaikoura. The ubiquitous *Carpophyllum maschalocarpum* was abundant in depths to around 5 m in all regions. *C. flexuosum* was generally found in > 10 m depth in all regions but extended into shallow water only in more protected sites. *Landsburgia quercifolia* could dominate patches in all regions, but it never dominated sites. This species was intermingled with the endemic *L. myricifolia* at the Chathams.

Laminarian algae had an odd distributional pattern. *Ecklonia radiata*, the ubiquitous kelp of the New Zealand mainland coast and nearshore islands, was not found at all at the Chathams. It formed a dominant habitat in deep water at the east coast sites as well as in Fiordland. At many sites it also occupied large patches in shallow water, or dominated the understorey of *Macrocystis* forests. The tough, leathery *Lessonia* species have a peculiar distribution bio-geographically. *Lessonia variegata* dominated some patches in exposed east coast and Fiordland sites, but overall it was not a dominant habitat-former in the sites investigated. In one locality where *Lessonia* was common, the inside of Five Fingers Peninsula in Fiordland, another species, probably *L. brevifolia*, occurred in dense isolated patches. It was seen nowhere else in these surveys. However, this species is the dominant understorey alga of the subantarctic Auckland Islands (D. Schiel unpubl. data) and has been reported from other sites in the southern fiords (C. Hay pers. comm.). At the Chatham Islands, a *Lessonia* species forms dense beds and dominates many sites. This endemic species, *L. tholiformis*, dominates the shallow areas normally shared with *Ecklonia radiata* in coastal sites. Giant kelp, *Macrocystis pyrifera*, is distributed widely and occurs in all regions. As clearly shown at the Chatham Islands, where a range of exposures occurs, this species occupies the more sheltered areas. At the Chathams, it was common in the Port Hutt Bays and the semi-sheltered northern sites. This species has a southern distribution in New Zealand. It is common around Stewart Island (D. Schiel pers. obs.) and the partially protected areas of southern Fiordland. However, it is not reported to occur north of Milford Sound on the west coast. Along the east coast of the South Island, it occurs in semi-protected sites on rocky substrata all along the coast, with the largest kelp bed occurring around Motunau Island (c. 50 km north of Christchurch). On Banks Peninsula, *M. pyrifera* tends to occur in < 10 m depth, primarily because rocky substrata run to sand in deeper water at many sites.

One of the most striking differences among the regions was the dominance of sessile invertebrates around Banks Peninsula. Sea tulips (*Pyura pachydermatina*) are extremely abundant, as is a rich understorey of bryozoans, mussels,

ascidians and sponges. This type of habitat is extensive around Banks Peninsula and occurs to at least Wainui in Akaroa Harbour (D. Schiel pers. obs.). In no other region was such a rich invertebrate understorey encountered.

Paua, *Haliotis iris*, were common in all regions but were especially abundant at the Chatham Islands. It is rare to find a site at the Chathams where paua are not common. Paua juvenile habitat is also particularly abundant at the Chatham Islands. Small tumbled boulders inshore with juvenile paua beneath them occurred at most sites except the extremely exposed southern shore of Chatham Island. This habitat was patchy in other regions.

Abundances of fish species also varied among regions (Fig. 36). The scarlet wrasse (*Pseudolabrus miles*) and butterfly perch (*Caesioperca lepidoptera*) were extremely abundant throughout Fiordland, but in no other region. Blue cod (*Parapercis colias*) were very abundant at the Chatham Islands but nowhere else. Spotties (*Notolabrus celidotus*) were the most abundant fish at
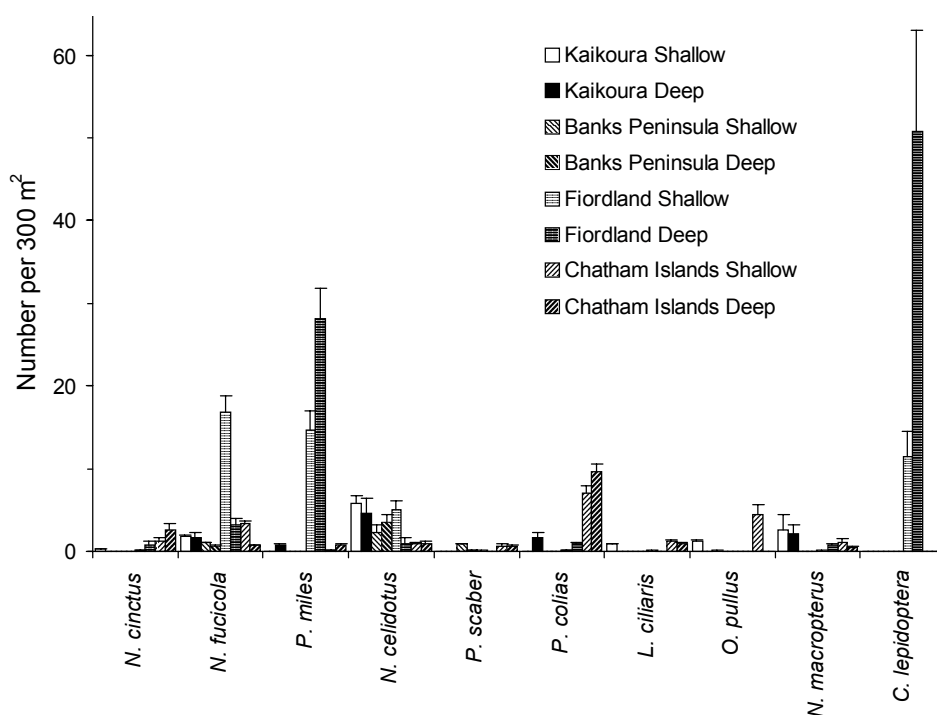
Figure 36. Mean number (+SE) of all species of fish that were found in shallow and deep transects across the four geographic regions. Transect size was adjusted to 300 m².

Kaikoura and Banks Peninsula. In terms of overall fish abundances, there were more fish per transect (300 m²) at Fiordland than in the other regions. The large numbers of *Caesioperca* at many Fiordland sites was the major cause of this trend. Banks Peninsula had the fewest fish per transect, with an overall average of 5 (Fig. 37). At Kaikoura, Fiordland and the Chatham Islands, the number of fish species per transect averaged 3-4 (Fig. 37). This was mostly due to the labrids co-occurring in most transects.
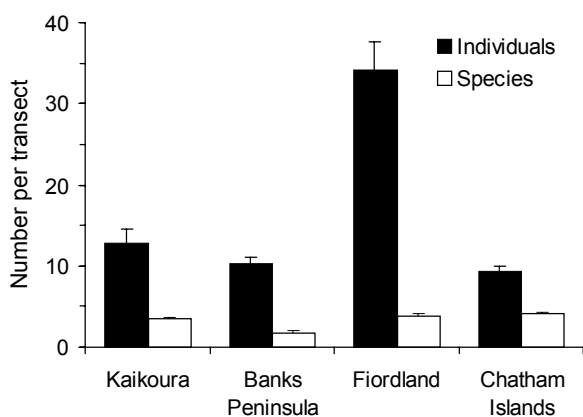
Figure 37. Mean number (+SE) of individual fish (solid bars) and fish species (open bars) per transect across the four geographic regions. Transect size was adjusted to 300 m².

5. Discussion

There was considerable variation in the abundances of algae and invertebrates with respect to depth, sites and regions. This patchiness was exemplified by the deep *Macrocystis pyrifera* forests that occurred at only two relatively sheltered sites at the Chatham Islands and in smaller patches in southern Fiordland, the occurrence of *Marginariella boryana* at only one site at the Chatham Islands, Kaikoura, and isolated patches elsewhere, *Cystophora* as isolated plants at a few sites, the extreme abundances of limpets at 6–9 m depth at two sites at the Chathams and Banks Peninsula, and the large variation in abundances and depth distribution of sea urchins and abalone. This patchiness provides clues to the underlying processes that may account for the structure of assemblages at these diverse localities. There is little distributional evidence for the types of strong top-down organising processes described in northern New Zealand and in other temperate areas of the world (Dayton 1985a; Schiel & Foster 1986; Harrold & Pearse 1987; Andrew 1988; Schiel 1988; Elner & Vadas 1990; Babcock et al. 1999). For example, the much documented sea urchin-dominated habitat of mid and deep water (Harrold & Pearse 1987) is largely missing from the Chatham Islands, except possibly for the very exposed southern coast, and from all of the sites we examined on the east coast of the South Island and Fiordland (although areas dominated by sea urchins occur in some shallow sites within Dusky Sound; E. Villouta pers. comm.). In only a few sites did we encounter 'barren' patches dominated by sea urchins. At the Chatham Islands, such patches were associated with large numbers of gastropods, including the abalone *H. iris*, despite the overall lack of correlation between *Evechinus* and *H. iris* at the Chathams.

In the absence of a dominant and universally abundant herbivore such as sea urchins, interactions among algae may assume greater importance in determining habitat structure (Dayton 1985a; Schiel & 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 recruit and persist in different physical regimes of exposure, sedimentation and availability of rocky substrata may have the major influences on the local array of species.

5.1 BIOGEOGRAPHY

The Chatham Islands was the most remote of the regions examined and is most affected by geographic isolation. Because of its position on the subtropical convergence, it has both northern and southern elements in its flora and fauna. Roberts (1991) described the affinities of the fish fauna of the Chathams. Sixty-three per cent of the 227 recorded fish species had widespread distributions and clear affinities with the Kaikoura-Banks Peninsula region. Eight per cent had a northern distribution and 4% a southern distribution. Of particular interest during our surveys was the sighting of spotties, *Notolabrus celidotus*, at most

sites. Roberts (1991) recorded this species as absent from the Chatham Islands. This species is ubiquitous throughout mainland New Zealand and the offshore islands, becoming particularly abundant in sheltered waters (Jones 1988). Jones (1984) recorded this as the most abundant reef fish species in northern New Zealand, with densities up to 300 fish per 500 m^2 in protected localities, and up to 30 per 500 m^2 in semi-exposed coastal sites. This species is common along the central South Island coast and would be expected to have reached the Chatham Islands, as did the other common coastal labrids. Our survey confirms its presence there. The other particularly striking trends in fish abundance were the great numbers of the scarlet wrasse *Pseudolabrus miles* in Fiordland and of blue cod, *Parapercis colias*, at the Chathams. *P. miles* commonly occurs at the offshore islands of northern New Zealand such as the Poor Knights (Choat et al. 1988; D. Schiel unpubl. data) and is seen in small numbers along most of the coast of New Zealand (Choat & Ayling 1987). However, its greatest density is in Fiordland, at the Three Kings Islands just off the tip of northern New Zealand, where it reaches densities of 34 fish per 500 m^2 (Choat & Ayling 1987), and possibly around Stewart Island. According to Ayling (1982), this species is most abundant in west coast sites (including the Three Kings Islands), and so may be influenced by the cooler water currents. The abundance of blue cod at the Chathams is probably related to the abundance of suitable habitat and also the reduced fishing pressure relative to mainland sites.

One of the most interesting biogeographic patterns is the striking presence of black coral in the inner-Sounds of Fiordland. We recorded black corals in similar densities to those found by Grange (1985) in his comprehensive survey of Fiordland. Most colonies were small (< 10 cm in height), but larger colonies are common and could be as old as 300 years (Grange & Goldberg 1993). The greatest abundances were found at depths of 15–20 m. The overall average density recorded by Grange (1985) was 1 colony per 4 m^2. There are many distinctive features to the physical environment and species' assemblages in Fiordland, not only because of the gradient of wave exposure away from the outer coast but also because of the influence of the low-salinity layer of surface water within the sounds. Low light penetration into the water column and the depth of the low-salinity layer affect the composition of assemblages and potentially important species interactions. For example, Witman & Grange (1998) found that grazers and predators avoided this low–salinity layer. In two inner sites within Doubtful Sound (far further into the Sound than the sites we sampled), mussels dominated depths of c. 3 m, which was usually within low-salinity water, and predation rates were intense immediately below this layer. During a period when the low-salinity layer was reduced, however, predators moved up a rock wall and greatly increased in abundance within the mussel zone.

The marine 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; Schiel et al. 1995). Large brown algae of the genera *Macrocystis*, *Lessonia* and *Durvillaea* are abundant from Cook Strait southwards 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 c. 40°. *Durvillaea*

species form the major component of the intertidal–subtidal boundary in much of Tasmania and south-eastern Australia (Womersley 1981; Cheshire & Hallam 1988, 1989), Chile (Santelices et al. 1980; Bustamante & Castilla 1990) down to Tierra del Fuego, and the islands of the Southern Ocean (Hay 1994). *M. pyrifera* is the dominant canopy species in many sheltered areas of southern Australia (Womersley 1981), and along the semi-protected and sheltered shores of Chile, especially in the southern Sounds areas, and Argentina (Santelices & Ojeda 1984a, b; Dayton 1985a, b) and many of the subantarctic islands (Womersley 1954).

The genus *Lessonia* has a wide southern geographic distribution. Most species in the genus are South American, but the taxonomy of some New Zealand species is unclear (C. Hay pers. comm.). It has some species, such as those at the Chatham Islands and Auckland Islands, with very restricted distributions, probably because of geographic separation, isolating currents, and the absence of an active means of dispersal. *Lessonia* species tend to be very tough, with leathery stipes and little buoyancy, and are found mostly in exposed situations. Various *Lessonia* species can dominate the intertidal–subtidal fringe and subtidal habitats along most of the northern and central coast of Chile (Villouta & Santelices 1984). *L. nigrescens* occupies the immediate subtidal region and competes with *Durvillaea antarctica* in central Chile (Castilla & Bustamante 1989). Further south, *L. vadosa* occurs in the shallow subtidal zone along much of the exposed coast of Chile and may set the upper limit of *M. pyrifera* in the semi-protected areas where these species co-occur (Santelices & Ojeda 1984a). *L. flavicans* is common in the understorey beneath the canopy of *M. pyrifera* in the southern Sounds of Chile (Santelices 1989). At the Auckland Islands, south of mainland New Zealand, the endemic species *L. brevifolia* is the dominant alga at a depth of c. 5 m, while *M. pyrifera* dominates in deeper water (Hay et al. 1985; Schiel 1990). *L. tholiformis,* endemic to the Chatham Islands, is very similar in appearance to *L. vadosa*. *Lessonia corrugata* is found around Tasmania in areas of moderate to strong water movement (Womersley 1987).

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

5.2 HYPOTHESES CONCERNING HABITAT STRUCTURE

At large spatial and taxonomic scales, several patterns become apparent. The bull kelps, *Durvillaea* spp., are restricted to the immediate subtidal region on exposed coasts, where there is severe water motion (cf. South & Hay 1979; Hay 1994). Other large brown algae seem incapable of persisting at a similar depth, either because of the physical regime or else through competition with *Durvillaea*. Beneath the canopy of *Durvillaea* is usually an area with few large brown algae. This is possibly due to the whiplash effect of *Durvillaea* (cf, Santelices et al. 1980; Santelices & Ojeda 1984b), reduced light beneath the canopy, and the inability of other algae to recruit into these exposed areas.

Beneath and just beyond this canopy there may be large numbers of abalone, particularly juveniles on the undersides of the tumbled boulders that are common inshore at the Chatham Islands and Banks Peninsula. The shallow depth zone (1.5–5 m) is usually partitioned finely. Fucalean species can survive well at 1.5 m depth, but were not seen in large numbers in areas of great water motion where *Durvillaea* flourished. In north-eastern New Zealand, where *Durvillaea* is rare, this shallow depth zone is normally occupied by a dense cover of fucalean algae, particularly *Carpophyllum angustifolium* (Choat & Schiel 1982), a species not found in southern New Zealand (Nelson et al. 1991).

Fucalean algae are found at all depths, but none except *C. flexuosum* are abundant beyond c. 10 m. At 2–5 m depth, however, fucalean and laminarian algae have approximately equal cover, and are assorted on a fine spatial scale with each occurring in dominant patches. 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 & Foster 1986). In the deepest areas of reefs (beyond 15 m), the dominant large brown algae were either *Macrocystis* or *C. flexuosum* at the Chatham Islands, and *C. flexuosum* and *Ecklonia* in the other regions. Because of its large size, *Macrocystis* required few plants to produce a dominant canopy in the northern sites of the Chatham Islands.

In parts of north-eastern New Zealand, especially some offshore islands, *Lessonia variegata* may form dense stands immediately below a zone occupied by *Carpophyllum angustifolium* (Choat & Schiel 1982). In Chile, *Lessonia nigrescens* competes with *Durvillaea antarctica* in the intertidal-subtidal boundary (Santelices et al. 1980). Another species, *L. vadosa* competes with *Macrocystis* in middle depths (Santelices & Ojeda 1984a, b). At the Chatham Islands there is evidence that fucalean species and *Lessonia* compete at a depth of 2–5 m. Across sites, fucaleans and *Lessonia tholiformis* each tend to be more abundant where the other is scarce. However, there were few correlations, either positive or negative, among the major algal taxa at any spatial scale. This supports the observation that all of 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 & Schiel 1982).

In waters beyond 15 m depth, it seems unlikely that competition affects the abundance of *Lessonia* species. In northern New Zealand, the Cook Strait region, the Auckland Islands, and the Chatham Islands, the abundance of this genus 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 degree of exposure may play a role in determining the abundance of species. For example, *Macrocystis* and *C. maschalocarpum* occupy sites on the north and west sides of Chatham I. that are somewhat protected from the full force of easterly and south-westerly storms. *Lessonia variegata* occurs in areas of intense water motion along north-eastern New Zealand (Choat & Schiel 1982; Schiel 1990) and along the Fiordland coast, but is never found in protected

areas. At the Chatham Islands, *Lessonia tholiformis* was found at most sites, but was particularly abundant along the very exposed south-eastern coast.

The stipitate kelp *Ecklonia radiata* is one of the dominant subtidal algal species of the Australasian region. It extends along the entire coast of New Zealand and the nearshore islands, it is the commonest kelp in New South Wales (Underwood et al. 1991) and it extends from Western Australia, around southern Australia, Tasmania and up to near the Queensland border (Womersley 1987). Its absence from the Chatham Islands results in major differences in the subtidal habitats there relative to other regions of New Zealand. Wherever it occurs in northern New Zealand, *E. radiata* shares dominance at depths of 2–8 m with fucalean species. On deeper reefs, however, it is almost invariably dominant except in sheltered waters where *Carpophyllum flexuosum* may be abundant (Choat & Schiel 1982; Schiel 1990). *E. radiata* grows quickly, disperses well, particularly when reproductive plants are nearby, and lives up to 10 years (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 and the east coast, *E. radiata* tends to dominate deeper water.

The absence of *Ecklonia radiata* at the Chatham Islands may also affect the large herbivorous invertebrates. The extensive sea urchin-dominated areas of northern New Zealand are invariably associated with the boundary, at c. 8 m depth, between shallow fucalean species and deeper *E. radiata* beds (Choat & 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* at the Chathams. Fucaleans (and probably *L. tholifornis*) 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 & Andrew 1986). This relationship was not seen at most sites surveyed in this study, although high densities of limpets were associated with sea urchins at a few sites.

Sea urchin 'barrens' in New Zealand appear to be related to latitude and are more characteristic of kelp communities north of Cook Strait. While they do occur in some sites in southern New Zealand (Dix 1970; E. Villouta, pers. comm.), they are not a common feature, as reported for many northern sites (Choat & Schiel 1982; Schiel 1990). This pattern may also exist in Australia, where sea urchin barrens are a common feature of the warm temperate areas of New South Wales (Andrew & Underwood 1989; Underwood et al. 1991) but apparently not of the algal-dominated kelp beds of southern Australia and Tasmania (Underwood & Kennelly 1990).

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 mix of species is so

different? The only reasonable clues seem to lie in the distribution and demography of the prominent component species. In unique offshore areas like the Chatham Islands, and remote areas such as Fiordland, these questions become important for conservation purposes and for the management of inshore fisheries. If biotic processes of grazing interactions are important to the structure of nearshore areas, and if high densities of grazers occur in some sites, then 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 distributions and life histories of species have the major effects, then comparisons of remote areas with more accessible areas becomes more difficult because of the different mix of species, some of which can be endemics. In the absence of strong structuring trophic 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 generally the most important structuring processes in the algal and invertebrate assemblages at these southern localities. Unfortunately, for most of these remote areas it is unlikely that an understanding of community organisation will be derived from in situ experimental studies.

6. Acknowledgements

7. References

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