

Community composition and structure of shallow subtidal reefs in northeastern New Zealand

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Cover: *Ecklonia radiata*, Cape Reinga. Photo: N. Shears

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Community composition and structure of shallow subtidal reefs in northeastern New Zealand

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ABSTRACT

Characteristics of shallow subtidal reef communities were quantified within nine locations, spanning approximately 500 km of the northeastern coast of the North Island of New Zealand from Cape Reinga to Tuhua (Mayor Island) in the Bay of Plenty. At each site, measurements of algal and mobile macro-invertebrate species composition, algal community structure (biomass), grazer abundance and environmental variables were made. Clear patterns were evident in community structure and species composition across a gradient from sheltered coastal sites to exposed coastal and offshore sites. At all locations, large brown algae were found to be the dominant components of the reef communities. *Ecklonia radiata* and *Carpophyllum maschalocarpum* were the most dominant species and were found at all locations. Algal species richness was highest at offshore islands and the northern-most locations, and lowest at the most sheltered location (Long Bay). Mobile macroinvertebrate species richness was lowest at Long Bay, but was also low at offshore island locations. Large variation in algal community structure was found within and among locations that generally reflected the wave exposure and the coastal or offshore setting of sites. Patterns in algal community structure were significantly related to a number of environmental variables (e.g. wave exposure and turbidity) and also to the density of sea urchins *Evechinus chloroticus*. The abundance of sea urchins varied with depth, and from sheltered to exposed locations. At sheltered sites they were rare, but with increasing exposure they became more abundant and their upper grazing limit moved deeper.

Keywords: Diversity, environmental gradients, kelp communities, macroalgae, macroinvertebrates, sea urchins.

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1. Introduction

The structure of communities is determined by complex interactions among the species making up the communities and their environment. A necessary step in understanding the important structuring processes and the trophic relationships in communities is the description of patterns across relevant spatial scales (Underwood et al. 2000). In general, observations over large scales (biogeographic regions) are required to understand variability at small scales. Furthermore, the importance of biotic interactions changes across environmental gradients (Menge & Sutherland 1987). Therefore, variation in environmental parameters within locations and across geographic regions needs to be taken into account when interpreting biogeographic patterns and identifying the important structuring processes.

Shallow subtidal reef communities in temperate areas are typically dominated by large brown algae of the orders Laminariales and Fucales (Schiel & Foster 1986). In many subtidal reef systems throughout the world, grazing by sea urchins has an important structuring influence on kelp communities (Lawrence 1975; Harrold & Pearse 1987). Overgrazing of kelp forests by sea urchins and the formation of urchin barrens habitat—areas devoid of large brown algae—has been linked to overfishing by humans of urchin predators such as sea otters (Estes & Duggins 1995), large fishes (Shears & Babcock 2002) and lobsters (Wharton & Mann 1981). The generality of this paradigm on temperate reefs has attracted much debate (Foster 1990). On Californian reefs, Foster & Schiel (1988) found otter-urchin trophic cascades only at specific sites, and Laur et al. (1988) demonstrated that the effects of this interaction differed according to the physical characteristics of the reef at particular sites. Similarly, Dayton (1985) found that the importance of the urchin *Loxechinus albus* varied along the southwest coast of South America and it was excluded from certain areas by a range of possible factors including larval recruitment, sedimentation, freshwater and human harvesting. Few studies have examined the importance of urchins as grazers across large areas and investigated how their abundance changes across environmental gradients.

Algal communities are strongly influenced by physical processes such as storms (Cowen et al. 1982), temperature (Leliaert et al. 2000), eutrophication (Eriksson et al. 2002), salinity (Schils et al. 2001), turbidity (Lumb 1989) and sedimentation (Airoldi & Virgillio 1998). Algal community structure (Harrold et al. 1988) and composition (Leliaert et al. 2000) have been shown to change across wave exposure gradients. However, it is often difficult to separate the effects of wave exposure from other interacting processes such as sedimentation and turbidity. In order to make generalities, in addition to describing biotic patterns (Fowler-Walker & Connell 2002), environmental gradients also need to be described.

Subtidal reef communities in New Zealand are typical of most temperate areas in that they are dominated by large brown algae (Schiel 1990), and sea urchins are a conspicuous component of many reefs, particularly in the north (Choat & Schiel 1982; cf. Schiel & Hickford 2001). In the northeastern North Island, New Zealand, the common sea urchin *Evechinus chloroticus* has an important

top-down structuring influence on algal assemblages (Andrew & Choat 1982; Shears & Babcock 2002). The majority of experimental studies investigating the mechanisms controlling subtidal reef communities have been carried out at Leigh in northeastern New Zealand (see reviews Andrew 1988; Creese 1988; Schiel 1988). The generality of findings from these studies to other areas, however, is not known. For example, in other parts of New Zealand, urchin-dominated areas are typically rare and urchins are not thought to have an important top-down effect on algal assemblages, e.g. Three Kings Islands, Owhiro Bay (Wellington) (Choat & Schiel 1982), Chatham Islands (Schiel et al. 1995) and the southern South Island (Schiel & Hickford 2001). In contrast, however, experimental manipulations by Villouta et al. (2001) found that *Evechinus* does play an important structuring role in Dusky Sound in southern New Zealand. In general, our understanding of the important factors structuring algal assemblages both within and across regions in New Zealand is poor.

The coast of northeastern New Zealand has been classified as a distinct biogeographic region and extends from North Cape to East Cape (Walls 1995). The coastline is highly complex and convoluted, with many headlands, peninsulas and offshore islands. Consequently, variation in environmental conditions within locations is high and may explain some of the small-scale variability in benthic communities recorded by Choat & Schiel (1982). These authors quantified the distribution and abundance of large brown algae and invertebrate herbivores at six locations in the North Island (1–2 sites in each) from the Three Kings Islands in the north to Wellington in the south. Despite the high variability at small scales, five broad-scale depth-related patterns were evident:

1. Shallow areas (0–3 m) dominated by fuclean algae—mainly members of the genus *Carpophyllum* with low numbers of *Ecklonia* and invertebrate grazers.
2. Mixed stands of fuclean and laminarian algae (3–6 m)—high density and biomass, also a high density of herbivorous invertebrates.
3. Areas dominated by sea urchins and encrusting red algae (c. 5–10 m)—high variation in *Evechinus* density, macroalgae typically absent, termed ‘urchin barrens’.
4. Sea urchin-laminarian border (c. 10 m)—abrupt transition from rock flats dominated by calcareous algae to *Ecklonia radiata* stands.
5. Deep algal stands (> 10 m)—typically monospecific stands of *Ecklonia radiata* (kelp forest habitat in Ayling 1978).

This pattern appears to be relatively stable and typical of moderately exposed reefs in northeastern New Zealand (Cole 1993; Walker 1999). However, in several studies, using varying methodologies, the vertical extent of these zones has been shown to decrease from the outer to the inner Hauraki Gulf (Grace 1983; Cole 1993; Walker 1999). At the most sheltered sites in the inner Gulf, urchin barrens are absent and replaced by *Carpophyllum flexuosum* forests; while at exposed offshore island sites, urchin barrens may extend down to depths of 20 m. Walker (1999) correlated patterns in benthic communities across this gradient to wave exposure, turbidity and sedimentation.

It is not clear how widespread or general the patterns described are throughout northeastern New Zealand and how they relate to environmental variables. In this study, patterns in subtidal benthic reef communities were examined

throughout northeastern New Zealand, combining broad-scale and intensive comparisons within locations using a consistent methodology. Eighty-one sites were sampled within nine locations, spanning about 500 km of coastline (Fig. 1). Reef communities were quantified at replicate sites within each location using a combination of line transects and depth-stratified quadrats. These locations spanned large environmental gradients and included coastal locations and offshore islands. The main objectives of our study were to:

- Describe biogeographic patterns in species composition among locations within northeastern New Zealand.
- Examine the generality of previously documented patterns in community structure throughout northeastern New Zealand and determine whether depth-related patterns in structure vary consistently across environmental gradients within locations.
- Investigate the relative importance of physical and biological factors that may contribute to the observed patterns; in particular, the relationship between macroalgal communities, the abundance of sea urchins and a range of environmental variables.

Such a large-scale study of these relationships is valuable for several reasons; in particular, demonstrating which patterns predominate under particular environmental conditions and defining generalisations for northeastern New Zealand. Information on these allow further testing of the important physical and biological processes responsible for the observed patterns.

2. Methods

Shallow subtidal reef communities were quantified at sites within nine locations throughout northeastern New Zealand (Fig. 1, Appendix 1). At each site, the distribution of habitat types down the depth gradient was recorded using a line transect, and the abundance of algae and invertebrates were measured within four given depth ranges (0–2, 4–6, 7–9 and 10–12 m below mean low water) using depth-stratified quadrats placed adjacent to the transect. Additional measurements of a number of environmental variables were also recorded for each site.

2.1 STUDY LOCATIONS

New Zealand's northeastern coast is protected from the prevailing westerly winds but is periodically subject to strong easterly storms. The East Auckland Current flows southeast down the eastern side of the North Island (Heath 1985). Water temperatures at Leigh (see Fig. 1) range annually from c. 13°C to 20°C (J. Evans unpubl. data); at the offshore islands the water is typically 1–2°C warmer. The nine sampling locations included three offshore island groups and six coastal locations from Cape Reinga to Hahei (Coromandel Peninsula). These locations were chosen to cover representative communities along the latitudinal

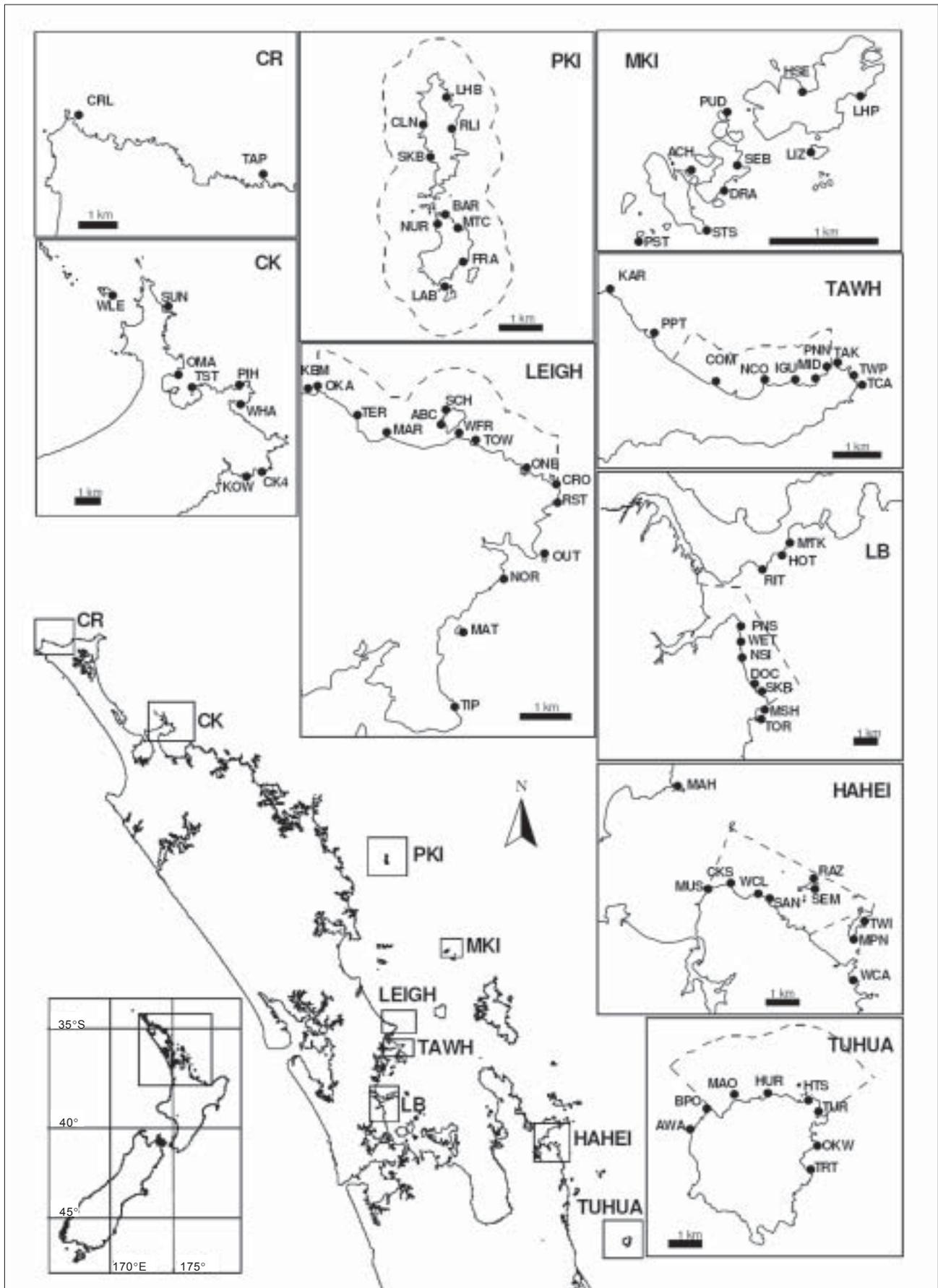


Figure 1. Position of study locations and study sites in northeastern New Zealand. CR = Cape Reinga, CK = Cape Karikari, PKI = Poor Knights Islands, MKI = Mokohinau Islands, TAWH = Tawharanui and LB = Long Bay. Site names given in Appendix 1.

gradient throughout northeastern New Zealand and also the onshore-offshore gradient. Coastal locations covered a range of wave exposure conditions from highly exposed (e.g. Cape Reinga) to very sheltered (e.g. Long Bay).

2.2 SITE LOCATION

Within the nine locations, sampling sites were located every 0.5 to 1 km (where possible) to obtain a representative description of the reef communities in the area. At the more exposed locations, the positioning of sites and the number of sites sampled was somewhat restricted by wave conditions during the sampling period. However, in most cases, sites with moderately sloping reefs were selected so that reefs could be sampled to a depth of 12 m. At the more sheltered coastal locations, the vertical extent of the reefs was occasionally insufficient to allow sampling at all depth ranges (see Appendix 1). For example, at Long Bay the reefs generally extended to a maximum depth of 5 m, but at some sites they were limited to less than 2 m, so only one depth stratum could be sampled. Within each location, sites generally covered a range of physical conditions. GPS co-ordinates (Appendix 1) were taken at each site, along with a photograph of the intertidal rock formations, so that exact relocation of the sites was possible. Most sampling was done during 1999. The exception was Tuhua (Mayor Island), which was sampled in March 2000 (Appendix 1).

2.3 SAMPLING PROCEDURE

2.3.1 Habitat distributions

At each sampling site within the nine locations, a line transect was sampled to quantify the depth distribution of habitats and to obtain information on the reef profile. Transects were run perpendicular to the shore on a fixed compass bearing from mean low water (top of the *Carpophyllum* band) out to the edge of the reef, or a maximum of 12 m depth (tidally corrected), whichever was encountered first. The habitat type, distance from shore and depth were recorded at 5-m intervals along each transect. The habitat types used in this study (Table 1) were adopted from Ayling (1978), but refined to include a number of additional habitats based on observations around northeastern New Zealand. The validity of this habitat classification system has been tested in Shears et al. (2004).

2.3.2 Depth-stratified sampling

At each site, five 1-m² quadrats were sampled in each of four depth ranges (< 2, 4-6, 7-9 and 10-12 m) to provide information on the abundance and size structure of macroalgae and macroinvertebrates. Depths were corrected to the mean low water mark to ensure accurate positioning of quadrats within the desired depth range. When available depths were less than 10 m, the deepest strata were omitted. Quadrats were positioned randomly adjacent to the transect line (within c. 10 m) in the desired depth range and the distance along each transect recorded to enable subsequent sampling in the same general area.

Within each quadrat, all macroalgae and macroinvertebrates were measured and counted. Measurements were made using a 5-mm-interval ruler for macroinvertebrates and using a 5-cm-interval 100-cm tape measure for macroalgae. Individual fronds were measured for macroalgae, as it is difficult to determine individual plants for many species. The total frond lengths of macroalgae were measured, along with stipe length and lamina length for *Ecklonia radiata* and *Lessonia variegata*. For *Lessonia*, the stipe length and total length of the whole plant was measured and the number of thalli counted. For *Carpophyllum angustifolium*, it was not always possible to measure all stipes, so these were counted and split into 25-cm size increments. Similarly, for small foliose algal species, it was impractical in some cases to count and

TABLE 1. DESCRIPTION OF HABITATS USED IN THIS STUDY (FROM SHEARS ET AL. 2004). FIGURES IN THE DESCRIPTIONS ARE INDICATIVE ONLY, HABITAT TYPES WERE DETERMINED BY SUBJECTIVE ASSESSMENT OF DOMINANT SPECIES.

HABITAT	DEPTH RANGE (m)	DESCRIPTION
Shallow <i>Carpophyllum</i> [†]	< 3	Dominated by high abundances (≥ 20 adult plants/m ²) of <i>Carpophyllum maschalocarpum</i> , <i>C. plumosum</i> , and <i>C. angustifolium</i> . <i>Ecklonia radiata</i> and the red algae <i>Pterocladia lucida</i> , <i>Osmundaria colensoi</i> , and <i>Melanthalia abscissa</i> also common. The sea urchin <i>Evechinus chloroticus</i> occurs at low numbers and generally occupies crevices.
<i>Ecklonia</i> forest*	5–20	Generally monospecific stands of mature <i>Ecklonia</i> forming a complete canopy (≥ 4 adult plants/m ²), occasional <i>C. flexuosum</i> plants. Urchins at low numbers (< 1 exposed urchins/m ²) and usually occupy crevices.
<i>Carpophyllum</i>	3–10	<i>Carpophyllum flexuosum</i> plants dominate (≥ 4 adult plants/m ²), on sheltered reefs plants are large <i>flexuosum</i> forest and associated with high levels of sediment. On more exposed reefs plants are short and generally associated with <i>Evechinus</i> .
Mixed algae [†]	2–10	Mixture of large brown algal species. No clear dominance of one particular species, usually only partial canopy (≥ 4 adult plants/m ²) and urchins may also occur at low numbers (< 2 exposed urchins/m ²).
Red foliose algae	2–9	Substratum predominantly covered (> 40%) by red foliose algae such as <i>P. lucida</i> or <i>O. colensoi</i> . Low numbers of large brown algae (< 4 adult plants/m ²).
Turfing algae [‡]	3–9	Substratum predominantly covered by turfing algae (e.g. articulated corallines and other red turfing algae.) (> 30% cover). Low numbers of large brown algae (< 4 adult plants/m ²) and urchins may be common.
<i>Caulerpa</i> mats		Green algae, usually <i>Caulerpa flexilis</i> , form dense mats over the substratum (> 40%). Urchins and large brown algae rare.
Urchin barrens [§]	3–9	Very low numbers of large brown algae present (< 4 adult plants/m ²), substratum typically dominated by crustose coralline algae. Usually associated with grazing activity of <i>Evechinus</i> (> 2 exposed urchins/m ²), which leaves the substratum relatively devoid of macroalgae. <i>C. flexuosum</i> and <i>Sargassum sinclairii</i> may occur.
Cobbles		Reef comprised of cobbles (< c. 0.5 m diameter), unstable and subject to high levels of agitation from wave exposure—in these areas crustose coralline algae are dominant along with a high cover of bare rock and sand. Large brown algae are generally absent.
Encrusting invertebrates		Usually vertical walls, substratum predominantly covered by community of encrusting ascidians, sponges, hydroids, and bryozoans. Large brown algae rare.
Sponge flats	> 10	Sponges visually dominant, high cover of sediment. Usually occurs on the reef-sand interface. Low numbers of <i>Ecklonia</i> may be present (< 4 adult plants/m ²).

* Habitat types described by Ayling (1978).

† Shallow *Carpophyllum* and mixed algae are both components of the 'Shallow broken rock' habitat described in Ayling (1978).

‡ Turfing algae are analogous to 'sediment flats' in Ayling (1978).

§ Urchin barrens are analogous to 'rock flats' in Ayling (1978).

measure all individual plants, so the percentage cover of these species was estimated. The primary (substratum) percentage cover of turfing algae, encrusting algal species, encrusting invertebrates and sediment were also recorded in each quadrat (1 m²) using a visual technique. Quadrats were divided into quarters, to assist in estimating covers of dominant forms, while the cover of minor forms was estimated on the basis that a 10 cm × 10 cm area equates to 1% cover. This technique was considered to be the most suitable in the context of this study, as it is efficient and ensures that the cover of all forms are recorded, unlike point-intercept methods (Benedetti-Cecchi et al. 1996). Furthermore, all quadrat sampling was carried out by the same two experienced divers in order to minimise inter-observer variability. Algae were identified using 'Seaweeds of New Zealand' (Adams 1994), with additional help from Dr Wendy Nelson (Museum of New Zealand Te Papa Tongarewa). Specimens are kept in a reference collection at the University of Auckland's Leigh Marine Laboratory. All algae species were identified at least to genus (Appendix 2), excluding small red turfing algae (< 5 cm), encrusting algae and epiphytic algae.

The test diameter of all urchins (> 5 mm) was measured, as well as whether each urchin was occupying crevices (cryptic) or was exposed. The shell width or shell length of gastropods were measured, the actual measurement varied depending on species' shell morphology (i.e. shell height for *Cantharidus purpureus*, shell width for *Turbo smaragdus*, *Trochus viridis* and *Cookia sulcata*). The total length of *Haliotis* species, limpets *Cellana stellifera* and chitons were also measured.

2.3.3 Environmental variables

Wave exposure, turbidity, sedimentation, overall reef slope and maximum depth were quantified at each site. Wave exposure was estimated using an index of potential fetch (Thomas 1986). The index was calculated by summing the potential fetch for each 10° sector of the compass rose. For open sectors of water, the radial distance was arbitrarily set to be 300 km. Turbidity was measured using a standard 25-cm-diameter black and white secchi disc (Larson & Buktenica 1998). The reading was taken as the depth (m) of descending disappearance and ascending reappearance. Sedimentation at each site was estimated using the percentage cover of sediment on the substratum, as recorded during depth-stratified quadrat sampling. The overall reef slope for each site was calculated as the total transect distance divided by the maximum depth.

2.4 STATISTICAL ANALYSIS

2.4.1 Species composition

Patterns in species composition of algae and mobile macroinvertebrates were investigated using presence-absence data for all sites. Similarities in species composition between sites were assessed using non-metric multidimensional scaling (MDS) based on a Bray-Curtis similarity matrix and hierarchical cluster analysis (Clarke 1993). Analysis of similarity (ANOSIM) was used to test differences between locations. This analysis was carried out separately for algae (66 species) and mobile macroinvertebrates (37 species).

Overall patterns in algal and mobile invertebrate species richness were investigated among locations. Because of the uneven number of sites sampled within each location, estimates of species richness were made using the Chao 2 incidence-based estimator (Colwell & Coddington 1994) with the program EstimateS (Version 6.0b1, R.K. Colwell). This technique estimates total number of species based on the total number of species observed and the number of species that only occur in one or two samples. This allows comparison of species richness among all locations despite the varying number of sites sampled.

2.4.2 Benthic community structure

Patterns in benthic community structure were investigated among sites and locations using a structural group-type approach (c.f. Steneck & Dethier 1994), whereby algal species were divided into nine groups. This was done to reduce the influence of species composition and emphasise structural patterns among communities. Algal measurements were converted to biomass (Table 2) in order to allow comparisons between all algal groups irrespective of sampling units (e.g. coralline turf measured in percentage cover while large brown algae were counted and measured), and also to adjust counts for different sizes of algae. The dry-weight of large algal species was calculated using a length-weight relationship, while a percentage cover-weight relationship was used for turfing and encrusting algal species. Biomass equations were calculated for all of the most common species and, where possible, at both island and coastal locations. For length-weight relationships, plants covering a range of sizes were measured to the nearest cm, dried at 80°C for a minimum of 3 days and weighed to the nearest 0.1 g. To convert percentage cover estimates of turfing and encrusting algae to dry-weight, a number of 10 cm × 10 cm (0.01 m² = 1%) samples were collected, dried and weighed. *Ecklonia radiata* was the only stipitate kelp, so the weights of the stipe and lamina were calculated using two separate equations (Table 2). It was not possible to calculate biomass equations for all species, so for some of the rarer species which were, typically, only very small contributors to total biomass, an equation from a species with similar morphology was used. All algal species were allocated to one of nine groups representing the main algal types responsible for defining algal community structure. *Ecklonia radiata* and *Carpophyllum flexuosum* formed their own groups, while other *Carpophyllum* species, other large brown algae, red foliose algae, fleshy red turfing algae, coralline turf, small brown algae and species of the green algal genus *Caulerpa* made up the remaining groups.

The biomass of each algal group was averaged across all depth ranges at each site to assess similarities in overall algal community structure between the sites and locations sampled. A Bray-Curtis similarity matrix was calculated on log(x+1) transformed data and similarities were investigated using hierarchical clustering and MDS. This procedure is suited to investigating similarities in community structure, as it effectively ensures that all groups, abundant or rare, contribute to the triangular matrix (Clarke & Warwick 1994). There were too many sites within each location to present data for each site, and pooling data across all sites masks important small-scale patterns within each location. Subsequently, sites were grouped using cluster analysis, and depth-related patterns in algal communities, urchin and gastropod abundance were described for each resulting group.

TABLE 2. LENGTH-WEIGHT AND / OR PERCENTAGE COVER-WEIGHT RELATIONSHIPS FOR MAJOR ALGAL SPECIES AND GROUPS.

GROUP/SPECIES	LOCATIONS	EQUATION	R ²	n	COLLECTED
<i>Ecklonia radiata</i>	CR	$\ln(y) = 2.625\ln(x) - 7.885$	0.97	21	CR
	All other locations				
	- Stipe	$\ln(y) = 1.671\ln(SL) - 3.787$	0.97	46	Leigh
	- Rest	$\ln(y) = 1.177\ln(SL \times LL) - 3.879$	0.94	55	Leigh
<i>Carpophyllum flexuosum</i>	LB/Hahei	$\ln(y) = 1.890\ln(x) - 4.823$	0.91	22	Long Bay
	Leigh/Tawh	$\ln(y) = 2.049\ln(x) - 5.251$	0.90	52	Tawh
	Islands/CK/CR	$\ln(y) = 1.792\ln(x) - 4.538$	0.89	59	MKI
Other <i>Carpophyllum</i>					
<i>Carpophyllum angustifolium</i> ^a	Coastal	$y = 0.068x - 0.27$		0.92	23
	Island	$\ln(y) = 1.131\ln(x) - 3.522$	0.89	117	MKI
<i>C. maschalocarpum</i>	LB	$\ln(y) = 2.078\ln(x) - 5.903$	0.88	116	Long Bay
	Leigh/Tawh/Hahei	$\ln(y) = 1.764\ln(x) - 4.311$	0.72	46	Leigh
	Islands/CK/CR	$\ln(y) = 1.567\ln(x) - 4.204$	0.96	38	MKI
<i>C. plumosum</i>	Leigh/Tawh/LB	$\ln(y) = 1.472\ln(x) - 3.850$	0.66	62	Leigh
	Hahei	$\ln(y) = 1.638\ln(x) - 4.413$	0.92	31	Hahei
	Islands/CK/CR	$\ln(y) = 1.517\ln(x) - 4.778$	0.69	60	MKI
<i>Lessonia variegata</i>	All locations	$\ln(y) = 1.677\ln(x) - 5.537$	0.83	9	MKI
<i>Landsburgia quercifolia</i>	All locations	$\ln(y) = 1.971\ln(x) - 5.058$	0.83	19	CR
<i>Sargassum sinclairii</i>	All locations	$y = 0.075x + 0.124$	0.58	25	CR
<i>Xiphobora chondrophylla</i>	Leigh/Tawh/Hahei	$\ln(y) = 1.786\ln(x) - 4.171$	0.62	18	Hahei
	Islands/CK/CR	$\ln(y) = 2.01\ln(x) - 5.377$	0.75	33	MKI
<i>Cystophora retroflexa</i>	All locations	$\ln(y) = 1.7436\ln(x) - 4.4144$	0.84	9	Leigh
Red foliose					
<i>Osmundaria colensoi</i>	All locations	$\ln(y) = 1.720 \ln(x) - 3.379$	0.70	14	MKI
		1% = 22.93 g		3	
<i>Pterocladia lucida</i>	All locations	$\ln(y) = 1.963 \ln(x) - 5.076$	0.73	47	Leigh
		1% = 10 g		3	
<i>Melanthalia abscissa</i>	All locations	$\ln(y) = 1.775 \ln(x) - 4.247$	0.64	22	MKI
<i>Plocamium</i> spp.	All locations	$\ln(y) = 2.649 \ln(x) - 8.812$	0.80	34	MKI
<i>Euptilota formosissima</i>	All locations	$\ln(y) = 1.616 \ln(x) - 4.971$	0.78	13	MKI
<i>Placentophora colensoi</i>	All locations	$\ln(y) = 2.582 \ln(x) - 6.392$	0.87	23	CR
Red turfing	All locations	1% = 1.74 g		3	MKI
Coralline turf ^b	All locations	1% = 1.5 g			Leigh
Crustose corallines ^b	All locations	1% = 0.35 g			Leigh
Small brown algae					
<i>Carpomitra costata</i>	All locations	$\ln(y) = 1.735\ln(x) - 5.856$	0.43	18	MKI
<i>Zonaria turneriana</i>	All locations	$\ln(y) = 2.587\ln(x) - 6.443$	0.83	27	MKI
		1% = 2.48 g		3	
<i>Caulerpa</i> spp.					
<i>Caulerpa flexilis</i>	All locations	1% = 5.81 g		3	MKI
Other green algae					
<i>Codium</i> spp.	All locations	1% = 4.68 g		3	MKI
<i>Ulva lucida</i>	All locations	1% = 1.71 g		3	MKI

^a From Choat & Schiel (1982).

^b The proportion of CaCO₃ in *Corallina officinalis* has been estimated as 45% of the dry-weight (M. Taylor unpubl. data). The value given is the total dry-weight of samples less 45%.

y = dry-weight (g), x = total length, SL = stipe length, LL = laminae length, LB = Long Bay, CK = Cape Karikari, CR = Cape Reinga, Tawh = Tawharanui, MKI = Mokohinau Islands.

2.4.3 Relationship between algal community structure and environmental variables

The relationship between algal community structure and the environmental variables measured was investigated using canonical analysis of principal coordinates (CAP, described in Anderson & Willis 2003). This technique was used to perform an unconstrained ordination (principal coordinates analysis) based on Bray-Curtis dissimilarities and a constrained ordination (canonical correlation analysis) with reference to the *a priori* hypothesis that there is no significant relationship between algal community data and a matrix of environmental variables. In addition, this technique carries out a permutation test to test the hypothesis and correlates the original variables with the canonical axes to identify which species or environmental variables are responsible for the multivariate patterns.

Analysis was carried out on fourth-root-transformed algal biomass data for each site. The same algal groups used in the community structure analysis were used, along with three additional groups: red encrusting algae, filamentous algae and other green algae. The importance of the environmental variables is likely to change with depth, so analyses were carried out separately for each of the four depth ranges. The environmental variables used included wind fetch, secchi depth, sediment cover (average for depth range), reef slope, maximum depth and exposed *Evechinus* density (average for depth range). While, strictly speaking, urchins are not an 'environmental variable', they are an important source of variation in algal communities that interact in a complex way with other environmental variables. Furthermore, densities of exposed urchins were used, as these generally reflect adults openly grazing the substratum—these are the urchins most responsible for influencing algal populations.

3. Results

3.1 SPECIES COMPOSITION AND RICHNESS AMONG LOCATIONS

Clear patterns were apparent between the sampling locations in the species composition (Fig. 2) and species richness (Fig. 3) of macroalgae and mobile macroinvertebrates. A list of the species identified in this study and their percentage occurrence at the locations sampled is given in Appendix 2.

3.1.1 Macroalgae

A clear gradient in algal species composition was apparent from the shallow sheltered sites at Long Bay to the northern and offshore island sites (Fig. 2A). While there was some overlap in overall species composition among locations, there was significant variation at the location level (ANOSIM, Global $R = 0.622$, $p = 0.001$ from 999 permutations). Pair-wise tests revealed differences in algal composition between all locations ($p < 0.05$), except between Leigh and Tawharanui ($R = 0.107$, $p = 0.073$, 999 permutations) and between Cape Karikari and Cape Reinga ($R = 0.427$, $p = 0.067$, 45 permutations).

Figure 2. Species composition of macroalgae (A) and mobile macroinvertebrates (B) for all sites. MDS ordinations based on presence-absence data.

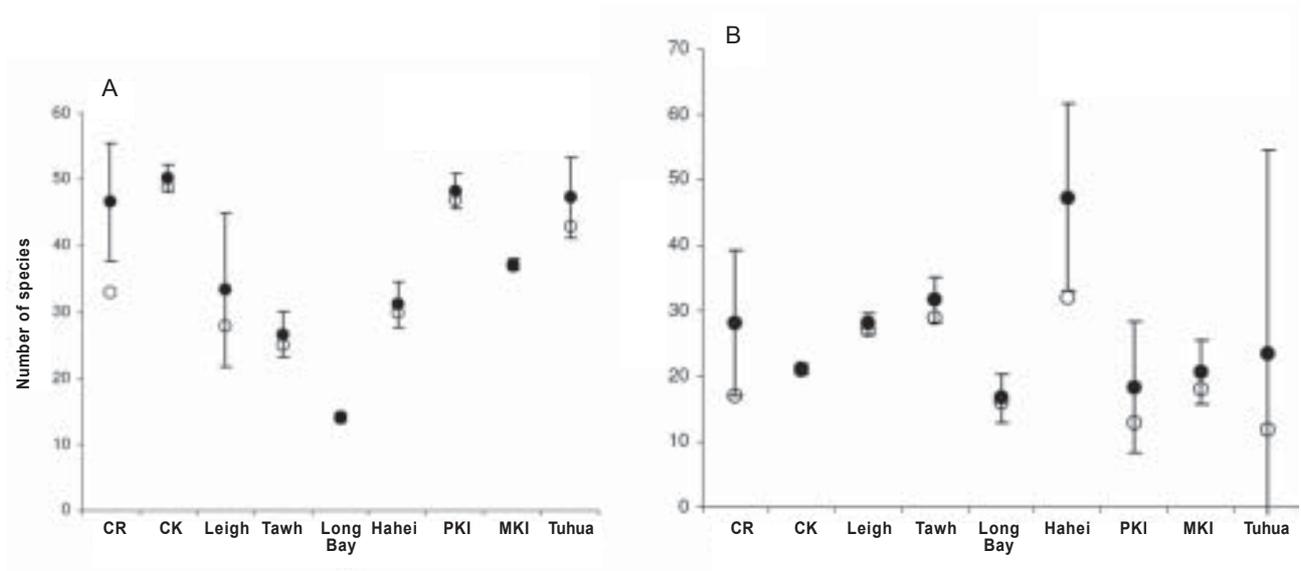
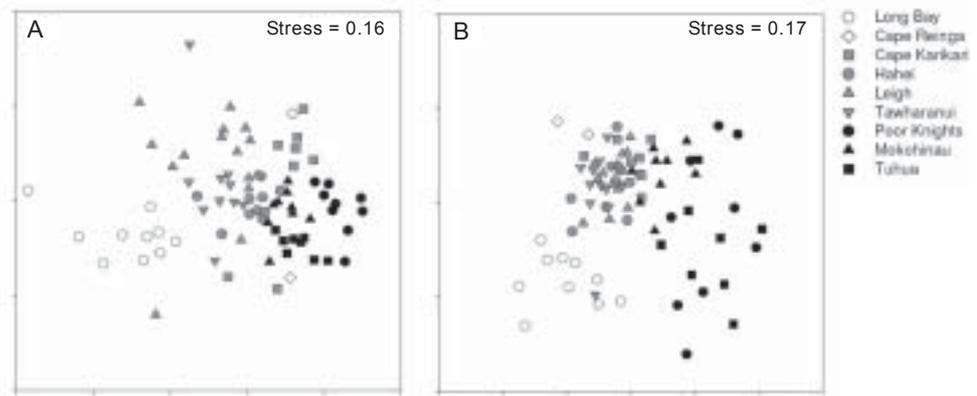


Figure 3. Observed and predicted (Chao2 estimator) species richness of macroalgae (A) and mobile macroinvertebrates (B) at each location. ○ = observed, ● = predicted (+/- SD).

Comparisons between Cape Reinga and other locations must be treated cautiously, as only two sites were sampled there.

In general, the algal communities at the locations sampled in this study were dominated by 5 species of large brown algae (86% of total algal biomass); of which *Ecklonia radiata* made up 48% (Table 3). There were clear differences in the dominant algal species between locations. *Ecklonia* dominated in all locations except for Long Bay and Cape Reinga, where *Carpophyllum maschalocarpum* was most abundant. *Carpophyllum maschalocarpum* tended to be the second-most important contributor to algal biomass at the other coastal locations (Table 3), while at offshore islands it only accounted for approximately 3% of the total biomass and was replaced by *C. angustifolium* (11–36%). *Carpophyllum angustifolium* was absent from Cape Reinga, Cape Karikari and Long Bay. *Carpophyllum flexuosum* was recorded at all locations except Cape Reinga, but was most dominant at Long Bay (20.9% total biomass). *Carpophyllum plumosum* occurred at relatively low levels in all locations, but was the greatest contributor at Long Bay (4.8%). *Lessonia variegata* was an important component of the algal assemblages at Cape Reinga, Cape Karikari and the offshore islands (except Tuhua, where it did not occur). Other large brown algae were generally less common, although *Sargassum sinclairii* and *Xiphophora chondrophylla* occurred at all locations

(Appendix 2). *Landsburgia quercifolia* was most common at Cape Reinga (occurred in 46% of quadrats), but was also present as isolated plants at the Poor Knights Islands, Hahei and Leigh.

A number of small brown algal species were recorded (Appendix 2). *Zonaria turneriana* was the most common, occurring in all locations, but was most important in terms of overall biomass at Long Bay (Table 3). *Carpomitra costata* was generally restricted to the more exposed locations and was absent from Leigh, Tawharanui and Long Bay. *Dictyota* sp. was only found at coastal locations, with *Perithalia capillaries* and *Sporocchnus* spp. only being found at Cape Karikari and Cape Reinga (Appendix 2).

Red foliose algae, such as *Osmundaria colensoi* and *Pterocladia lucida*, and red turfing algae were important contributors to total algal biomass at Cape Reinga, Cape Karikari and the offshore islands (Table 3). At Long Bay, these groups were generally absent. Crustose coralline algae and coralline turf were ubiquitous at all locations and each contributed 1.4% to overall algal biomass. On average, crustose corallines covered $55.0 \pm 0.7\%$ of the substratum and coralline turf $12.3 \pm 0.5\%$. While articulated corallines were not identified to species level in each quadrat, some clear patterns were apparent: *Corallina officinalis* was ubiquitous at coastal locations, while *Amphiroa anceps*, *Arthrocardia corymbose*, *Cheilosporum sagittatum*, *Haliphtilon roseum* and *Jania* sp. were more common at offshore islands and the northernmost locations. Many other red algal species were recorded (Appendix 2), but their contribution to overall biomass was minimal. A number of species were restricted to (e.g. *Nesophila boggardii* and *Rhodymenia* spp.), or more common at (e.g. *Euptilota*

TABLE 3. PROPORTIONAL BIOMASS OF DOMINANT MACROALGAL SPECIES AND STRUCTURAL GROUPS AMONG LOCATIONS. A COMPLETE LIST OF THE SPECIES IDENTIFIED IN THIS STUDY AND THEIR PERCENTAGE OCCURRENCE AT THE LOCATIONS SAMPLED IS GIVEN IN APPENDIX 2.

	TOTAL AVERAGE BIOMASS (g/m ²)	<i>Ecklonia radiata</i>	<i>Carpophyllum maschalocarpum</i>	<i>C. angustifolium</i>	<i>C. flexuosum</i>	<i>Lessonia variegata</i>	Red turfing	<i>Osmundaria colensoi</i>	<i>Pterocladia lucida</i>	<i>C. plumosum</i>	RED ENCRUSTING	CORALLINE TURF	OTHER SPECIES (> 1% TOTAL BIOMASS)
All locations	400.5	48.1	20.1	11.0	3.9	3.2	2.1	1.9	1.7	1.4	1.4	1.4	
Coastal locations													
Cape Reinga	267.9	12.9	63.1	-	-	8.2	2.5	3.2	3.3	0.1	1.2	1.3	<i>Landsburgia, Melanthalia</i>
Cape Karikari	434.4	53.9	16.6	-	5.4	9.2	2.0	1.1	1.4	1.0	2.2	0.9	<i>Xiphophora, Codium convolutum, Sargassum</i>
Leigh	267.8	58.4	27.8	0.5	0.4	-	1.3	0.1	2.3	1.7	2.4	2.8	
Tawharanui	339.9	66.7	26.0	0.1	1.0	-	0.5	0.1	0.7	0.6	1.8	1.5	
Hahei	497.9	51.0	26.3	2.3	4.5	5.9	1.1	0.4	1.0	2.3	1.4	0.4	<i>Xiphophora</i>
Long Bay	379.0	19.2	49.9	-	20.9	-	-	-	-	4.8	1.8	0.3	<i>Zonaria turneriana</i>
Offshore Islands													
Poor Knights	475.6	52.8	2.8	18.2	0.2	5.7	6.4	3.0	1.5	0.8	0.8	2.0	<i>Ulva</i> spp. <i>Caulerpa flexilis</i>
Mokohinau	256.9	54.0	3.2	11.5	1.6	10.2	4.0	0.8	2.5	0.3	2.0	3.4	<i>Ulva</i> spp. <i>C. convolutum</i>
Tuhua	824.9	44.0	3.3	35.9	0.2	-	1.6	5.9	3.3	0.3	0.4	1.1	<i>C. flexilis</i>

formosissima, *Delisea compressa* and *Curdiea coriacea*) the offshore islands (Appendix 2). An undescribed *Rhodymenia* species (previously recorded only from the Three Kings Islands, W. Nelson pers. comm.) was very common at the Poor Knights Islands in shallow water (< 5 m) and reached a maximum length of approximately 30 cm. *Placentophora colensoi* and *Pachymenia crassa* were only found at offshore islands, Cape Reinga and Cape Karikari.

A number of green algal species including *Ulva lactuca*, *Caulerpa flexilis*, *C. geminata* and *Pedobesia clavaeformis* were also common at the offshore islands and Cape Karikari but rare at other mainland locations. *Ulva lactuca* was the most common green algae (Appendix 2) and contributed more than 1% of total algal biomass at the Poor Knights Is and Mokohinau Is. *Codium convolutum* occurred at all locations, except Long Bay, but was most common at Cape Karikari and the offshore islands. The green algae *Caulerpa fastigiata*, *C. articulata* and *Cladophora feredayi* were only found at Cape Karikari, while *Cladophoropsis herpestica* was only found at Long Bay.

These patterns in algal composition were reflected in the overall species richness among locations (Fig. 3A). The offshore islands and the locations in the far north (Cape Reinga and Cape Karikari) tended to have the highest observed and predicted species richness, while Long Bay had the lowest (14 species). The number of species at Cape Reinga was predicted to be much higher than observed (although only two sites were sampled) and was similar to Cape Karikari and the offshore islands. The number of species at the Mokohinau Islands, however, was lower than at other offshore islands. Leigh, Tawharanui and Hahei all had similar observed species richness (28, 25 and 30 species respectively).

3.1.2 Mobile macroinvertebrates

The species composition of mobile macroinvertebrates (Fig. 2B) differed among locations (Global $R = 0.569$, $p = 0.001$ from 999 permutations) and generally reflected the patterns seen for macroalgae. Pair-wise comparisons between locations revealed no difference in mobile invertebrate composition between Cape Karikari and Hahei ($R = 0.124$, $p = 0.056$, 999 permutations), Hahei and Leigh ($R = 0.056$, $p = 0.200$, 999 permutations), Leigh and Tawharanui ($R = 0.118$, $p = 0.061$, 999 permutations), or between the Poor Knights Is and Tuhua ($R = 0.044$, $p = 0.271$, 999 permutations). The Poor Knights Is and Tuhua were clearly separated from coastal locations (Fig. 2B). In general, mobile invertebrates were much more common at coastal locations.

The herbivorous gastropods *Cookia sulcata*, *Trochus viridis* and *Cantharidus purpureus* commonly occurred at all coastal locations but were generally scarce at offshore islands (Appendix 2). The majority of other herbivorous gastropods showed similar patterns except *Modelia granosus*, which was most common at Cape Karikari and the Mokohinau Is. *Turbo smaragdus* was very common at Long Bay (occurred in 92% of quadrats) but rare at other coastal locations (< 7%) and absent from the offshore islands. Predatory gastropods were also rare at offshore islands (Appendix 2).

Evechinus chloroticus was the most ubiquitous sea urchin, occurring at all locations. *Centrostephanus rodgersii* was generally rare, but was most common at offshore islands and Cape Karikari. Starfish species were only recorded from coastal locations and the crinoid, *Comanthus novaezelandiae*,

was only found at the Mokohinau Is (Appendix 2). The cushion star *Patiriella regularis*, the ambush starfish *Stegnaster inflatus* and the filter-feeding gastropod *Maoricolpus roseus* were most common at Long Bay.

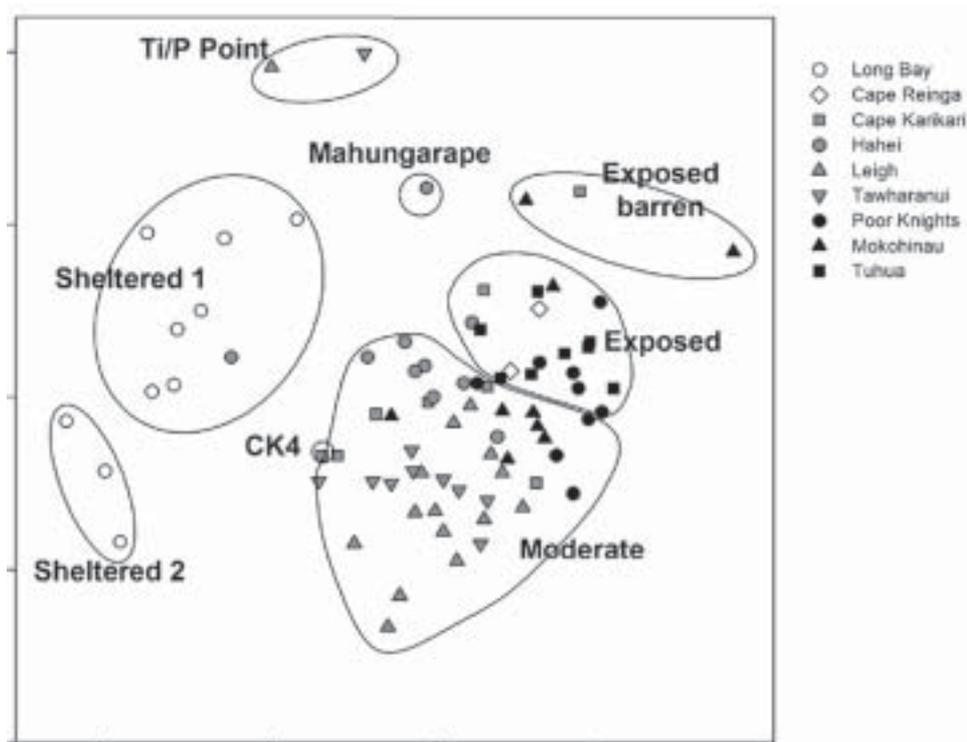
In contrast to macroalgae, the species richness of mobile invertebrates was generally lowest at the offshore islands and Long Bay (Fig. 3B). The high variation in predicted richness at offshore islands was due to the majority of species being recorded at single sites, reflecting the very low densities of mobile invertebrates at these islands. The highest mobile invertebrate richness was observed at Hahei, Leigh and Tawharanui.

3.2 BENTHIC COMMUNITY STRUCTURE AMONG SITES AND LOCATIONS

Patterns in algal community structure (based on algal biomass) among sites and locations (Fig. 4) were broadly similar to patterns of algal species composition (Fig. 2B), with a clear gradient from sheltered coastal to offshore island sites. Overall, algal communities differed among locations (ANOSIM, $R = 0.462$, $p = 0.001$, 999 permutations). Pair-wise tests revealed no difference at site level between Leigh and Tawharanui ($R = 0.016$, $p = 0.350$, 999 permutations), Cape Karikari and Hahei ($R = 0.063$, $p = 0.162$, 999 permutations), or between Cape Karikari and the Mokohinau Is ($R = 0.054$, $p = 0.197$, 999 permutations). There was no difference between Cape Reinga and all other locations, except Long Bay ($R = 0.759$, $p = 0.015$); however, only 2 sites were sampled at Cape Reinga and the tests were based on only 45 to 136 permutations.

The high variation within (e.g. Hahei and Cape Karikari) and among locations generally reflected the gradient of environmental conditions over which sampling occurred in a location. Based on biomass of the nine algal groups, sites were divided into 8 groups at the 27% dissimilarity level (Figs 4 and 5). There was

Figure 4. MDS ordination of algal communities at all sites. Based on $\log(x+1)$ transformed biomass data for the nine dominant algal groups averaged across all depths. Stress = 0.19. Solid circles = 27% dissimilarity.



a strong concordance between these groupings and both wave exposure (measured as wind fetch) and the coastal or offshore locality of sites (Fig. 5). The wind fetch measure does not take into account the swell climate of specific locations, therefore between-location comparisons are indicative only. For example, offshore island sites with relatively low fetch may be subject to wave exposures similar to those at sites from coastal locations with a higher fetch.

The sheltered mainland sites were divided into two groups: 'Sheltered 1' and 'Sheltered 2'. The majority of coastal sites from Leigh, Tawharanui, Hahei and Cape Karikari, along with the most sheltered sites from the Poor Knights and Mokohinau Is, were grouped into a large 'Moderate' group. The Cape Reinga sites, along with the majority of offshore island sites, mainly from the Poor Knights Is and Tuhua, made up the 'Exposed' group. The 'Exposed barren' group included the most exposed sites from Cape Karikari and the Mokohinau Is. The remaining three groups included a few sites of generally low to moderate wave exposure: 'Ti Point' and 'P-Point' at Leigh and Tawharanui respectively, 'Mahungarape' at Hahei and 'CK4', the most sheltered site at Cape Karikari. Both the 'exposed' and 'moderate' groups were further divided at the 23% dissimilarity level (Fig. 5).

3.2.1 Cape Reinga

The two sites sampled at Cape Reinga were grouped in the 'E1' group (Fig. 5). Both are north-facing, highly exposed to the northwest and northeast, and had the highest wind fetch of all the sites sampled. At both sites, the reefs were gradually sloping and inundated with sand at depths greater than 10 m. Shallow *Carpophyllum* habitat dominated to depths of 4 m, below which the reefs were covered with a mixture of turfing, red foliose and mixed algal habitats (Fig. 6). Urchin barrens and *Ecklonia* forest were rare.

Stands of *Carpophyllum maschalocarpum* dominated the immediate subtidal (< 2 m) at both sites (Appendix 3, Fig. A3.1). The biomass and abundance of *C. maschalocarpum* was considerably higher than at any of the other locations sampled. In addition, the plants there were the largest measured in the study, up to 240 cm total length. The average length of *C. maschalocarpum* at the Cape Reinga sites was 69.5 ± 2.1 cm, as opposed to average lengths of between 28 and 40 cm for all other locations. At greater depths, mixed algal stands of large brown algae, including *C. maschalocarpum*, *Lessonia variegata*, *Ecklonia radiata* (hereafter *Ecklonia*), *C. plumosum* and *Landsburgia quercifolia* occurred. *Carpophyllum maschalocarpum* was present in high-density monospecific patches down to depths of 10 m, although its biomass declined with depth and the biomass of *Ecklonia* increased. *Ecklonia* did not show its typical canopy-forming morphology (long stipes and short primary laminae), as seen in other locations; instead, plants had short stipes with long primary lamina and were mixed in with other large brown algae.

Patches of red foliose algae (mainly *Osmundaria colensoi* and *Pterocladia lucida*) and coralline turf (including *Arthrocardia corymbosa*, *Amphiroa anceps* and *Haliptilon roseum*) were also interspersed amongst the large brown algae at all depths (Appendix 3, Fig. A3.1). Other red algal species were present, including *Placentophora colensoi*, *Melanthalia abscissa*, *Pterocladia capillacea*, *Plocamium* spp., *Laurencia thyrsifera*, *L. distichophylla*, *Asparagopsis armata*, *Curdiea coriacea* and *C. codioides*.

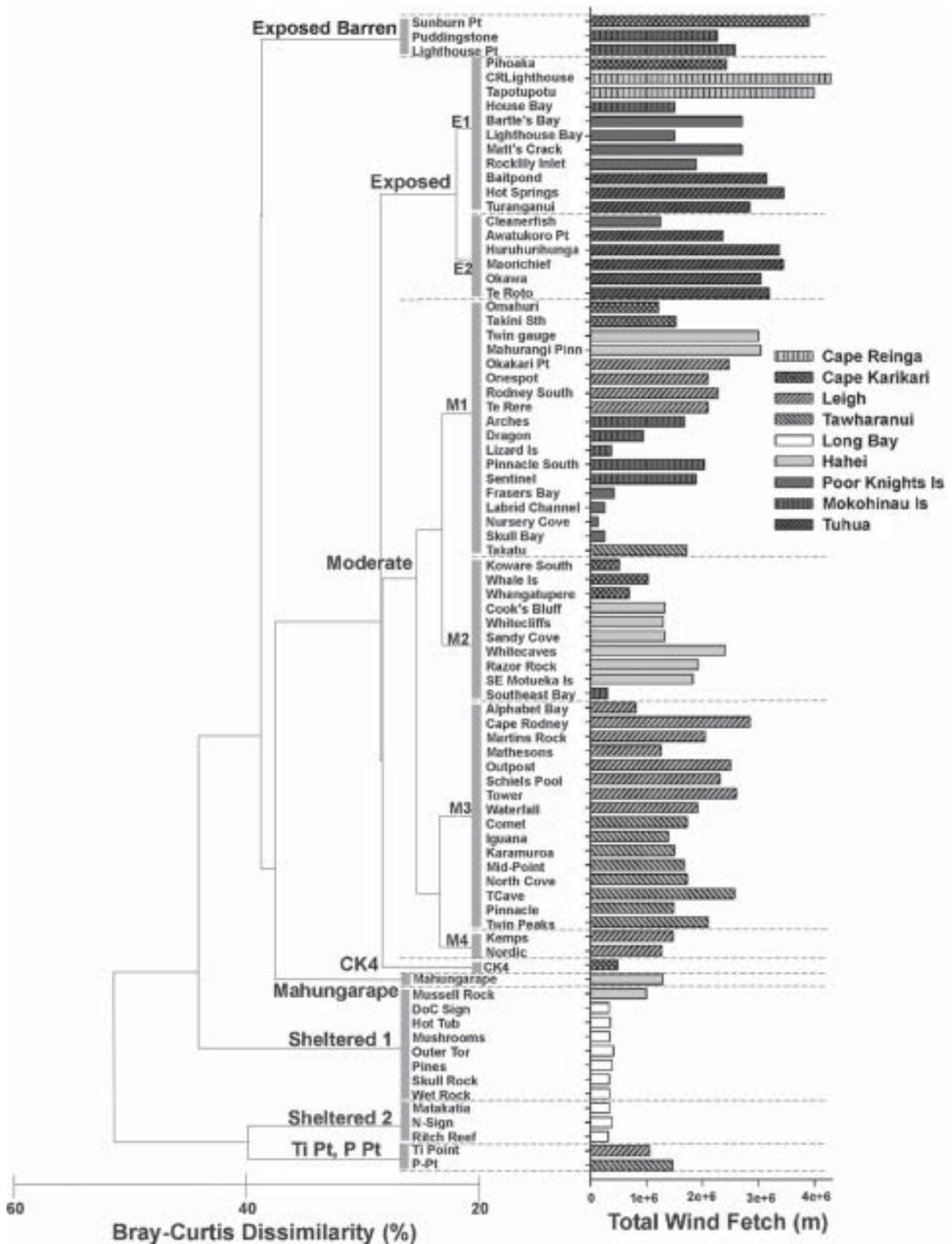
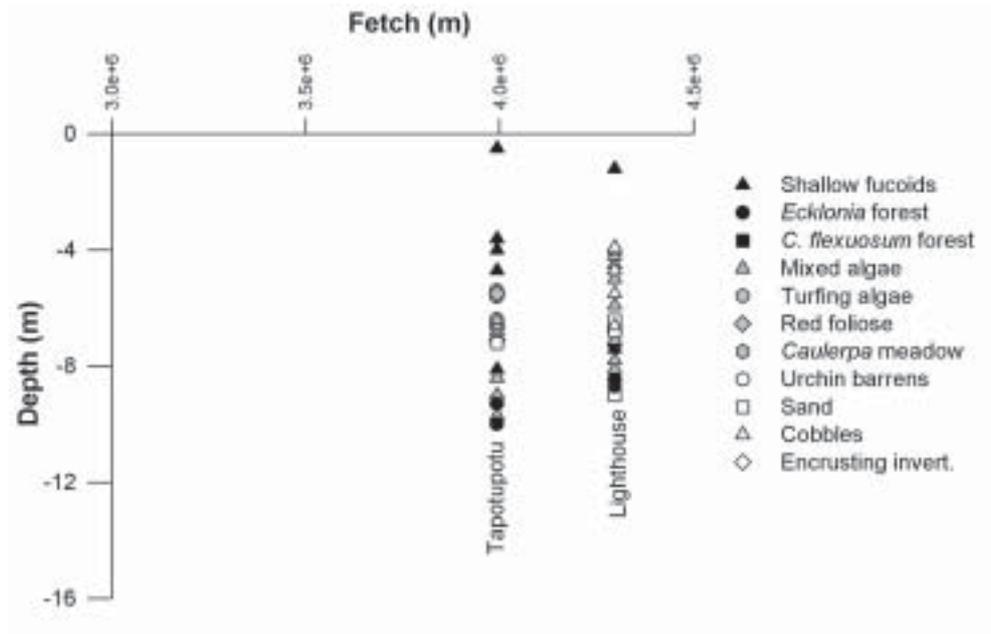


Figure 5. Hierarchical cluster analysis of sites showing site groupings at the 27% and 23% dissimilarity based on biomass of the 9 dominant algal groups. The bar chart shows the total wind fetch for each site.

Figure 6. Habitat distributions for Cape Reinga sites from transect data arranged according to total wind fetch at each site. Symbols indicate the habitat type assigned to points every 5 m along the transect line.



The sea urchin *Evechinus chloroticus* (hereafter *Evechinus*) was common, but densities were variable. Both *Evechinus* and *Haliotis iris* were only found at high densities in isolated patches, typically around the base of large boulders or within the shelter of crevices. All paua were below legal size (> 125 mm). The gastropod species—*Cookia sulcata*, *Trochus viridis*, *Cantharidus purpureus*, *Modelia granosus* (indicated by ‘Other herb’) and *Dicathais orbita*—were present in low numbers (Fig. A3.1).

3.2.2 Cape Karikari

The eight sites at Cape Karikari spanned a range of wave exposure conditions and there was high variability in algal communities among sites (Figs 4 and 5). The distribution of habitats varied according to wind fetch (Fig. 7). At the most sheltered sites, urchin barrens habitat was patchy between 3 m and 5 m depth and *Carpophyllum flexuosum* forest was present (Koware South and, to a lesser extent, CK 4). With increasing exposure, the vertical extent of both shallow *Carpophyllum* habitat and urchin barrens tended to increase and the upper limit of *Ecklonia* became deeper. The arrangement of sites with fetch was consistent with the groups identified from clustering (Fig. 5). Sunburn Pt, the most exposed site, was located in the ‘Exposed barren’ group, Pihoaka Pt in group ‘E1’, Takini South and Omahuri were in the ‘M1’ group and Koware South, Whale Island and Whangatupere in ‘M2’. The most sheltered site, CK4, was in its own group.

The biomass of large brown algae at Cape Karikari showed clear depth-related patterns between groups with decreasing wave exposure (Appendix 3, Fig. A3.2). These patterns appeared highly related to urchin density; with increasing wave exposure, urchins were more abundant at greater depths and, subsequently, the biomass of *Ecklonia* was lower at the most exposed sites (Fig. A3.2(a, b)). At Sunburn Pt, *Ecklonia* forest only occurred at depths greater than 12 m. *Carpophyllum maschalocarpum* and, to a lesser extent, *C. plumosum*, dominated the < 2 -m depth stratum at all sites. At the most exposed sites (Pihoaka Pt and Sunburn Pt), the biomass of red foliose algae, predominantly *Osmundaria colensoi* and *Pterocladia lucida*, was considerably