

Macroalgal assemblages in New Zealand: structure, interactions and demography

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Abstract

Quantitative descriptions of macroalgal distributions from low intertidal regions to a sublittoral depth of 20 m are presented for rocky reefs from several localities ranging over 16° latitude in New Zealand. These include the northern and southern main islands as well as the Chatham Islands and the sub-antarctic Auckland Islands. Fuclean algae are dominant in the shallow sublittoral regions throughout NZ. Laminarian species are rare and generally reach their greatest abundances at 7–17 m depth. The colder waters in central and southern NZ tend to have different dominant species from those in northern NZ. Sea urchins form a characteristic zone devoid of kelp at 5–8 m in the north, but tend to occur only in patches on reefs in southern localities. Summaries of experiments in the north show that strong inter-specific effects occur among algal species, particularly due to canopy shading, and between sea urchins and algae. Much of the patchiness in algal assemblages, however, is not accounted for by these effects. A knowledge of the demographic processes of individual species is necessary to understand assemblage organization; life histories, phenology and biogeography significantly affect distributions and interactions.

Introduction

Neither the structure of the biota of rocky shores nor the processes responsible for the organization of macroalgal assemblages have been examined extensively in New Zealand. Studies in the 1940s – 50s provided qualitative descriptions of intertidal assemblages of macroalgae and invertebrates in terms of zonation schemes, but these were concentrated in the regions around Auckland in the north and Dunedin in the south (Chapman, 1943; Dellow, 1950, 1955; Batham, 1956, 1958). Studies of rocky sublittoral regions have been much more recent. Choat & Schiel (1982) gave a general description of the patterns

of distribution and abundance of fuclean and laminarian algae as well as herbivorous invertebrates in northeastern NZ. They also discussed hypotheses about the processes affecting these patterns. In most cases, however, experimental studies are lacking, and most of the information concerning the organization of algal assemblages derives from work done in northeastern NZ (reviews by Andrew, 1988; Creese, 1988; Schiel, 1988).

This paper does not review all of this work but instead limits its focus to the structure of macroalgal assemblages from the low tide mark to a sublittoral depth of 20 m. I assume that the structure gives clues about organizational proc-

esses and therefore a description of algal assemblages from a range of sites over 16° latitude will provide a context for a discussion of structuring processes.

Studies from elsewhere highlight the large variability in the structure of sublittoral algal assemblages but also reveal a considerable discrepancy in views concerning organizational processes and under what conditions and places they operate. For example, in the species-rich kelp forests off California, sea urchins may overgraze kelp in some areas (Lawrence, 1975; Harrold & Pearse, 1987) while extensive parts of the coastline suffer no large-scale effects (Foster & Schiel, 1988). 'Stabilizing predatory relationships' (Dayton, 1985) by sea otters (Estes *et al.*, 1978; Estes & Harrold, 1988), fishes (Bernstein *et al.*, 1981; Tegner & Dayton, 1981; Cowen, 1983), crabs and lobsters (Breen & Mann, 1976a; Bernstein *et al.*, 1981; Wharton & Mann, 1981; Tegner & Levin, 1983) may diminish the effects of sea urchins by reducing their abundance. In the kelp forests of Chile, where only a few kelp species are present, sea urchins do not seem to graze extensively on attached plants (Moreno & Sutherland, 1982; Dayton, 1985) and algal interactions may strongly influence the structure of algal stands (Santelices & Ojeda, 1984). Studies in Nova Scotia, where a few species of stipitate laminarians are dominant, have shown that demographic processes of algal species affects the structure of assemblages (Chapman, 1984) and also that sea urchins can devastate algal populations over considerable areas of coastlines (Miller, 1985). Both predators and disease have been invoked as limiting echinoid effects in this region (Bernstein *et al.*, 1981; Wharton & Mann, 1981; Miller & Colodey, 1983; Scheibling, 1884).

Sublittoral areas in New Zealand contain analogues of most of these communities (Choat & Schiel, 1982; Schiel, 1988). As in Australia, however, the species composition in NZ is quite different from North America, with many fucal species and only a few laminarians. Only one species of sea urchin, *Evechinus chloroticus*, is common and it occurs throughout coastal NZ and most nearshore islands (Dix, 1970). Are the

structure and organization of these components also different?

This paper first considers the structure of algal assemblages in NZ and then assesses the strength of interactions between algal species and between algae and sea urchins. Particular emphasis is given to factors affecting the patchiness of algal species in shallow water and the abundances of fucal algae in deeper water. Welden & Slauson (1986) stress the distinction between the strength of interactions and their importance in explaining an effect. I point to evidence that strong interactions occur between species but their overall importance in accounting for the structure of algal assemblages may not be great. Several spatial scales are considered, from localized patches within depths to a geographic scale throughout NZ.

Methods

Descriptions of the distribution and abundances of large invertebrates, particularly sea urchins, and fucal and laminarian algae were done for seven areas of NZ, ranging over 16° latitude from the Three Kings Islands in the north to the subantarctic Auckland Islands (Fig. 1). The purpose of these descriptions is to show the depth distribution of the most abundant large brown algae and sea urchins within localities and to compare these patterns and species among localities. Data from northern NZ come from Choat & Schiel (1982). The descriptions for the southern localities were taken from semi-exposed sites – those that were neither in protected bays nor exposed directly to oceanic swells in the prevailing wind direction. Conditions were therefore comparable to northern sites. The Auckland Is. and Chatham Is. sites, however, are probably exposed occasionally to more severe conditions than are the mainland and nearshore islands. Southern sites were sampled using random quadrats at each of several depth strata (see Choat & Schiel, 1982 for description of methods).

Summaries of experiments on the interactions between species are taken from the published

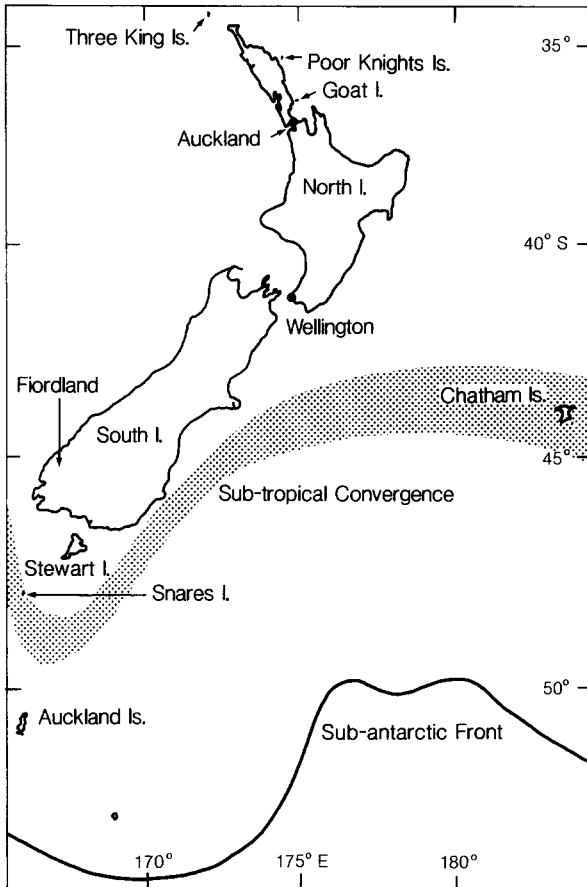


Fig. 1. Map of New Zealand and the offshore islands showing localities that were sampled for the distribution and abundance of large brown algae. The positions of the Sub-tropical Convergence and the Sub-antarctic Front are indicated (from Heath, 1985).

literature and from Schiel (1981). Methods are given in the text and in table captions.

Results

Depth distribution of macroalgae and herbivores

Choat & Schiel (1982) described the depth-associated patterns of macroalgae and herbivorous invertebrates at several sites in the North Island (Fig. 2). Along the northeast coast, the main patterns are an abundance of fuclean algae from low intertidal areas to a sublittoral depth of ~7 m. The predominant species are *Carpophyl-*

lum angustifolium and *C. maschalocarpum* in the shallowest areas, and *Sargassum sinclairii*, *C. plumosum* and *Landsburgia quercifolia* (not shown) which occupy depths of 4–7 m. Herbivorous gastropods and the sea urchin, *Evechinus chloroticus*, are abundant in shallow water, but occupy a zone exclusive of large algae at a depth around 8 m. In most areas of northern NZ, the only laminarian is *Ecklonia radiata*. It has a bimodal distribution, forming stands at ~5 m depth and in deeper water at 10–20 m. This pattern, with minor variations, is reasonably consistent throughout northeastern NZ and the islands nearby. At some localities, such as the Poor Knights Islands, another laminarian, *Lessonia variegata*, is abundant at 3–5 m depth, while *Carpophyllum flexuosum* forms dense stands in deeper water at 15–20 m. A feature of the algal assemblages in northeastern NZ is that single-species aggregations are common within a depth

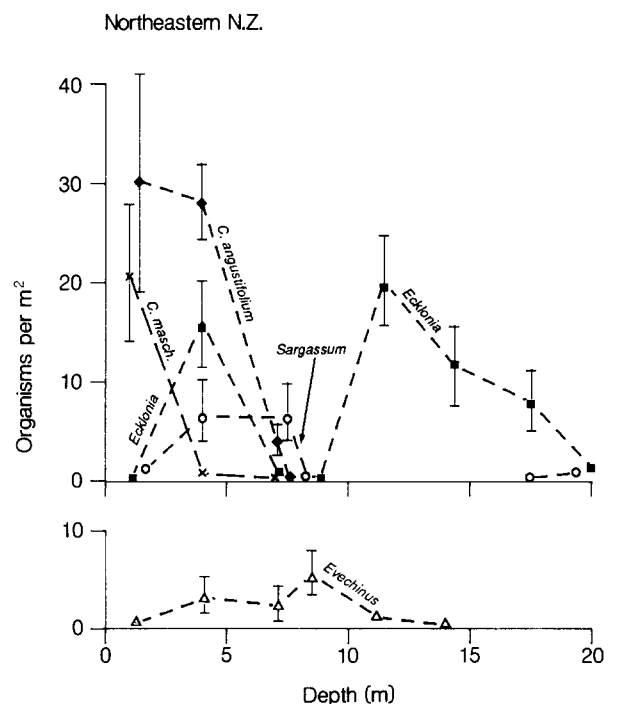


Fig. 2. Abundance patterns (means \pm standard error) with depth of large brown algae and sea urchins from localities in northeastern NZ (from Choat & Schiel, 1982). Sampling methods and patterns for other localities in northern NZ are given in Choat & Schiel (1982).

stratum, but adjacent boulders may be occupied by different species.

Cooler waters prevail below the subtropical convergence (Fig. 1). Around Wellington, the laminarian *Lessonia variegata* is more abundant in shallow water than it is in northeastern NZ (Fig. 3). The fucaleans *Landsburgia quercifolia*, *C. flexuosum* (not shown), *C. maschalocarpum* and *C. angustifolium* are also common. Unlike northern NZ, sea urchins do not form 'barren grounds' (Pearse *et al.*, 1970; 'coralline flats' of Ayling, 1981) around the coast near Wellington, so there is no intermediate depth zone devoid of large algae.

Fiordland is considered to be a different algal province from Wellington, being exposed to the Westland Current and a cooler water mass

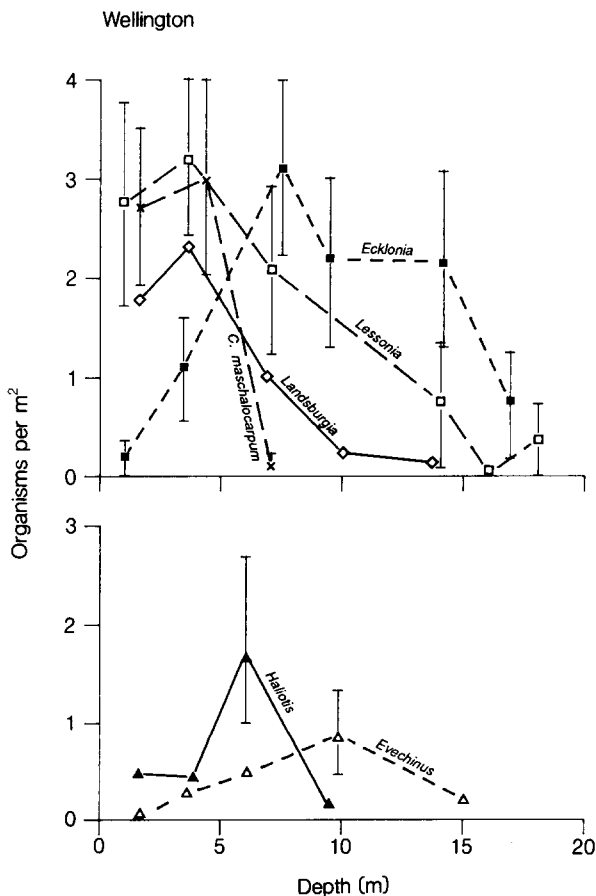


Fig. 3. Depth distribution pattern of large brown algae, sea urchins, and abalone at Wellington (from Choat & Schiel, 1982 and Schiel, unpublished).

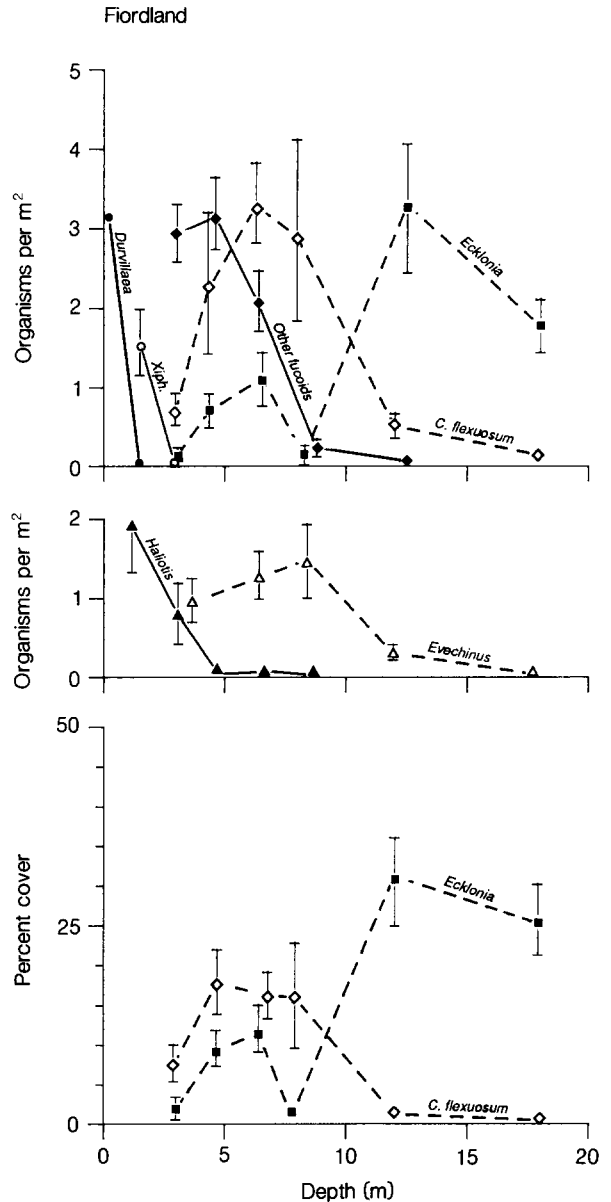


Fig. 4. Abundance patterns with depth of large brown algae and invertebrates herbivores at localities in Fiordland. This is a composite of data from 6 localities of similar exposure in the outer areas of the fiords. Sampling methods were similar to those described by Choat & Schiel (1982). Species: Xiph. = *Xiphophora chondrophylla*. 'Percent cover' = cover of the canopy over the substratum.

(Moore, 1949; Knox, 1963; Heath, 1985). The large bull kelp, *Durvillaea antarctica*, dominates the low intertidal and extends to a depth of ~1 m (Fig. 4). At about 2 m depth the fucalean

Xiphophora chondrophylla is abundant. Several species of fucaleans (= 'other fucoids' in Fig. 4), particularly *C. plumosum* and *Cystophora* spp. are abundant to a depth of 12 m. *Ecklonia radiata* has a bimodal distribution, being common at 3–6 m and slightly less abundant at 12–18 m. This is an interesting feature because sea urchins are not particularly abundant at any depth, but rather are patchy in occurrence from 3–10 m. The abalone *Haliotis iris* is the most abundant invertebrate herbivore at 0–2 m. There is no depth stratum barren of large foliose algae. One common feature of many Fiordland sites is the presence of cobbles, gravel and sand at intermediate depths (8–10 m) between shallow boulders and deeper reefs.

Offshore islands present several different patterns from localities near the mainland. In the far north, the Three Kings Islands exhibit a flora dominated by an endemic fucalean, *Sargassum johnsoni*, to a depth of 18 m (Fig. 5). Dense stands of smaller plants of this species occur at 0–5 m while very large individuals are common to 20 m. Other common fucaleans are *Landsburgia quercifolia* in shallow water and *C. plumosum* (not shown) at all depths to 20 m. *Ecklonia radiata* is present in deeper water. Sea urchins occur in patches, but the distribution of algae tends to be continuous along a depth gradient.

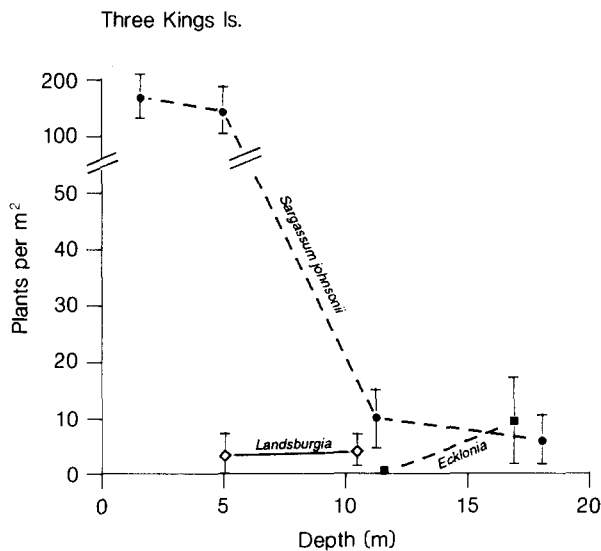


Fig. 5. Abundance patterns with depth of large brown algae at the Three Kings Islands. From Choat & Schiel (1982).

Chatham Is.

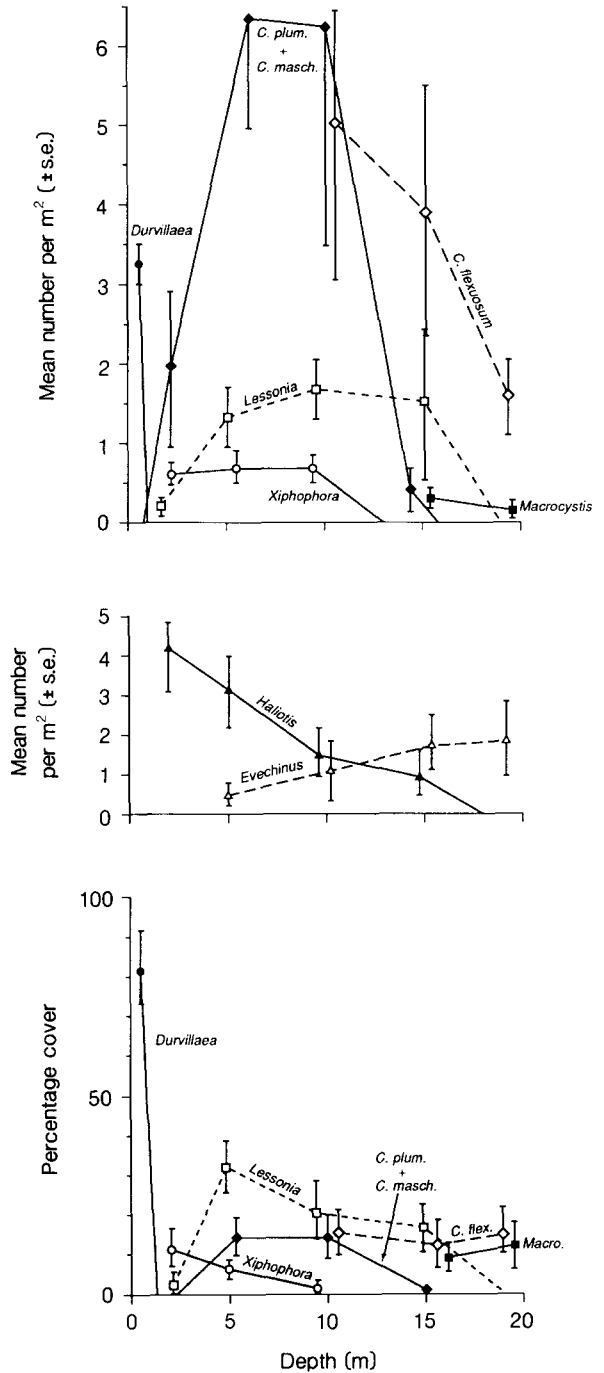


Fig. 6. Abundance patterns with depth of large brown algae and invertebrate herbivores at the Chatham Islands. This is a composite of data from 5 localities of similar exposure. Species: *C. plum.* = *Carpophyllum plumosum*; *C. masch.* = *C. maschalocarpum*. 'Percentage cover' = cover of the canopy over the substratum.

The Chatham Islands lie 800 km east of the central mainland and comprise another algal province. *Durvillaea* dominates the shallowest areas, with virtually total canopy cover at most sites (Fig. 6). The fucal species, *Xiphophora chondrophylla*, *Carpophyllum plumosum* and *C. maschalocarpum* form mixed stands and are abundant to 12 m. *Landsburgia quercifolia* and the endemic *L. myracifolia* are common at some sites (not shown in Fig. 6). *C. flexuosum* occurs from 9–20 m. *Lessonia variegata* and *Lessonia* sp. nov. are abundant from 3–15 m depth. Giant kelp, *Macrocystis pyrifera*, forms dense stands at 15–25 m depth at some sites, but is absent from many others. The commonest NZ kelp, *Ecklonia radiata*, has not been recorded at the Chatham Islands. Abalone, *H. iris*, are very abundant in shallow water, reaching densities of 40 m⁻² in some places. These islands support a large fishery for this species. Sea urchins are found in patches at 5–20 m, but do not appear to generate the characteristic ‘barren’ zones found at intermediate depth in northeastern NZ.

The final locality described here is the Auckland Islands, lying 400 km south of the

South Island. Waters here are cold, reaching 6 °C in winter. The shallowest areas are dominated by *Durvillaea antarctica* throughout the islands (Fig. 7). At 2 m, *Xiphophora chondrophylla* is the commonest large alga. From ~2–5 m depth, there is a carpet of the brown alga *Halopteris funicularis*. The laminarian, *Lessonia brevifolia* forms stands at 4–12 m, while giant kelp is the commonest large alga in deep water. *Macrocystis pyrifera* forms very dense stands at some sites. *Ecklonia radiata* has not been recorded at the Auckland Islands. The only common herbivore is *Haliotis virginea*, a small abalone (75 mm shell length) which occurs just below the *Durvillaea* canopy and also on deep reefs at 15–20 m depth.

Discussion of processes affecting depth distribution patterns

There are actually few data and experiments on the factors affecting the distributions of algae at various depths in NZ. Choat & Schiel (1982) identified five depth-related zones and discussed hypotheses on factors responsible for them. The

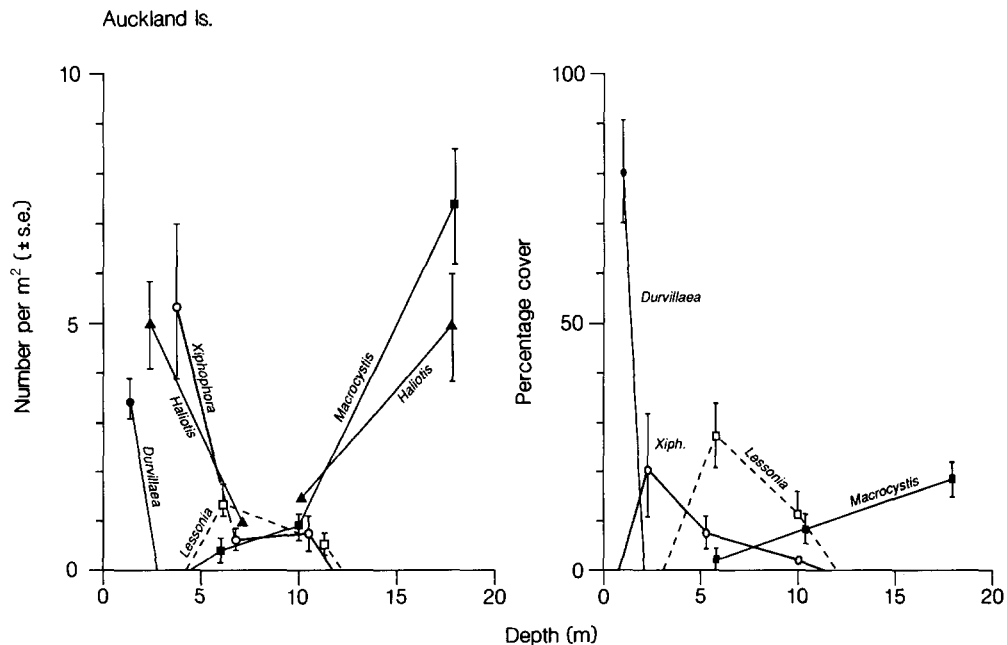


Fig. 7. Abundance patterns with depth of large brown algae and invertebrate herbivores at the Auckland Islands. This is a composite of 7 localities of similar exposure on the eastern side of the islands (Schiel, unpublished).

zones identified were 1) shallow areas dominated by fuclean algae, 2) mixed stands of fuclean and laminarian algae (3–6 m depth), 3) areas dominated by sea urchins and encrusting red algae (5–10 m depth), 4) sea urchin-laminarian borders (10 m depth) and 5) deep algal stands. These were described for localities in northeastern NZ and each does not occur throughout the country. Even though there is considerable variability among sites in any geographic region, the general differences between northern and southern localities seem to be consistent. *Durvillaea antarctica* occupies the low intertidal – shallow sublittoral region in most of southern NZ, while this zone is comprised of *Carpophyllum* species in northeastern areas. Fuclean species are prominent to 10 m depth at sites throughout the country. The laminarian *Ecklonia radiata* forms both shallow and deep stands in northern and southern mainland localities.

One major difference between northern and southern localities is the distribution of sea urchins. Many northern sites have characteristic and extensive areas dominated by echinoids. These are reduced to small patches in most southern sites. Dix (1970) reported extensive areas dominated by sea urchins in some sheltered habitats at the northern end of the South Island, but this phenomenon is not widespread in southern NZ. Deeper areas in both northern and southern NZ are occupied by *Ecklonia radiata* and *C. flexuosum*. Where *Macrocystis* occurs, it is generally found below 10 m depth.

Not all of the hypotheses discussed by Choat & Schiel (1982) will be presented here. The following discussion focuses on a few questions which have been addressed experimentally in NZ.

What effects do grazers have on the upper distribution of large brown algae?

Two studies experimentally examined this question in northern NZ. Creese (1988) discusses a study by Edwards (1982) which assessed the effects of molluscan grazers in low intertidal areas at Leigh, North Auckland. In experimental condi-

tions of fixed densities, the combined grazing activities of the limpet *Cellana radians* and the turbinid *Turbo smaragdus* prevented the establishment of stands of macroalgae adjacent and above the zone of fuclean algae. Macroalgae became established in the absence of grazers. The gastropods were therefore capable of limiting the shoreward extension of sublittoral algae. The density of molluscan grazers is much reduced in the fucoid zone of the low intertidal (Creese, 1988). Experiments in Australia have shown that once macroalgae become established in this zone, grazers such as limpets are incapable of feeding on them (Underwood & Jernakoff, 1981).

In southern NZ, Hay (1979) removed several species of limpets, including the large *Cellana denticulata*, from two shores. In one of these localities, he found that a large recruitment of the bull kelp *Durvillaea antarctica* occurred at a higher level of the shore than in control areas. The germlings eventually died back from desiccation during summer. In this case, grazers exerted a strong effect on the shoreward distribution of *Durvillaea* but physical effects were clearly important in setting the upper limit.

What effects do grazers have on the smaller-scale distribution of sublittoral algae?

Several experiments have been done in northern NZ to test the effects of sea urchins on reef biota. Ayling (1981) found that *Evechinus chloroticus*, at a density of 18 m^{-2} on a rock flat area, grazed over 35% of the reef surface in 100 days. Large numbers of gastropods were associated with the sea urchins on these rock flats and their combined grazing activities allowed only encrusting coralline algae and some sponges to establish on the reef.

Choat & Andrew (1986) showed there are strong interactions between the large invertebrate grazers in sublittoral regions. Where there are high densities of the turbinid *Cookia sulcata* and the limpet *Cellana stellifera*, substrata are dominated by encrusting coralline algae. Turfing algae have increased cover where the densities of gas-

tropods are reduced or where each species of gastropod occurs on its own. Species combinations can also affect the patchiness of large brown algae. Schiel (1981) used cages which enclosed fixed densities of gastropods to demonstrate that the recruitment of fuclean algae can be greatly reduced by *Cookia*, either alone or in combination with *Cellana*. Although these interactions among gastropods can be locally strong, their major effects occur in the presence of sea urchins and it is unlikely that gastropods themselves are important to the overall distribution of large brown algae.

As in other areas of the world, sea urchins provide the most demonstrable impacts on the patterns of abundance of macroalgae. Schiel (1982) recorded the movement of a vanguard of *Evechinus* through an algal stand at 8 m depth. The kelp, *Ecklonia radiata*, was one of the first species removed, while *Carpophyllum* species were least vulnerable to removal. *Ecklonia* was also one of the most preferred species when *Evechinus* was given a choice of algal foods. It is clear, therefore, that in northern NZ sea urchins can have both strong and important effects on algal distributions on a local scale.

The removal of echinoids has variable effects. Andrew & Choat (1982) showed that the removal of *Evechinus* from rock flats resulted in a rapid recruitment of laminarian and fuclean algae. This produced an abrupt change in community structure from sea urchins and encrusting red algae to domination by macroscopic brown algae. Other community effects were decreases in the numbers of *Cellana stellifera* and in feeding rates of predatory fishes.

Schiel & Choat (in Schiel, 1981) recorded more subtle effects of sea urchins over three years on boulders at 7 m depth. Boulders kept free of sea urchins had over twice the number of *Ecklonia* than those with average echinoid densities of 1–2 m⁻². Differences in other species between these echinoid treatments over three years ranged from 10–90% for *Sargassum*, about 50% for *Landsburgia*, and virtually no difference for *Carpophyllum* species.

These results are consistent with findings else-

where that sea urchins can have strong interactions with macroalgae (reviews in Lawrence, 1975; Harrold & Pearse, 1987). This has led some authors to discuss sublittoral algal assemblages in terms of 'alternate stable states', each being mediated by the presence or absence of sea urchins (Simenstad *et al.*, 1978; Moreno & Sutherland, 1982; Harrold & Reed, 1985). These echinoid – algae interactions may be locally intense but how important are they generally to the structure of macroalgal assemblages in New Zealand?

There are various ways of gauging the importance of an effect to an overall result. Welden & Slauson (1986) suggest that one estimate of importance is given by dividing the treatment sums of squares in an analysis of variance model by the total sum of squares. The relative importance of other, uncontrolled, factors is then given by the residual SS divided by the total SS. Using these criteria, the effect of removing *Evechinus* by Andrew & Choat (1982) was relatively important (Table 1A). Sixty percent of the variation in numbers of large brown algae was accounted for by the factor *Evechinus*, while 26% was due to uncontrolled factors. This experiment was done on a rock flat where the density of *Evechinus* averaged 2–4 m⁻². The ANOVA on the data collected by Schiel and Choat (in Schiel, 1981) shows there was a significant difference in the abundance of algae between boulders with and without *Evechinus* and also a difference in the abundance of species of algae (Table 1B). In this case, however, only 14% of the variance in the model was accounted for by sea urchins while 54% was due to uncontrolled factors.

These results provide only one relative measure of importance of the effects of echinoids. Presumably, the strength of an effect may be independent of its importance, and the addition of other factors into an ANOVA model will further reduce the residual SS. The caveat here is that 'importance' is sensitive to both sample size and the number of treatments, so that contrasts should be made between experiments of the same size (Underwood, pers. comm.). The results do, however, support the argument that the effects of

Table 1. ANOVA summaries of echinoid experiments. Variables were the number of algal recruits. A) The result of an experiment from Andrew & Choat (1982). *Evechinus* were either present or absent, with or without cages. Replicates were 2 m² in area ($n = 5$). This experiment was done on a rock flat area. 'Importance' is the treatment SS/total SS, using non-transformed data (Welden & Slauson, 1986). B) The result of an experiment by Schiel (1981) and Choat (unpublished). Replicates were boulders, either with or without *Evechinus*. 'Species' were *Ecklonia radiata*, *Sargassum sinclairii*, *Landsburgia quercifolia* and *Carpophyllum* spp. (note that *C. maschalocarpum* and *C. agustifolium* are very difficult to distinguish as recruits and so are lumped together). Significance indicated by *(0.05), **(0.01), *** (0.001).

| A. | | | | |
|-------------------------|------|----------|----------|------------|
| Source of variation | d.f. | SS | F | Importance |
| Caging (+, -) | 1 | 1.458 | 4.94* | 0.08 |
| <i>Evechinus</i> (+, -) | 1 | 11.041 | 37.48* | 0.60 |
| CXA | 1 | 1.049 | 3.56 | 0.06 |
| Residual | 16 | 4.720 | | 0.26 |
| B. | | | | |
| Source of variation | d.f. | SS | F | Importance |
| Species | 3 | 1156.639 | 6.94*** | 0.23 |
| <i>Evechinus</i> | 1 | 660.756 | 11.90*** | 0.14 |
| SXE | 3 | 460.798 | 2.75 | 0.09 |
| Eesidual | 48 | 2666.029 | | 0.54 |

removing echinoids are quite variable in terms of the subsequent structure of algal assemblages.

Other authors have argued that there is a threshold effect of echinoid numbers and grazing effects, above which there are large changes to community structure and below which effects are more subtle (Breen & Mann, 1976b; Schiel, 1982; Harrold & Pearse, 1987). Rather than alternate stable states, however, evidence from NZ points to a range of effects based partially on the density of *Evechinus*. Some of these effects have only been clarified in northern NZ because experiments have explicitly assessed grazer densities as a factor (Andrew, 1988 for review). Rock flat areas represent one extreme of this range, where high densities of echinoids have removed brown macroalgae, while reduced numbers of echinoids and high densities of gastropods have maintained the habitat (Ayling, 1981; Andrew & Choat, 1982; Choat & Andrew, 1986).

What uncontrolled factors influence the effects of removing echinoids? The most important of these are the reproductive periodicity and dispersal capabilities of algae. One source of recruit-

ment variability in echinoid-removal areas is the failure of propagules to arrive and settle. *Ecklonia*, *Sargassum*, *Landsburgia* and *Carpophyllum* spp. have distinct peaks of reproductive output in northern NZ. Furthermore, most recruits appear within a few metres of fertile adult plants. The season in which clearances appear and their distance from fertile algae, therefore, strongly influence the outcome of free space becoming available in the absence of grazers. There may also be considerable variability between years in recruitment of each species (Schiel, 1985). A reduction in grazing pressure, therefore, has variable results because of variability in the effects of echinoids and because of the ability of algae to respond to the availability of free space.

On a geographic scale, echinoids assume less importance to community structure in southern NZ and the offshore islands. Current evidence indicates it is rare for sea urchins to dominate extensive areas of reefs from Wellington southwards (although this may occur in some protected localities [Dix, 1970; Andrew, 1988]). *Evechinus* was seen only as isolated individuals or

in relatively small patches (1–10 m²) at Wellington, Fiordland, and the Chatham Islands. Extensive surveys at Steward Island, off southern NZ, also revealed no echinoid-dominated areas (Schiel, unpublished), although large patches dominated by sea urchins have been reported for a nearby islet (M.S. Foster, pers. comm.). The distribution of *Evechinus* extends only to the Snares Islands off southern NZ (Fell, 1960; Pawson, 1965) and does not reach the Auckland Islands.

The most abundant large, herbivorous invertebrate in most of southern NZ is *Haliotis iris*. This species, reaching 180 mm in shell length, occurs primarily at depths of 0–3 m and is not found in protected localities. It may feed on attached red algae, but is primarily a passive feeder capturing drift algae (Poore, 1972). An endemic subspecies, *Haliotis virginea virginea* (reaching 75 mm shell length), occurs at the Auckland Islands. These haliotids are generally found attached to coralline crusts and may help maintain this understory. It is unlikely that they have more far-reaching community effects.

What effects do algal interactions have on distribution and abundance patterns of macroalgae?

In any kelp bed or forest, there is a layering of species from encrusting algae, turfing forms, larger foliose species, fucal and laminarian juveniles, to adult canopies of large brown algae (Foster, 1975; Foster & Schiel, 1985; Santelices & Ojeda, 1984; Kain, 1979; Chapman, 1984). Given the multiplicity of species, forms and canopy heights, many types and degrees of interactions are possible among species. Only those involving fucal and laminarian canopies will be discussed here.

Because large brown algae often occur in discrete stands, the commonest method used to detect the effects of one species on another is the removal of canopies, with observations on subsequent recruitment or persistence of each species (review in Schiel & Foster, 1986). Canopies may affect the resources to understory algae by signifi-

cantly reducing the available light (Reed & Foster, 1984) and possibly nutrient levels (Jackson, 1977), with consequent effects on the recruitment, growth and survival of understory species. The experimental removal of canopies in patches mimics natural clearances by storms and grazing (Kennelly, 1987a, 1987b) and therefore can be of considerable use in examining patch maintenance.

In northern NZ, canopy clearances of three species were done to test for effects on recruitment (Schiel, 1981, 1988). The results of three such experiments are summarized to show which factors were significant and the proportional sums of squares (i.e., treatment SS/total SS) for each factor and the Residuals (Table 2). The removal of *Ecklonia* canopies resulted in significantly greater recruitment of *Sargassum* and *Carpophyllum* spp. compared to areas where canopies were left intact (Table 2A). For all species, there were differences between years in the levels of recruitment. *Landsburgia* recruited in equal numbers beneath and outside of canopies, while *Ecklonia* recruited mostly outside of canopies but showed a difference in numbers between years (Schiel, 1988). Despite the significant recruitment of *Sargassum* and *Carpophyllum*, cleared patches were recaptured by *Ecklonia* due to larger numbers of recruits and more rapid growth. The proportional SS in the Residual was smallest for *Sargassum sinclairii*, which is an opportunistic species with an annual habit. This figure was large for the other species, indicating that much of the variance in recruitment was not due to the canopy.

The removal of *Carpophyllum maschalocarpum* canopies produced similar results (Table 2B). Both *Sargassum* and *Carpophyllum* spp. recruited almost exclusively in the cleared patches. *Ecklonia* had only a small recruitment. The proportional SS in the Residual was largest for *Ecklonia* and least for the original canopy alga, *Carpophyllum maschalocarpum*. Again, the recruitment of *Landsburgia* was largely unexplained by any effect of the canopy.

Removal of *Landsburgia quercifolia* canopies produced a significant effect only for *Ecklonia*. *Landsburgia* again recruited both beneath and

Table 2. Summaries of ANOVA models and treatment sums of squares divided by total sums of squares ('importance') for canopy removal experiments. Replicates = 5 in each case; clearances were 1 m². Variable = number of recruits of each species. More details of experiments given in Schiel (1988). Significance of treatment effects is indicated by * (0.05), ** (0.001), *** (0.001), n.s. (not significant). E.r. = *Ecklonia radiata*, S.s. = *Sargassum sinclairii*, L.q. = *Landsburgia quercifolia*, C. = *Carpophyllum* spp. (*C. maschalocarpum* and *C. angustifolium* are indistinguishable as small juveniles in the field). Numbers shown are 'importance'.

A. *Ecklonia* canopy removal

| Source of variation | E.r. | S.s. | L.q. | C. |
|---------------------|-----------|-----------|-----------|-----------|
| Canopy (+, -) | 0.05 n.s. | 0.50** | 0.01 n.s. | 0.14* |
| Year ($b = 3$) | 0.10* | 0.19** | 0.30*** | 0.46*** |
| CXY | 0.28** | 0.04 n.s. | 0.13 n.s. | 0.37 n.s. |
| Residual | 0.57 | 0.27 | 0.56 | 0.37 |

B. *Carpophyllum maschalocarpum* canopy removal

| Source of variation | E.r. | S.s. | L.q. | C. |
|---------------------|-------|---------|-----------|---------|
| Canopy | 0.28* | 0.61*** | 0.14 n.s. | 0.67*** |
| Residual | 0.72 | 0.39 | 0.86 | 0.33 |

C. *Landsburgia quercifolia* canopy removal

| Source of variation | E.r. | S.s. | L.q. | C. |
|---------------------|-------|----------|-----------|-----------|
| Canopy | 0.36* | no | 0.35 n.s. | 0.24 n.s. |
| Residual | 0.64 | recruits | 0.65 | 0.76 |

outside of canopies, while *Sargassum* failed to recruit. The proportional SS in the Residual was large in all cases.

The patterns of recruitment are affected by numerous factors. These include the season of canopy removals, proximity of fertile adults, the densities of reproductive adults, and the dispersal capabilities of each species (Schiel, 1981, 1985, 1988). Not surprisingly, the removal of *Ecklonia* canopies during a period when nearby plants were fertile resulted in a large recruitment of *Ecklonia*. An analogous result occurred for *Carpophyllum* in patches where its canopy was removed. In these cases, the interactions of algae due to canopies were clearly significant and in many cases were 'strong'. Nevertheless, it was the life history or phenological features of each species which largely determined whether or not it recruited into a patch in sufficient numbers to recapture that space.

Why do fucalcan algae occur predominantly in shallow water?

In northern NZ, the four dominant fucalcan species have different size-frequency distributions with depth (Fig. 8). The *Carpophyllum* species have bi-modal length distributions at 3 m and 7 m depth, but more plants and the greatest biomass occur at 3 m. Few plants occur at > 11 m depth. *Landsburgia* has a larger proportion of small plants at 3 m and plants are rare by a depth of 11 m. *Sargassum sinclairii* has a large proportion of small plants and a few large plants at 3 m, while mostly small plants occur at 7 m. Plants at > 11 m are generally small and sizes are approximately normally distributed. By way of comparison, *Ecklonia radiata* is abundant at all depths, with stipe lengths up to 50 cm at 3 and 7 m, and longer stipe lengths at > 11 m. The largest biomass of this species occurs in dense beds at a depth of 11–15 m with numerous small

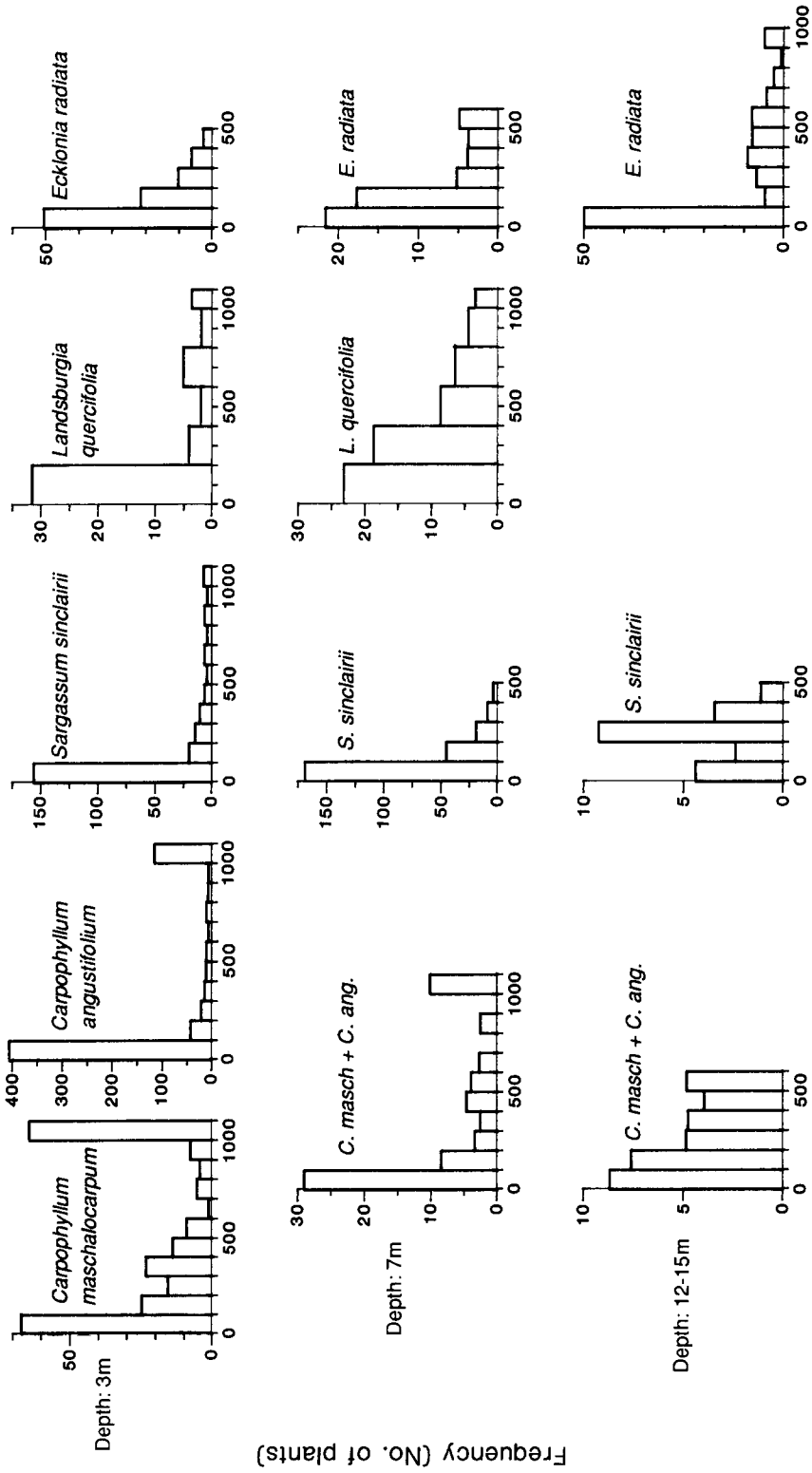


Fig. 8. Size frequency distributions of four species of algae at different depths at Goat Island localities in northeastern NZ. Data were compiled from the stratified random quadrat surveys of Schiel (1981) and Choat & Schiel (1982). Note that the two *Carpophyllum* species are combined for 7 and 12–15 m, and *Landsburgia* does not occur in 12–15 m.

sporophytes beneath the canopy (see also Choat & Schiel, 1982).

In terms of numbers and sizes, therefore, *Ecklonia* does much better than the fucal species in deeper water. One cause for this poor representation of fucal algae is their slow growth rates in deeper water. This is illustrated by *Sargassum sinclairii*, the fucal species which occurs to depths of 20 m. Plants show distinctly seasonal growth, with fastest rates beginning in spring (August), peaking in summer, and tapering off again in autumn (Fig. 9). Growth rates are much faster, however, at 5 m depth than at 15 m depth. Elongation rates reach an average of 10 mm/day in shallow water but are not greater than ~1.5 mm/day in deeper water. Because of their slower growth rates, plants in deep water do not reach a large size by autumn, when growth at all sites is curtailed. This affects the reproductive potential of deep plants because both the number

of reproductive receptacles and their proportion of the biomass of a plant increase with plant size (Schiel, 1985). Less than 5% of plants become fertile in deep water compared to about 65% of shallow plants.

Most recruits of *Sargassum sinclairii* appear within only a few metres of fertile adults (Schiel, 1988). Recruitment of *Sargassum*, and probably most other fucal species, is sparse in deep water due to reduced reproductive output of local plants and the limited dispersal of these species.

Carpophyllum flexuosum is the one fucal species that is regularly found in deep water at mainland sites. It is common both at protected and semi-exposed sites and in turbid as well as clear waters. Little demographic information exists for this species and it is not known why it performs well in deep water.

Are there 'controlling' predators in the sublittoral zone of NZ?

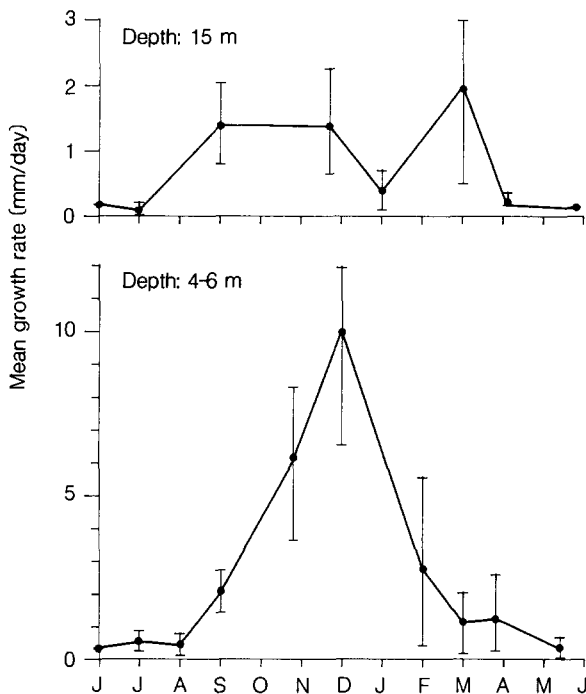


Fig. 9. The mean (\pm s.e.) growth rate (mm/day) of *Sargassum sinclairii* from two depths at Goat Island in northeastern NZ. Data were compiled from tagged plants that were remeasured at each sampling time. The measurement used is total plant length (i.e., primary plus secondary branches).

It has been hypothesized that some predators in northern hemisphere waters may control the abundance of sea urchins, thereby influencing the abundance patterns of macroalgae. For example, sea otters are voracious predators of invertebrates and are known to have been responsible for the removal of large numbers of echinoids in some areas (reviewed in VanBlaricom & Estes, 1988). Sea otters, however, do not occur in New Zealand. Other studies in California and Nova Scotia have cited the predatory activities of fishes and lobsters as causing a reduction in numbers of sea urchins and a modification of their behaviour and effects on macroalgae (Tegner & Dayton, 1981; Cowen, 1983; Bernstein *et al.*, 1981). It is also argued that the influence of these predators was greater historically, before commercial fishing pressure reduced their numbers. The data are subject to other interpretations (Pringle *et al.*, 1980; Andrew & Choat, 1982; Choat, 1982; Schiel & Foster, 1986; Miller, 1985; Foster & Schiel, 1988), but it is clear that these mobile predators may at least exert strong local effects on patterns of abundance of echinoids.

The effects of fish on echinoids were specifically tested in northeastern NZ by Andrew & Choat (1982). Using 2 m² enclosures they showed that the abundance of juvenile sea urchins (*Evechinus chloroticus*) was enhanced by excluding fishes. Despite the feeding pressure by a large suite of predacious fishes in other treatments, however, a consistent but small number of *Evechinus* recruits escaped predation. This recruitment was great enough to sustain an urchin-dominated rock flat area. Another abundant predator, the rock lobster *Jasus edwardsii*, readily consumes *Evechinus* but does not reside in rock flat areas and also does not appear to forage there (McDiarmid, 1987; Andrew, 1988).

Another study showed that *Evechinus* juveniles were rare in kelp beds and on deep reefs, and that when transplanted to these habitats had poor survival for reasons other than predation (Andrew & Choat, 1985). Despite the fact that fishes and lobsters may reduce the abundance of echinoids, it is not clear that these predators have wider community effects by controlling the influence of *Evechinus* (Andrew & Choat, 1982; Andrew, 1984; Choat & Ayling, 1987). The evidence (reviewed by Andrew, 1988) suggests predation does not trigger large-scale community effects. Choat & Ayling (1987) concluded that the type of reef habitat, dominated either by brown macroalgae or sea urchins, plays an important role in determining the associated fish fauna, rather than fish being the primary determinant of habitat type.

The patterns of abundance of fish have not been examined for many sites in southern NZ (Kingsford *et al.*, in press), so it is unknown whether their effects are similar to those in northern NZ.

Discussion

Perhaps the most unusual feature of the NZ sublittoral zone is the dominance of fucal algae and *Durvillaea* in waters < 10 m deep. This pattern is fairly consistent despite changes in species composition at localities throughout NZ. Only in temperate Australia is there a similar large repre-

sentation of fucal algae in shallow water (Womersley, 1981a, 1981b; Schiel, submitted).

The patterns of biogeography of marine algae in this part of the world have received recent attention (Hay *et al.*, 1985; Nelson & Adams, 1984), but are still not well-described. Within NZ, the Snares Islands, just south of Stewart Island, appear to be the southern limit for many fucal species (Dr Cameron Hay, NZ Oceanographic Institute, pers. commun.). The probable reasons for this southern boundary are limited dispersal ability, lower water temperatures, and the West Wind Drift moving away from the land mass.

It is hardly novel to argue that the structure of stands of algae can be strongly affected by grazers, interactions between species of algae, and life histories. Within particular sites, grazing invertebrates have strong effects on the distribution of algae, abbreviating their upper and lower limits. Limpets affected the upper limit of colonization by *Durvillaea* at one locality in southern NZ, and a similar effect occurred for *Carpophyllum* in northern NZ. In both cases, however, it appeared that regardless of grazing, desiccation of new recruits set the upper limit of distribution to previous levels. In sublittoral areas, gastropods may enhance the effects of grazing by echinoids where the two groups co-occur on rock flats (Ayling, 1981; Andrew & Choat, 1982; Choat & Andrew, 1986), but otherwise have only small effects on algal recruitment and patchiness.

Sea urchins clearly play an important role in the organization of algal assemblages at some northern sites. Despite predation by numerous fishes, areas dominated by echinoids at 6–8 m depth have been maintained for > 10 years in at least one locality (Ayling, 1981; Andrew & Choat, 1982). Their large-scale influence, however, seems to be confined to this particular depth stratum in northern sites. Sea urchins are not abundant enough at most southern localities to exert an important or dominant effect on reef biota.

Within kelp forests, Dayton *et al.* (1984) cleared canopies of kelp to assess interactions among species of algae, and they constructed life tables for several species. They argued that the ability of species to recapture space after a dis-

turbance, combined with the longevity of species, determined the stability of patches of algae. These characteristics varied between species. Reed & Foster (1984) showed that canopies of *Macrocystis* and the stipitate laminarian *Pterygophora californica* suppressed their own recruitment and that this was correlated with drastically reduced levels of light beneath adult canopies. Several other studies have shown that canopies have a suppressive effect on recruitment to areas below (reviews in Kain, 1979; Schiel & Foster, 1986). What is less well-examined is the relative importance of canopy effects vs. other factors in the patch dynamics of algal stands.

It is difficult to find a useful and consistent measure with which to gauge the importance of interactions. The use of Sums of Squares from Analyses of Variance can give varying results, depending on sample size and the number of treatments. Furthermore, these results are directly applicable only to the spatial and temporal scales examined. In the experiments cited here (Tables 1 & 2), the effects of canopies and grazers were significant, yet the Residual was proportionally large in most cases. Clearly, other factors have strong effects on patch dynamics. It is worth noting that there is also an element of randomness superimposed on the more deterministic processes considered here. This is comparable to other systems where patch dynamics are affected by spatial and temporal heterogeneity (Sales, 1978, 1982; Chesson & Warner, 1981; Sousa, 1984).

The information summarized here indicates that the effects of canopy removals on recruitment varies among species, both in terms of the dominant canopy and also of the recruiting species. The removal of *Ecklonia* canopies results in significant recruitment of other species, but there are differences in the levels of recruitment between years. These latter differences appear to be largely unrelated to the actual effects of removal of the canopy. Results are similar when *Carpophyllum maschalocarpum* canopies are removed. The greatest differences between treatments occurs in the recruitment of *Carpophyllum* and *Sargassum*. It could be expected that patches of *Carpophyllum*

species would have strong effects on recruitment. In addition to the effects associated with the presence of a canopy, the densely-packed holdfasts of adult plants may preclude recruitment due to a scarcity of available primary space for attachment to the substratum. Removal of adult plants provides a significant increase in available substratum relative to canopy-covered patches.

Species are clearly different in their abilities to colonize space after the removal of canopies. *Landsburgia* recruits both beneath and outside of canopies, and its recruitment is unexplained by the canopy treatment. *Sargassum* recruits well into open areas regardless of the initial type of canopy. Even though most recruits tend to appear near fertile adults, this is the one species possessing a considerable ability to disperse. Fertile portions of plants break away and are carried to the sea surface by buoyant vesicles. Reproductive *Sargassum* plants comprise a major portion of algal drift on the sea surface (Kingsford, 1986). Of the other species, *Ecklonia radiata* has a relatively wide dispersal and also the longest period of fertility (Schiel, 1981, 1988). Its recruitment is strongly affected by the presence of canopies. In cases where it does recruit beneath canopies, it tends to have poor survival. *Landsburgia* releases fertilized ova directly and these do not remain attached to adult plants as is the case for *Sargassum* and *Carpophyllum* species. *Landsburgia* appears to have poor dispersal ability. It is the least abundant of the four species considered here and therefore has a lesser capacity to recruit in large numbers to distant areas. The demography of this species may be much different in southern NZ where it is more abundant. It is not surprising that the results of canopy removals are variable. The ability of a species to capture space after the removal of a canopy is influenced by many factors including the size of the patch, the proximity of reproductive adults, and the timing of recruitment. The general importance of 'canopy effects' to the organization of algal assemblages is limited, therefore, because they can only be expressed by virtue of the particular life history and phenology of each species.

The restricted depth distribution of fucalcan

algae is also directly related to life histories. The demography of *Sargassum* is different at different depths, with reduced growth, sizes and reproductive output characterizing deep areas. These differences may be due to insufficient light in deeper areas (Chapman, 1965). Another potentially important factor is grazing by small crustacea on germlings and juveniles (Kennelly, 1983). Because growth rates are reduced in deeper water, plants may be vulnerable to these micro-grazers for longer periods of time.

It is not known why *Carpophyllum flexuosum* is able to thrive on deep reefs or how its life history characteristics compare with those of other fucaleans. This is one of the dominant species on deep reefs in many localities, particularly in southern NZ, and is obviously tolerant of reduced light levels due to depth and turbidity.

Conclusion

In the search for identification and explanation of the processes structuring algal assemblages, a few concepts have been generalized. Other authors have pointed this out, highlighting methodological problems in experimental evidence (Underwood & Denley, 1984; Hurlburt, 1984) and the limited number of localities at which experiments have been done (Foster, this volume). For most areas of the world, relatively few localities have been described quantitatively for their patterns of distribution of algae and herbivores. As more sites are examined, it appears that few generalizations are appropriate. For example, even in southern California where research in kelp forests led to the postulation of dominant effects of sea urchins, Foster & Schiel (1988) found that sites dominated by echinoids comprised only 19/224 (8.5%) of those examined over a wide geographic region. This relatively small occurrence of dominant effects diminishes arguments for generality.

Andrew & Mapstone (1987) pointed out that it is difficult to design and interpret ecological experiments without extensive information on natural history and distribution. There is neither a large body of quantitative information on distribution nor have many experiments been done on ecological processes affecting the organization

of algal assemblages in New Zealand. What is known emphasizes the fact that the effects of predators, grazers, the nature of the substratum, and algal canopies interact in complex ways in the patch dynamics and organization of algal assemblages. These interactions cannot be understood without reference to the specific life history and phenological characteristics of particular species and the demographic consequences of settling and growing under different conditions.

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