

Figure 7. Habitat distributions for Cape Karikari 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.

higher in the shallow stratum than at the more sheltered sites. *Lessonia variegata* dominated the 4–6-m depth stratum (Fig. A3.2(a, b)). *Carpophyllum maschalocarpum* was also present at this depth and extended down to 9 m at Sunburn Pt. At these sites, *Ecklonia* was rare in the deepest stratum and urchins were common. *Carpophyllum flexuosum* was present in urchin-grazed areas and exhibited an exposed morphology (cf. Cole et al. 2001). Similarly, *Ecklonia* morphology was comparable to that observed at Cape Reinga with short stipes. The densities of gastropods, in particular *Cookia* and *Cellana stellifera*, were relatively high compared with the more sheltered sites. *Modelia granosus* was locally abundant at Pihako Pt (Fig. A3.2(d), indicated by ‘Other herb’). The large sea urchin *Centrostephanus rodgersii* was found at low numbers at Cape Karikari, the highest densities of this urchin were recorded at Pihako Pt at 10–12 m depth ($1.0 \pm 0.3 \text{ m}^{-2}$).

Depth-related patterns in algal community structure were very similar between the Koware South, Whangatupere, Whale I. and CK4 sites (Fig. A3.2(d, e)). The separation of the CK4 site from the other sites of similar wave exposure was probably the result of the relatively high biomass of small brown algae (*Distromium scottsbergii* and *Zonaria turneriana*) and green algae (*Caulerpa flexilis* and *C. articulata*) in the deepest stratum at CK4. Urchins were generally most abundant at 4–6 m and large brown algae rare. However, at Koware South (grouped in ‘M2’), *C. flexuosum* forest (sheltered variety) dominated the 4–6 m depth stratum ($12.0 \pm 4.4 \text{ plants m}^{-2}$, $202.2 \pm 97.1 \text{ g dry weight m}^{-2}$) and urchins occurred at low numbers ($2.2 \pm 1.2 \text{ m}^{-2}$) at this depth. At greater depths (7–9 m and 10–12 m), urchins were rare and *Ecklonia* forest dominated. Gastropod numbers tended to be low with *Cookia sulcata* being the most abundant species in shallow (< 6 m) strata and *Trochus viridis* more abundant in the deeper strata. At Takini and Omahuri (‘M1’), the patterns in algae, urchins and gastropods (Fig. A3.2(c)) were relatively similar to the more sheltered groups; however, urchins were abundant to depths of 9 m and, subsequently, *Ecklonia* only occurred at a relatively low biomass in the 7–9-m stratum. Another difference was the occurrence of *Lessonia variegata* in the shallow stratum (< 2 m).

3.2.3 Leigh

All sites sampled at Leigh, except Ti Point, were in the 'Moderate' group (Fig. 5). Shallow *Carpophyllum* habitat dominated from 0 to 2 m and *Ecklonia* forest dominated at depths greater than 7 m (Fig. 8). Intermediate depths were characterised by a mixture of urchin barrens, turfing and mixed algal habitats. At Ti Point, the urchin barrens habitat extended to the bottom of the reef (c. 7 m) and deep algal habitats were absent.

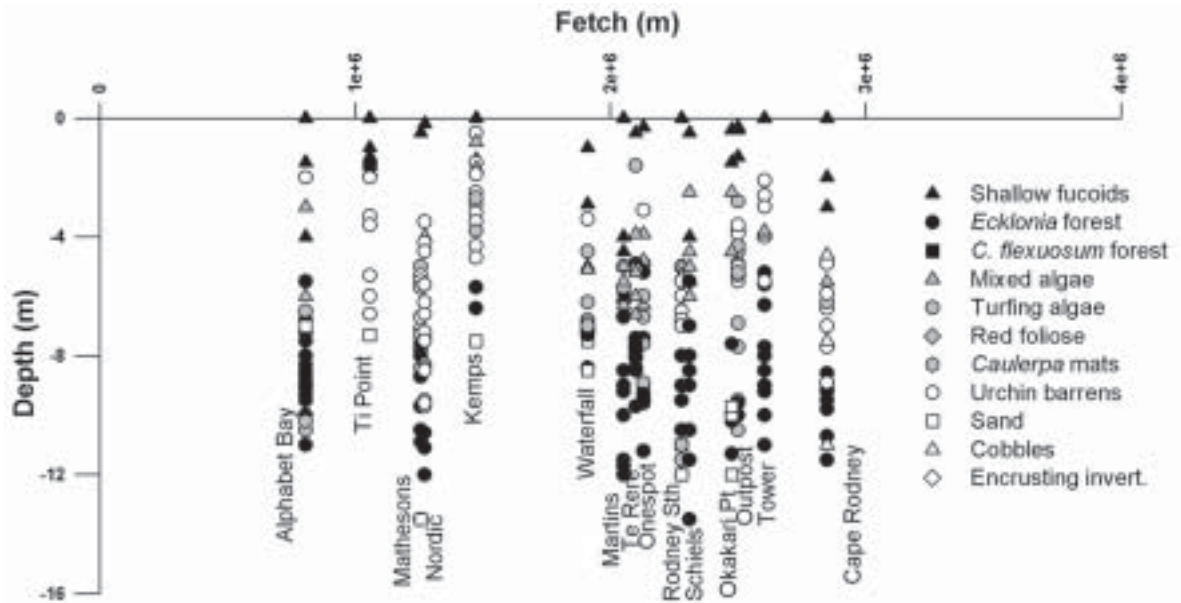


Figure 8. Habitat distributions for sites at Leigh from transect data arranged according to total wind fetch at each site. Symbols indicate the habitat type assigned to points every 5 m along the transect line.

All sites, excluding Ti Point, exhibited a bimodal pattern in algal biomass with depth (Appendix 3, Fig. A3.3). The shallow stratum was dominated by *C. maschalocarpum*, although *C. angustifolium*, *C. plumosum*, *Ecklonia* and *Xiphophora chondrophylla* were also common at some sites. Low numbers of *Landsburgia quercifolia* plants were also recorded at Waterfall Reef. *Evechinus* was most abundant in the 4–6-m stratum where algal biomass was generally lowest. However, in the 'M1' and 'M3' groups (Fig. A3.3(a, b)), *Ecklonia*, *C. maschalocarpum* and *C. flexuosum* (exposed variety) were common in the 4–6-m depth range. *Ecklonia* dominated the 7–9-m and 10–12-m strata with low numbers of *C. flexuosum*, *C. plumosum*, *C. maschalocarpum* and *Sargassum sinclairii* occasionally occurring. *Zonaria turneriana* was the most abundant understory species, but *Distromium skottsbergii*, *Halopteris* spp., *Pterocladia lucida*, *Melanthalia abscissa*, *Plocamium* spp. and *Kallymenia berggrenii* also occurred.

The main difference between groups 'M1' and 'M3' was the higher biomass of red turfing algae in the shallow stratum (< 2 m) at 'M1' compared with 'M3', which had a higher biomass of red foliose algae, mainly *Pterocladia lucida* and, to a lesser extent, *Melanthalia abscissa* and *Osmundaria colensoi*. Sites in the 'M4' group (Kemps Beach and Nordic) were characterised by a high abundance of *Evechinus* and the absence of large brown algae at 4–6 m (Fig. A3.3(c)). This group also had a very high biomass of small brown algae, mainly *Zonaria turneriana* and *Distromium skottsbergii*, in the 10–12 m stratum.

Gastropods occurred at relatively high densities at all sites. *Cookia sulcata* was generally the most abundant in the 0–2-m and 4–6-m strata, while *Trochus viridis* and *Cantbaridus purpureus* were most abundant in the deeper strata. *Cellana stellifera* and *Dicathbais orbita* were also common at all sites. The main difference between the site groups was the relatively low numbers of *Cookia* found at Ti Point, Kemps Beach and Nordic.

3.2.4 Tawharanui

All sites sampled at Tawharanui were moderately exposed and their habitat distributions (Fig. 9) exhibited similar patterns to those seen at the Leigh sites. Shallow *Carpophyllum* dominated from MLW to 2–3-m depth; there was a mixture of urchin barrens, turfing algae, mixed algal habitat and *C. flexuosum* forest from 3 m to 6 m, and *Ecklonia* forest dominated below 6 m. At the most exposed site (T-Cave), urchin barrens habitat extended down to 8 m.

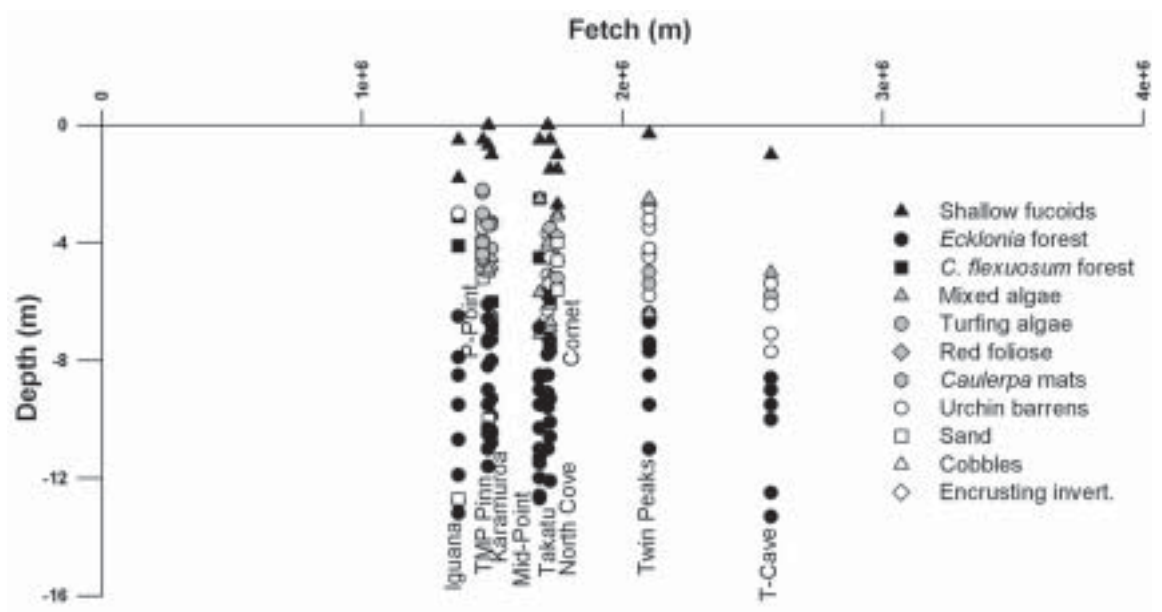


Figure 9. Habitat distributions for sites at Tawharanui from transect data arranged according to total wind fetch at each site. Symbols indicate the habitat type assigned to points every 5 m along the transect line.

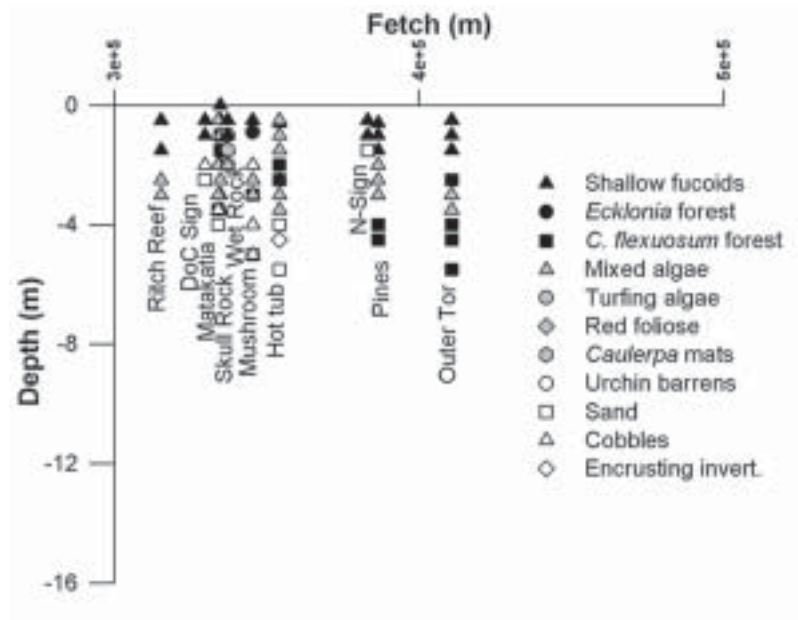
All sites generally clustered in the ‘M3’ group except Takatu (‘M1’) and P-Point (Fig. 5). The ‘M1’ and ‘M3’ groups (Appendix 3, Fig. A3.4(a, b)) exhibited the same bimodal pattern in algal biomass as sites at Leigh, with *C. maschalocarpum* dominating the shallow stratum and *Ecklonia* dominating the deepest strata. Urchins dominated the 4–6-m depth range and there was only a low biomass of *Ecklonia* and *C. flexuosum* (exposed variety). The main difference between Takatu and the sites in the ‘M3’ group was a higher biomass of red turfing algae in the shallow stratum. Gastropods occurred at relatively high densities, in particular, *Cantbaridus purpureus* and *Trochus viridis* in the deeper strata. *Micrelenchus* spp. was abundant but patchy in the shallow stratum at Takatu (Fig. A3.4(a)).

At P-Pt the reef was inundated with sand at c. 5 m, and apart from *Carpophyllum maschalocarpum* in the shallow stratum, the reef was relatively devoid of large brown macroalgae—probably due to the high numbers of urchins (Fig. A3.4(c)). P-Pt also differed from the other sites at Tawharanui, as it had high numbers of *Turbo smaragdus*.

3.2.5 Long Bay

The sites at Long Bay are all very sheltered with low-relief sandstone reefs. The reefs at the sites with higher wind fetch tended to extend deeper and were dominated by *C. flexuosum* forest (Fig. 10—note that the scale of fetch measurements are an order of magnitude lower than for other locations). Shallow *Carpophyllum* generally dominated to between 1 m and 2 m depth; below this, mixed algal habitat was common.

Figure 10. Habitat distributions for Long Bay 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. Note different fetch scale to other locations.



The sites at Long Bay were separated into two groups ('Sheltered 1' and 'Sheltered 2') based on the biomass of dominant algal groups (Figs 4 and 5). These groups generally reflected the maximum depth sampled; 'Sheltered 2' included three sites (N-sign, Matakatia and Ritch Reef) where the reef only extended to depths less than 2 m (Appendix 3, Fig. A3.5(b)), while 'Sheltered 1' included all the sites where the reef extended to 5 m (Fig. A3.5(a)). The < 2-m depth stratum for the 'Sheltered 2' group was dominated by *C. maschalocarpum* and other macroalgae were generally scarce. At the 'Sheltered 1' sites, a number of other large brown algal species were also common in the shallow stratum (e.g. *Ecklonia*, *C. flexuosum*, *C. plumosum* and *Sargassum sinclairii*). The 4–6-m depth range was dominated by *C. flexuosum* and the small brown algae *Zonaria turneriana*. Other large brown algae, including *Cystophora retroflexa*, *Ecklonia* and *Sargassum*, were also present. Red algae, with the exception of crustose and turfing corallines, were typically absent. *Evechinus* was rare at all sites. *Turbo smaragdus* was found at very high densities in the < 2-m stratum, and *Trochus* was abundant at 4–6 m. Both *Cookia* and *Cantharidus* were rare.

3.2.6 Hahei

Sites at Hahei were located across a broad wave exposure gradient, which was reflected by the large variation in algal communities (Fig. 5) and habitat distributions (Fig. 11). The most sheltered site (Mussell Rock) was dominated by shallow fucoids and *Carpophyllum flexuosum* forest. With increasing wave exposure, the occurrence of *C. flexuosum* forest declined and *Ecklonia* forest

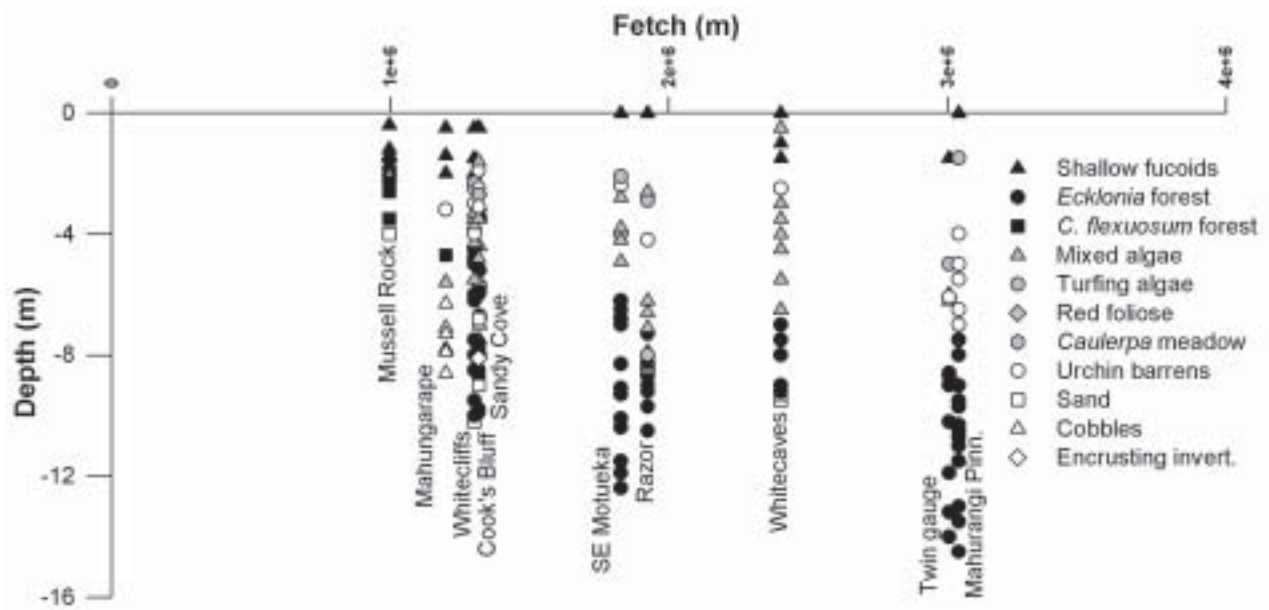


Figure 11. Habitat distributions for Hahei sites from transect data arranged according to total wind fetch at each site. Symbols indicate the habitat type assigned to points every 5 m along the transect line.

became prevalent, generally below 6 m. Mixed algae dominated at intermediate depths (2–6 m), although patches of turfing algae and urchin barrens also occurred at approximately 2–4 m. The extent of urchin barrens was greatest at the two most exposed sites, dominating between depths of 3 m and 8 m.

These broad differences in habitat distributions were reflected in the grouping of sites based on the biomass of the dominant algal species (Fig. 5). The majority of sites were located in the ‘Moderate’ group, except the two most sheltered sites—Mussell Rock and Mahungarape Island—which were in separate groups. The most exposed sites, on the eastern side of Mahurangi Island (Twin gauge and Mahurangi Pinn.), were grouped in ‘M1’, while the remaining sites were in the ‘M2’ group.

At the most exposed sites at Hahei (‘M1’), a bimodal algal distribution occurred, with *Carpophyllum angustifolium*, *C. maschalocarpum* and *Lessonia* dominating the shallow depth stratum, urchins dominating at 4–6 m, and *Ecklonia* at greater depths (Appendix 3, Fig. A3.6(a)). Short *C. flexuosum* (exposed morphology) and *Sargassum sinclairii* were common in the urchin barrens habitat. For the sites in the ‘M2’ group (Fig. A3.6(b)), the bimodal pattern was not as apparent, with *Ecklonia* dominating the 4–6-m depth stratum, despite moderate densities of *Evechinus*. At these sites, the urchin barrens habitat was generally restricted to a narrow band between 2 m and 4 m. Other species of large brown algae, including *C. maschalocarpum*, *C. plumosum*, *C. flexuosum* (sheltered morphology), *Xiphophora* and *Sargassum*, were interspersed with *Ecklonia* in the 4–6-m stratum. Understorey algal species were generally sparse (e.g. *Zonaria turneriana*, *Pterocladia lucida*, *Plocamium* spp. and *Sargassum*). However, the understorey flora at SE Motueka Island was more diverse than at other sites, and included *Halopteris* spp., *Pedobesia clavaeformis*, *Melanthalia abscissa*, *Callophyllis* sp., *Curdiea coriacea*, *C. codioides*, *Codium cranwelliae*, *Kallymentia berggenii* and *Carpomitra costata*. Herbivorous gastropods exhibited a similar pattern for both the ‘M1’ and ‘M2’ groups; *Cookia* were most abundant in the shallow depth strata (< 6 m), and *Trochus* were most abundant at greater depths.

The organisation of benthic communities at Mahungarape I. (Fig. A3.6(c)) was considerably different from other sites and, subsequently, they were grouped separately. The reef at this site was comprised of cobbles at depths greater than 5 m, where both large brown algae and urchins were absent. The shallow depth stratum (< 2 m) exhibited an unusually high biomass of red foliose (mainly *Pterocladia lucida*) and red turfing algae. In the 4–6-m depth stratum, urchins were common and the biomass of large brown algae (*C. maschalocarpum*, *C. flexuosum* and *Ecklonia*) was relatively low. High densities of *Cookia* were present in the 4–6-m stratum.

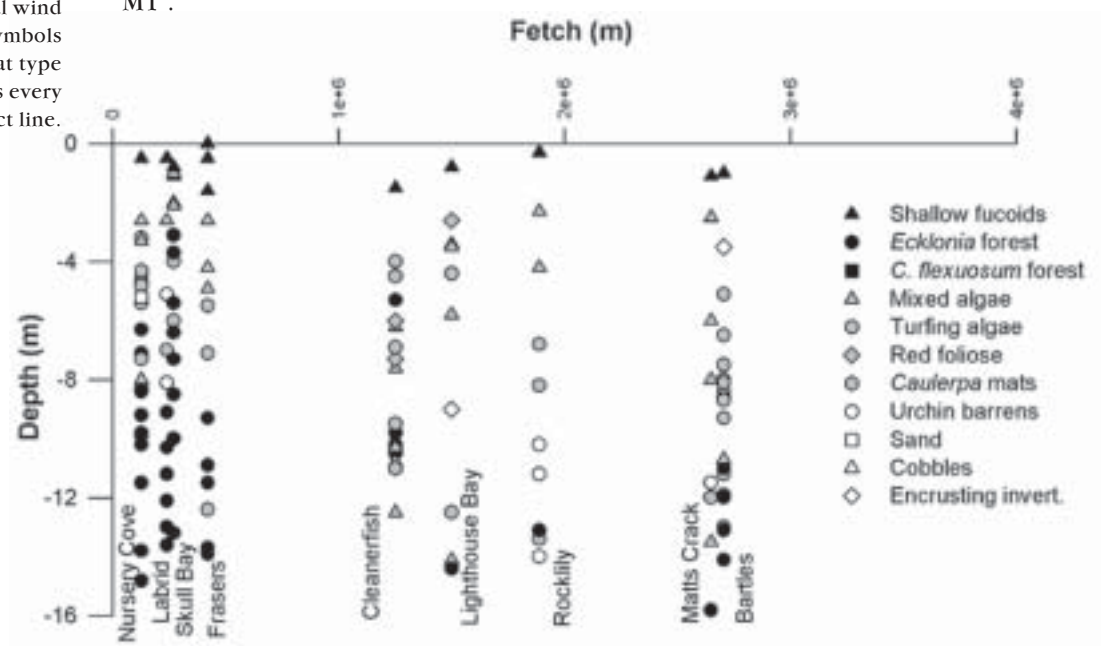
At Mussell Rock, the most sheltered site, *Carpophyllum maschalocarpum* and other fucallean algae, in particular *C. plumosum*, dominated the immediate subtidal (Fig. A3.6(d)) and *Ecklonia*, *Pterocladia* and *Zonaria* also occurred. This shallow *Carpophyllum* habitat graded into stands of large *C. flexuosum* plants, with low numbers of *Ecklonia* and *Sargassum* also being present. *Evechinus* occurred at low numbers and did not form urchin barrens. The herbivorous gastropod *Turbo smaragdus* occurred at low numbers.

3.2.7 Poor Knights Islands

Nine sites were sampled around the two main islands of the Poor Knights group, spanning a range of wave exposure conditions (Fig. 12). Shallow *Carpophyllum* habitat dominated the shallow stratum (< 2 m) at all sites and *Ecklonia* forest occurred at greater depths. The upper limit of *Ecklonia* forest tended to be deeper at the more exposed sites. Urchin barrens were not very common and, instead, the mid-depths were characterised by a mixture of turfing, mixed and red foliose algal habitats. *Caulerpa* mats were common at Nursery Cove and Cleanerfish Bay.

The Poor Knights Is sites were divided among three groups (Fig. 5), which were consistent with the differing wave exposure conditions (Appendix 3, Fig. A3.7). The four exposed sites on the eastern side of the islands (Lighthouse Bay, Rocklily Inlet, Matt's Crack and Bartle's Bay) were grouped in 'E1', Cleanerfish Bay (exposed to the northwest) fell in the 'E2' group, and the four most sheltered sites (Nursery Cove, Labrid, Skull Bay and Frasers Bay) were grouped together in 'M1'.

Figure 12. Habitat distributions with depth for Poor Knights Island's 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 shallow depth stratum at 'E1' sites was dominated by *C. angustifolium*, along with red turfing and red foliose algae, including *Pterocladia lucida*, *Rhodymenia* sp., *Osmundaria* and *Pachymenia crassa* (Fig. A3.7(a)). *Lessonia variegata*, coralline turf and red turfing algae dominated the 4–6 m stratum. Urchins were abundant in the deeper strata (7–9 m and 10–12 m), where coralline turf and red turfing algae dominated. Short *Ecklonia* plants (< 50 cm total length), along with patches of *C. maschalocarpum* and *Lessonia*, were also present. In some cases, urchin-grazed habitat was interspersed with *Ecklonia* to greater than 20-m depth; for example, at Matt's Crack. *Phacelocarpus labillardieri*, *Euptilota formosissima* and *Callopybllis* spp. were common understorey species beneath the *Ecklonia* forest canopy.

At Cleanerfish Bay, the shallow stratum (< 2 m) was dominated by *C. angustifolium* and red turfing algae, urchins were most abundant at 4–6 m, and *Ecklonia* dominated the deeper strata (7–9 m and 10–12 m) but was often interspersed with patches of *Caulerpa flexilis* (Fig. A3.7(b)). *Ecklonia* was patchily distributed in the 4–6-m stratum with red turfing algae (including *Gigartina macrocarpa*), red foliose algae (*Osmundaria*, *Placentophora colensoi*, *Pachymenia crassa*, *Nesophila hoggardii*) and the green alga *Ulva lactuca*.

For the 'M1' group, the shallow stratum (< 2 m) was dominated by a mixture of *C. angustifolium*, *C. maschalocarpum*, *Lessonia* and *Ecklonia* (Fig. A3.7(c)). Coralline turf, red turfing algae and red foliose algae (*Osmundaria*, *Pterocladia lucida*, *P. apillacea*, *Rhodymenia* spp. and *Melanthalia abscissa*) were also prominent. *Ecklonia* was dominant in all other strata, although patches of *C. plumosum* and the green alga *Caulerpa flexilis* were also common. Beneath the *Ecklonia* canopy a diverse understorey was present, including *Distromium scottsbergii*, *Carpomitra costata*, *Phacelocarpus labillardie*, *Delisea elegans*, *Melanthalia*, *Rhodymenia* sp., *Euptilota formosissima*, *Nesophila hoggardii*, *Plocamium* spp. and *Curdiea coriacea*. *Evechinus* were abundant in the two shallow depth strata (< 6 m) but absent from deeper strata.

The large sea urchin *Centrostephanus rodgersii* was commonly observed at the study sites but, in general, only low abundances were recorded (< 1 m⁻²). The highest densities were recorded at the Labrid site in the 7–9-m depth stratum where *Centrostephanus* occurred amongst the *Ecklonia* forest at densities of 2.0 ± 1.1 m⁻². Both herbivorous and predatory gastropods were rare at all sites.

3.2.8 Mokohinau Islands

The nine sites sampled at the Mokohinau Is were located around the Burgess Island group. Habitat distributions were variable among sites; however, the vertical extent of both urchin barrens and shallow *Carpophyllum* generally increased with increasing wave exposure (Fig. 13). The Pinnacle South site was an exception to this pattern, as *Ecklonia* forest occurred up to depths of 7 m. While this site had a high fetch, it is mainly exposed to the southwest and southeast, and is relatively protected from large northeasterly swells.

Six of the Mokohinau Is sites were located in the 'Moderate' group, House Bay was classified in the 'E1' group, and the most exposed sites (Puddingstone and Lighthouse Pt) were in the 'Exposed barren' group (Fig. 5). Of the 'Moderate' sites, Dragon, Lizard Island, Arches, Sentinel and Pinnacle were in the 'M1'

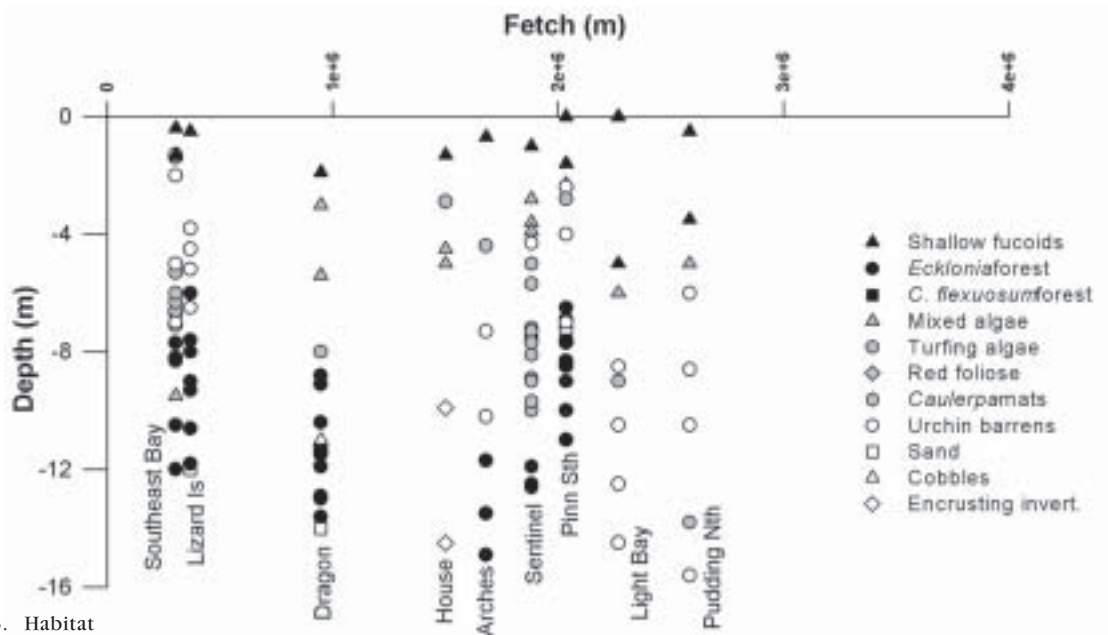


Figure 13. Habitat distributions for Mokohinau Island's sites from transect data arranged according to total wind fetch at each site. Symbols indicate the habitat type assigned to points every 5 m along the transect line.

group, while the most sheltered site, Southeast Bay, was grouped in 'M2'. At the most exposed sites, *C. angustifolium* dominated the shallow stratum with red turfing and red foliose algae (mainly *Pterocladia* and *Osmundaria*) (Appendix 3, Fig. A3.8(a, b)). At these sites *Lessonia*, coralline turf and red foliose algae dominated at 4–6 m. At greater depths, *Evechinus* were abundant and large brown algae were scarce, with crustose corallines, coralline turf, red turfing algae and *Ulva* dominating.

The most sheltered site—Southeast Bay—exhibited a pattern comparable to moderately exposed coastal locations, with *C. maschalocarpum*, *C. angustifolium*, *C. plumosum* and *Xiphophora chondrophylla* dominating the shallow stratum (< 2 m), *Ecklonia* dominating the deepest strata (7–9 m and 10–12 m), and high densities of urchins at 4–6 m (Fig. A3.8(d)). The 'M1' group (Fig. A3.8(c)) followed a similar pattern; however, *Lessonia*, red turfing and red foliose algae (*P. lucida*) were also common in the < 2-m stratum, urchins were also abundant and *Ecklonia* biomass reduced at 4–6 m and 7–9 m. *Ulva lactuca* was also abundant in the 4–6-m stratum. In the deeper strata, patches of *C. flexilis* were common amongst the *Ecklonia* forest and there was a relatively diverse range of understory species including *Zonaria turneriana*, *Carpomitra costata*, *Melanthalia abscissa*, *Euptilota formosissima*, *Plocamium* spp. and *Pedobesia clavaeformis*.

Low numbers of gastropods were recorded at all sites. *Cookia* and *Cellana* were generally the most abundant, together with *Modelia granosus* at Puddingstone and Lighthouse Pt (Fig. A3.8(d)).

3.2.9 Tuhua (Mayor Island)

The sites at Tuhua were mainly located on the northern side of the island and were all relatively exposed. Consequently, all had similar habitat distributions (Fig. 14). Shallow *Carpophyllum* habitat occurred to depths of between 3 m and 4 m and *Ecklonia* forest generally dominated below 10 m. Intermediate depths were largely dominated by urchin barrens and turfing algae, although mixed algal stands, red foliose algae and *Caulerpa* mats were also common.

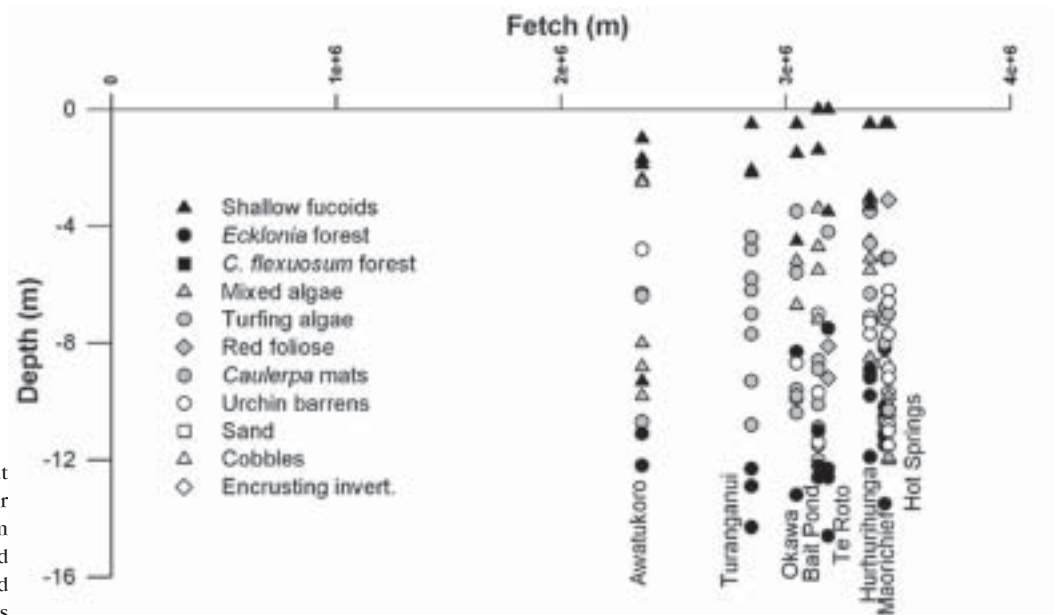


Figure 14. Habitat distributions with depth for Tuhua Island sites from transect data arranged according to total wind fetch at each site. Symbols indicate the habitat type assigned to points every 5 m along the transect line.

All sites sampled at Tuhua were divided into the two exposed groups—‘E1’ and ‘E2’ (Fig. 5). For all sites, algal communities in the < 2-m stratum were characterised by a high biomass of *C. angustifolium* (average density of $387 \pm 40 \text{ m}^{-2}$), a low biomass of *C. maschalocarpum* and a high biomass of red foliose algae (*Osmundaria*, *Pterocladia lucida*, and *Melanthalia*) and red turfing algae.

Evechinus was abundant at sites in the ‘E1’ group and occurred down to depths of 10–12 m (Appendix 3, Fig. A3.9(a)). Large brown algae were subsequently sparse in the 4–6-m and 7–9-m strata, with coralline turf, red turf, red foliose algae (mainly *Osmundaria*) and *Ulva* dominating. *Ecklonia* and coralline turf dominated the 10–12-m stratum. Large *C. flexuosum* plants, *Sargassum* and *Xiphophora* occurred at low numbers amongst the *Ecklonia*. The occasional *Cookia*, *Cellana* or *Modelia* were observed, but gastropods were generally rare.

At sites in the ‘E2’ group, *Evechinus* was only abundant in the 4–6-m stratum (Fig. A3.9(b)), co-occurring with patches of *C. maschalocarpum*, *Ecklonia*, *Cystophora retroflexa* and *Sargassum*. Turfing and red foliose algae (mainly *Osmundaria*) also occurred at a relatively high biomass. At 7–9 m, moderate numbers of urchins were interspersed with patches of *Ecklonia* forest, *C. plumosum*, red foliose algae and *Caulerpa flexilis*. *Ecklonia* dominated the 10–12-m stratum and achieved the highest biomass and density ($21.6 \pm 2.6 \text{ m}^{-2}$) recorded in this study. *Ecklonia* plants were generally tall (> 1 m total length) and had a relatively diverse understory including *Distromium skottsbergii*, *Zonaria turneriana*, *Carpomitra costata*, *Pedobesia clavaeformis*, *Osmundaria colensoi*, *Phacelocarpus labillardieri*, *Euptilota formosissima*, *Delisea elegans*, *Rhodymentia* sp. and *Plocamium* spp. *Lessonia variegata* was absent from all Tuhua sites sampled.

3.3 RELATIONSHIP BETWEEN ALGAL COMMUNITY STRUCTURE AND ENVIRONMENTAL VARIABLES

The observed grouping of sites suggested a strong relationship between the algal communities and environmental variables. CAP analysis revealed that for all depth ranges there was a significant relationship between algal communities and the environmental variables measured (Table 4). The general groupings of sheltered, moderate coastal and exposed offshore sites seen for all depths pooled (Fig. 5) were also apparent at each depth (Fig. 15A). The unconstrained ordinations of principal coordinate axes 1 and 2 are not shown as for all depths these exhibited very similar patterns to the plots of the first two canonical axes (Fig. 15A). This demonstrates that the unconstrained axis of maximum variation among sites (principal coordinate axis 1) is in the same direction as the constrained axis (canonical axis 1) that best fits the environmental data. The number of principal coordinate axes (m) included in the analyses ranged between 2 and 5 and explained 65–92% of the variation in the original dissimilarity matrix (Table 4). The correlations between the canonical axes and both environmental variables and individual algal species are shown graphically in Fig. 15B, C). Superimposition of these plots onto the ordination of algal communities (Fig. 15A) revealed which species and which variables were most responsible for the multivariate patterns.

3.3.1 Environmental variables

Strong relationships were apparent between environmental variables and algal communities and these reflected the patterns in community structure seen within and between locations (Fig. 15B). The environmental variables include a range of inter-related measurements that reflect the overall exposure of a site. Consequently, all depths are orientated in similar directions to one another in relation to the canonical axes. The environmental variables are strongly correlated with CA1 in the shallow strata (< 2 m and 4–6 m), with slope and sediment being negatively correlated and maximum depth, fetch and secchi depth being positively correlated. This axis therefore reflects the physical gradient from shallow sheltered coastal sites with high sediment to the more exposed coastal and offshore sites with higher water clarity and deeper reefs. This gradient was not as pronounced in the deeper strata (7–9 m and 10–12 m) and only secchi depth had a strong positive correlation with CA1. There was a strong correlation between *Evechinus* and CA2 for all depths except the < 2-m stratum where

TABLE 4. RESULTS FROM CAP ANALYSIS INVESTIGATING THE RELATIONSHIP BETWEEN ALGAL COMMUNITY DATA AND ENVIRONMENTAL VARIABLES. PROPORTION OF VARIATION EXPLAINED BY PRINCIPAL COORDINATES (PC) AXES 1 AND 2, THE NUMBER OF AXES USED IN CAP ANALYSIS (m) AND THE PROPORTION OF VARIATION EXPLAINED BY m PC AXES.

DEPTH RANGE	PC 1	PC 2	m	PROP. G	TRACE STATISTIC	δ_1^2
< 2 m	36.8	23.6	4	0.86	0.01	0.01
4–6 m	37.2	28.0	2	0.65	0.01	0.01
7–9 m	40.8	23.9	2	0.65	0.01	0.01
> 10 m	32.8	22.8	5	0.92	0.01	0.01

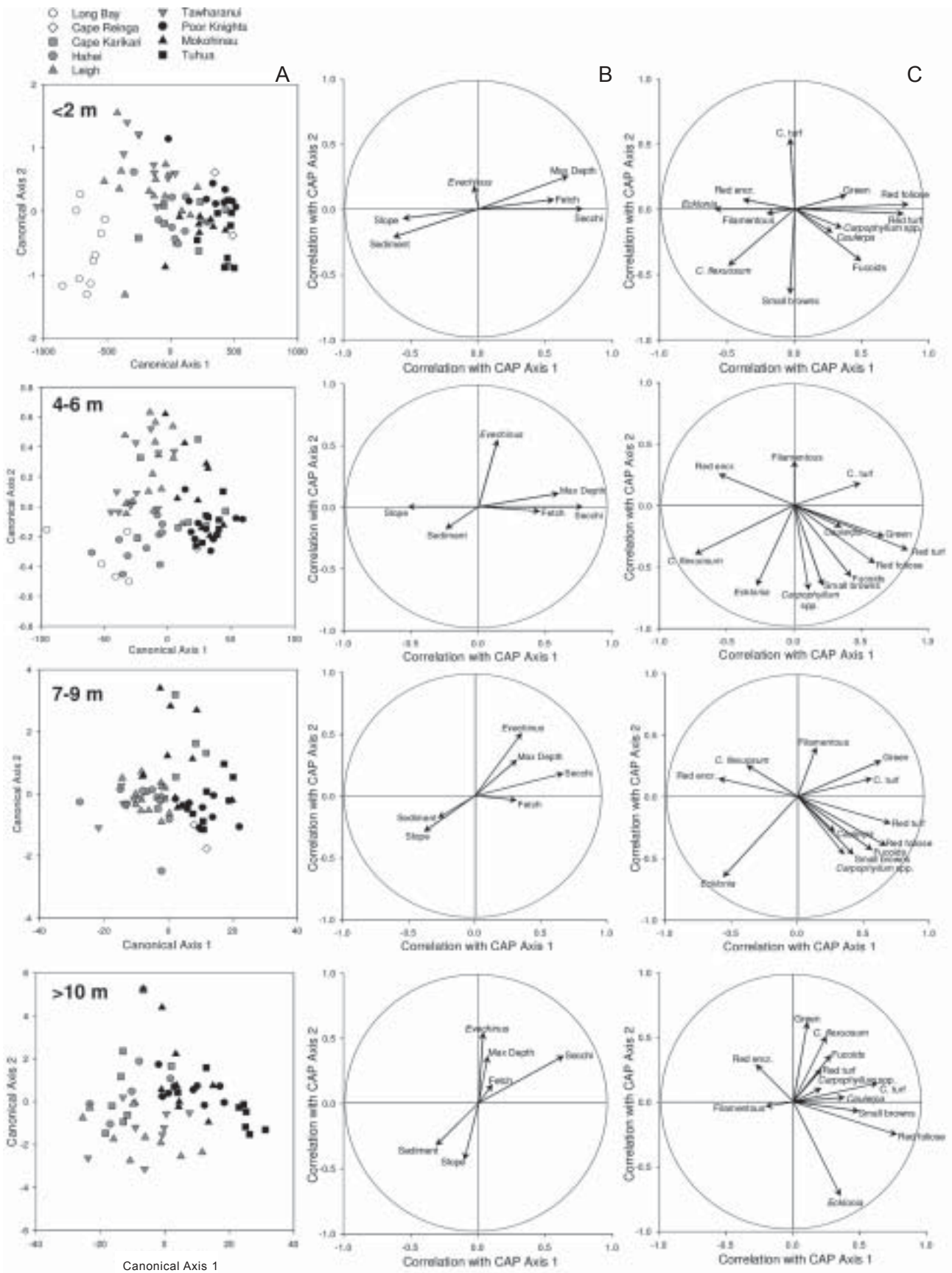


Figure 15. Constrained ordination (CAP) of algal community data (A) and correlations between the two canonical axes and environmental variables (B) and the original species variables (C).

Evechinus generally occurs at low numbers (Fig. 15B). The correlation between *Evechinus* and CA2 was strongest in the 4–6-m stratum and the direction is perpendicular to the other environmental variables. In the deeper strata, *Evechinus* tends to lie along the same axis as slope and maximum depth, i.e. at steeper sites *Evechinus* is an important contributor to the observed patterns.

3.3.2 Algal groups

In the shallow stratum (< 2 m) there was a strong negative correlation between CA1 and both *Ecklonia* and *C. flexuosum* (Fig. 15C). This reflects the higher biomass of these species at sheltered sites. In contrast, red turfing algae, red foliose algae and other large brown algal species such as *Lessonia*, were strongly positively correlated with CA1, reflecting their greater contribution at the more exposed and offshore sites. The same patterns are evident at 4–6 m, although both *Ecklonia* and *Carpophyllum* spp. show a strong negative correlation with CA2 which is consistent with the strong positive correlation between *Evechinus* and CA1. At greater depths (7–9 m and 10–12 m), *Ecklonia* showed the same pattern, with correlations occurring in an inverse direction to those of *Evechinus*. For these depths, red foliose algae, red turfing algae, coralline turf and, to a lesser extent, *Caulerpa* and other green algae, were correlated with secchi depth. At 10–12 m, the axes of *Evechinus* and *C. flexuosum* were orientated in the same direction. This can be explained by the occurrence of *C. flexuosum* (exposed morphology) in the urchin barrens habitat at some of the exposed sites, e.g. Pihoaka Pt.

4. Discussion

4.1 BIOGEOGRAPHIC PATTERNS AMONG LOCATIONS

At all study locations, the reefs were dominated by large brown algae, predominantly the laminarian alga *Ecklonia radiata* and the fucal *Carpophyllum maschalocarpum*. These were the most dominant species overall. *Carpophyllum flexuosum* generally only dominated at shallow sheltered reefs. However, the short exposed form of *C. flexuosum* (Cole et al. 2001) was also found in urchin-grazed areas at Cape Karikari and Tawharanui. At offshore islands, *Carpophyllum angustifolium* replaced *C. maschalocarpum* in the shallow subtidal (< 2 m).

The locations sampled in this study were located within Moore's (1949; 1961) Auckland algal province. More recently, the study area has been divided into two separate biogeographic regions—northeastern New Zealand and Cape Reinga-Three Kings Islands (Walls 1995). In the present study, while further geographical patterns in algal species assemblages are clearly discernable within the region (Fig. 3A), there was no evidence to suggest Cape Reinga was in a separate biogeographic region from the rest of the area. No difference in algal species composition was found between Cape Reinga and Cape Karikari,

and no algal or mobile macroinvertebrate species were found exclusively at Cape Reinga, which suggests that the two locations are in the same biogeographic region. There were some differences, though, between these two far north locations and the other locations sampled. Most obvious was the absence of *Carpophyllum angustifolium* at Cape Karikari and Cape Reinga. This species typically dominates the sublittoral fringe on exposed reefs throughout northeastern New Zealand, but its northerly range is restricted to about Cape Brett (Moore 1961). While a number of species were found only at Cape Karikari (e.g. *Perithalia calillaris*, *Caulerpa fastigiata* and *C. articulata*), the overall algal communities and dominant species were fairly typical of northeastern New Zealand.

The large brown algae *Landsburgia quercifolia* and *Lessonia variegata* were most common at the Cape Reinga sites and were both conspicuous components of the algal communities to depths of 12 m. While these species were also found at the offshore islands, they are generally more abundant at exposed locations further south, e.g. Wellington (N. Shears unpubl. data; Choat & Schiel 1982). The higher abundance of these species at Cape Reinga compared with other locations may be related to the high wave exposure at these sites (Choat & Schiel 1982). In general, *Lessonia* tends to have a rather patchy distribution. For example, *Lessonia* is absent from Tuhua and other offshore islands in the Bay of Plenty (Grange et al. 1992), but is present at islands closer to the coast e.g. Slipper Island (G. Nesbit pers. comm.), and at East Cape (C. Duffy pers. comm.).

Algal diversity was highest at the offshore islands and the northernmost locations—Cape Reinga and Cape Karikari. This may be explained by the influence of warmer, clearer water from the East Auckland Current (Heath 1985) at the northernmost locations and the offshore islands. Some species of algae (e.g. *Nesophila boggardii*, *Rhodymenia* spp.) were only found at the offshore islands where the water temperatures are raised by the seasonal influx of tropical water (Harris 1985). The Mokohinau Is tended to have lower algal species richness than other offshore islands and may be less influenced by the East Auckland Current (Heath 1985). Algal diversity was lowest at the most sheltered coastal sites (e.g. Long Bay) where, typically, there are higher levels of sediment and higher turbidity. The algal communities on these reefs were generally dominated by a few species of large brown algae (e.g. *Carpophyllum flexuosum*) and crustose coralline algae. Both fleshy red and green algal species were very rare on these sheltered reefs.

Mobile macroinvertebrates generally showed the opposite pattern to macroalgae with species richness being higher at coastal locations than at offshore islands, where many coastal species were rare, e.g. *Trochus viridis* and *Cantharidus purpureus*. However, the offshore islands and Cape Karikari had some warm temperate or subtropical species that were absent or rare at other coastal locations, e.g. the sea urchin species *Centrostephanus rodgersii* and *Heliocidaris tuberculata*.

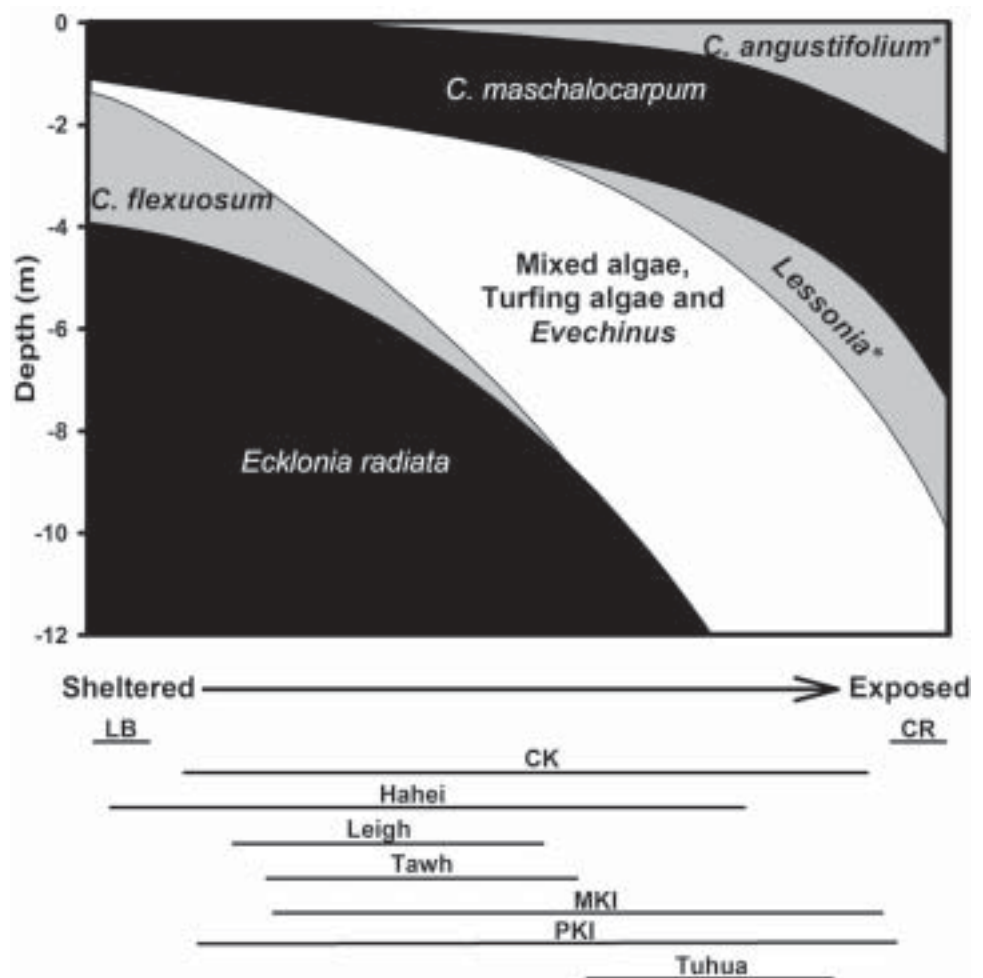
4.2 PATTERNS IN COMMUNITY STRUCTURE

A high degree of variability in algal community structure was apparent among the sites sampled. The grouping of sites based on algal community structure generally reflected the wave exposure of particular sites and whether they were located on the mainland coast or at offshore islands. Depth-related patterns in algal community structure were clearly apparent from sheltered to exposed sites both within and across the locations. These patterns are summarised in Fig. 16. While a similar pattern has previously been described from the inner to outer Hauraki Gulf (Grace 1983; Cole 1993; Walker 1999), the present study demonstrates that the pattern is present over a much greater geographic scale for northeastern New Zealand. Furthermore, we have shown that such variation in algal communities can occur across wave exposure gradients on much smaller spatial scales, e.g. within locations such as Cape Karikari and Hahei.

In general, the most sheltered coastal sites were characterised by shallow reefs that were inundated with sand at depths less than 5 m, e.g. all sites at Long Bay and at Mussell Rock at Hahei. At these sites, *Carpophyllum maschalocarpum* characteristically graded into tall mono-specific stands of *C. flexuosum* forest, with high levels of sediment at depths greater than 2 m. *Evechinus* was present at low densities and the urchin barrens habitat absent. This *Carpophyllum flexuosum*-dominated assemblage appears to be typical of shallow sheltered reefs in northeastern New Zealand, e.g. inner Hauraki Gulf (Grace 1983; Cole 1993; Walker 1999), the Bay of Islands (Brook & Carlin 1992) and Mimiwhangata (Ballantine et al. 1973). At the most sheltered sites at Cape Karikari (Koware South and CK4), *C. flexuosum* forest occurred in the 4-6-m stratum but gave way to *Ecklonia* at greater depths. Although not observed in this study, deeper water (> 10 m) stands of *C. flexuosum* occur on the sheltered side of the offshore islands, e.g. Poor Knight Is (Choat & Schiel 1982), Mokohinau Is (Cole et al. 2001) and Little Barrier Island (Walker 1999). Similar stands of *C. flexuosum* also appear to be relatively common in central (Gisborne, Kapiti Island, Wellington, Marlborough Sounds, Nelson (N. Shears unpubl. data)) and southern (Chatham Islands, Fiordland, Banks Peninsula (Schiel & Hickford 2001)) parts of New Zealand.

The majority of coastal sites sampled in this study were grouped into a 'Moderately exposed' group, which included most of the sites from Leigh, Tawharanui, Cape Karikari, Hahei and also the Mokohinau Is. The most sheltered sites from the Poor Knights Is were also included in this group. While there was a high degree of variability among sites within this group, these sites typically had a bimodal algal distribution with depth, consistent with that described by Choat & Schiel (1982) for moderately exposed sites in northeastern New Zealand. Briefly, fucaleans dominated from 0-3 m, with a low algal biomass zone grazed by urchins from c. 4-7 m and *Ecklonia radiata* forest at greater depths. Within this group, however, the vertical extent of these zones changed in relation to wave exposure (Fig. 16). At some of the most sheltered sites (e.g. at Hahei and Cape Karikari), large brown algae (*Ecklonia*, *C. maschalocarpum* and *C. flexuosum*) dominated the 4-6-m depth stratum and the bimodal algal distribution was not as apparent. Also, the most sheltered sites at the Poor Knights Is (Nursery Cove and Skull Bay) did not exhibit a bimodal algal distribution but, rather, mixed fucaleans and *Lessonia* grading

Figure 16. Schematic representation of depth-related patterns in algal community structure across a wave exposure gradient in northeastern New Zealand (After Ballantine et al. 1973 and Grace 1983). The approximate range of communities sampled is indicated for each location by a horizontal line.



*Both *Carpophyllum angustifolium* and *Lessonia* were not found at all localities (see Section 4.1 for details).

into *Ecklonia* forest at depths of 5 m. In contrast, at some of the more exposed sites in this group, in particular from Cape Karikari and the Mokohinau Is, the urchin-grazed zone extended to depths of c. 10 m. The most exposed sites from these locations, however, were grouped separately ('Exposed barren' group). At these sites, a band of *Lessonia* often occurred at 4–6 m, consistent with Choat & Schiel (1982). Beneath this, the urchin barrens habitat extended down to depths greater than 12 m. At Leigh and Tawharanui, urchin barrens were most common between c. 3 m and 7 m, whereas Choat & Schiel (1982) reported the urchin barrens habitat to be dominant from 5 m to 10 m. This apparent shift in the depth of algal biomass minima since the 1980s may be related to decadal-scale climate variation and a calmer wave climate in northeastern New Zealand since 1978 (R. Babcock unpubl. data).

The most exposed sites from the Poor Knights Is and all the Tuhua sites were grouped together ('Exposed' group). Depth-related patterns in biomass of large brown algae at the Poor Knights and Tuhua varied with wave exposure in a manner similar to those of coastal sites, but the Poor Knights and Tuhua sites had a much higher biomass of green, red foliose and turfing algae. While the vertical extent of the zone of high urchin densities and reduced algal biomass increased with wave exposure, this habitat was not typical of urchin-grazed areas at coastal locations. Despite relatively high urchin densities, this zone was often characterised by a relatively high biomass of coralline turf, red turfing and red

foliose algae, along with the green alga *Ulva lactuca* and, sometimes, patches of *Ecklonia* and *C. maschalocarpum*. The density of herbivorous gastropods at these offshore islands sites was very low compared with coastal sites. This may be due to offshore populations being recruitment-limited (Watanabe 1984), or due to the higher abundance of predatory wrasses at offshore islands (Willis & Denny 2000).

The Cape Reinga sites were also grouped with the offshore island sites, but the patterns in algal community structure with depth differed considerably from the other locations sampled. These were the most wave-exposed sites sampled in this study, and the organisation of algal communities reflected those described for other areas of high wave energy, e.g. Three Kings Is and Owhiro Bay (Wellington) (Choat & Schiel 1982). The bimodal depth distribution of algal biomass and the urchin barrens habitat were not present and *Evechinus* was restricted to small cleared areas amongst the algal stands. Instead, a continuous stand of *Ecklonia*, *C. maschalocarpum*, *Landsburgia quercifolia* and *Lessonia* were present down to c. 10 m. This is comparable to the algal assemblages at Kawerua on Northland's west coast (Dickson 1986). It is important to note, however, that the reefs sampled at Cape Reinga only extended down to a maximum depth of 11 m. If deeper reef were available, both the urchin barrens habitat and deeper stands of *Ecklonia*, characteristic of other locations, may have been present. For example, *Ecklonia* forest dominates at depths of 50–60 m at the Three Kings Is (Choat & Schiel 1982), approximately 30 nautical miles northwest of Cape Reinga. The *Ecklonia* present at Cape Reinga and at the most exposed sites at Cape Karikari had short stipes and long strap-like primary lamina. While this morphology differed from other locations sampled, it was consistent with that described from the Three Kings Is (Choat & Schiel 1982).

4.3 PROCESSES RESPONSIBLE FOR PATTERNS

Grazing by *Evechinus* is generally thought to be a major determinant of algal community structure on reefs in northeastern New Zealand (Andrew 1988; Shears & Babcock 2002). However, the importance of *Evechinus* appears to change in a complex and interactive way with depth and across environmental gradients. At the most exposed (Cape Reinga) and most sheltered (Long Bay) locations sampled in this study, *Evechinus* occurred at low numbers and did not appear to play an important role in structuring algal communities. At such locations where urchins do not exert a strong top-down control on algal communities, physical factors, demography and life history characteristics of individual species are generally thought to be the most important structuring processes (e.g. in southern New Zealand, Schiel & Hickford (2001)). However, at sites where *Evechinus* did appear to influence algal community structure, it was generally restricted to a relatively narrow depth range (Fig. 16). Algal communities in shallow and deeper parts of reefs are, therefore, determined by an interaction between physical factors and life histories of individual species. The mechanisms controlling these depth-related patterns seen within sites may also explain the large-scale pattern in urchin abundance seen among sites.

At shallow depths, the high water motion typically restricts sea urchins to crevices. Consequently, they have a reduced foraging efficiency (Lissner 1980). The effects of high water movement on urchins have, however, been shown to

occur to depths of 12 m (Cowen et al. 1982). The limiting effect of high water movement on sea urchins probably explains the greater width of the shallow *Carpophyllum* zone with increasing wave exposure seen in this study. At the most exposed sites (Cape Reinga), the *Carpophyllum* zone extended down to 10–12 m and urchins were generally cryptic.

While wave action may set the upper limit to urchin grazing, the factors setting the lower limit are poorly understood. The fact that the lower limit tends to increase with exposure suggests that it is set by some physical process. Andrew & Choat (1985) suggested that lower survival of juveniles at depth is a result of higher sedimentation levels. This hypothesis is consistent with the change seen across wave exposure gradients and may explain the very low numbers of urchins seen at the most sheltered sites where sedimentation is highest. Low abundances of urchins have been shown for other sheltered areas, e.g. Fiordland New Zealand (Villouta et al. 2001; Wing et al. 2003) and Chilean fiords (Dayton 1985). Such areas have been shown to have very low levels of recruitment (Wing et al. 2003), possibly due to reduced larval supply, larval sensitivity to low salinity or unsuccessful settlement in areas with a high sediment load. Other factors which may prevent urchins grazing deeper at more exposed sites may be the presence of the algae itself, e.g. higher levels of recruitment at greater depths may 'swamp' urchins (Reed & Foster 1984) or abrasion by algae may act as a physical barrier (Konar 2000).

4.4 CONCLUSIONS

Large variation in species composition and algal community structure was found on shallow subtidal reefs throughout northeastern New Zealand. These patterns were strongly related to the environmental characteristics of sites and, in general, reflected the gradient from sheltered coastal sites to more exposed coastal and offshore sites, rather than any clear latitudinal gradients. The influence of sea urchins on algal communities appeared to vary across environmental gradients among sites, but also within sites, with depth. The observed patterns in urchins and macroalgae with depth and from sheltered to exposed sites are broadly consistent with the hypothesis of Menge & Sutherland (1987) that the importance of biotic interactions changes across environmental gradients and that food-web complexity decreases with increasing stress. At both the most exposed and most sheltered sites, the biotic effect of sea urchin grazing appears to be minimal, and algal community structure is likely to be determined by interactions among the algal species present and environmental conditions. Further investigation is needed into the actual processes restricting urchins from particular sites and depths.

The variability within locations across environmental gradients observed in this study highlights the need to sample a sufficient number of sites within a locality in order to adequately describe the communities and develop hypotheses regarding the important structuring processes. There are very few reported examples of such gradients occurring in other parts of New Zealand.

5. Acknowledgements

The authors thank Robert Russell, Jarrod Walker and Clinton Duffy (Science & Research Unit, DOC, Hamilton) who provided invaluable diving assistance during the study. Drs Richard Taylor, Graham Edgar, Bill Ballantine and two anonymous referees provided valuable comments on this manuscript. Phil Bendle of the M.V. *Norseman* provided help and knowledge of the Poor Knights Is. Similarly, Brady Doak and Murray Birch skippered the R.V. *Proteus* to the Mokohinau Is. Dr Eduardo Villouta (Science & Research Unit, DOC, Wellington) provided valuable advice and software for calculation of wind fetch measurements. Other DOC staff: Peter Carter, Gillie and Roger at Hahei, and Alan Jones and Craig at Tuhua (Mayor Island) provided help with logistical support and local knowledge. The staff of the University of Auckland Leigh Marine Laboratory, particularly Arthur Cozens, provided logistical support. Dr. Wendy Nelson assisted with seaweed identification. This study was funded by the Department of Conservation (Science Investigation no. 2481).

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