Shallow subtidal reef communities at the Poor Knights Islands Marine Reserve after eight years of no-take protection

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ABSTRACT

The Poor Knights Islands Marine Reserve became completely no-take in 1998 resulting in large increases in populations of snapper *Pagrus auratus*. To investigate potential community-level effects of the increase in this predatory species, subtidal reef communities were surveyed at the Poor Knights in 2006 and compared with data from the first year of no-take protection (1999). Patterns were also compared with analogous data from Leigh and the Mokohinau Islands to place these in a regional context. A high degree of variability was found in shallow subtidal reef communities among the Poor Knights sites, which appeared to be related to differences in wave exposure among sites. For macroalgal species composition, macroalgal community structure, and sessile benthic communities there was no significant difference between the two surveys. Significant differences in the abundance and/or biomass of some key species were found between surveys. In particular, there was a doubling in the biomass of the canopy forming kelp *Ecklonia radiata* between years, which may explain some of the changes seen in a number of understorey taxa, in particular the decline in cover of red turfing algae, coralline turf and *Ulva* sp., and increase in crustose corallines, sponges, hydroids and bryozoans. There was no change in the abundance of the dominant sea urchin *Evechinus chloroticus* at the Poor Knights, but there was an increase in the extent of barrens habitat associated with the sea urchin *Centrostephanus rodgersii*. The patterns in *Ecklonia* and *Evechinus* populations reflected those seen at Leigh and the Mokohinau Islands over the same time period and appear to reflect region-wide variation rather than being associated with increased numbers of predators at the Poor Knights.

1. Introduction

With increasing awareness of human impacts on the marine environment the New Zealand government is currently implementing the Marine Protected Areas Policy and Implementation Plan (www.biodiversity.govt.nz/seas/biodiversity/protected/mpa_policy), which aims to increase the level of protection afforded to the marine environment in a network of representative marine protected areas by 2010. In general, however, our understanding of how whole ecosystems respond to marine reserve protection is poorly understood, and continued monitoring of marine reserves is necessary to better understand such effects and to set realistic objectives with regard to the outcomes of marine protection.

It has widely been shown throughout New Zealand that populations of species that are heavily targeted by commercial and recreational fishermen recover in marine reserves following the implementation of no-take protection, e.g., spiny lobster *Jasus edwardsii*, snapper *Pagrus auratus* and blue cod *Parapercis colias* (Kelly et al., 2000; Davidson, 2001; Davidson et al., 2002; Willis et al., 2003; Denny et al., 2004; Shears et al., 2006). These species are typically high level predators on shallow reefs and in some cases their recovery in marine reserves has lead to community level changes at lower trophic levels (Babcock et al., 1999; Shears & Babcock, 2002; 2003; Langlois et al., 2005; Langlois et al., 2006). There is a growing literature worldwide on how benthic communities change in temperate marine reserves following a recovery of large predatory species (Shears & Babcock, 2002; Lafferty, 2004; Guidetti et al., 2005; Micheli et al., 2005). In all of these cases, changes in macroalgal assemblages have been attributed to the effects of predators on sea urchin populations. Such indirect effects, or trophic cascades, however are not general to marine reserves throughout New Zealand (Shears & Babcock, 2004a).

The Poor Knights Islands are located 24 km of the northeastern coast of northeastern New Zealand (Fig. 1) and are influenced by the East Auckland Current (Stanton et al., 1997) which brings a subtropical element to the flora and fauna of the island's surrounding habitats (Ayling & Schiel, 2003). The Poor Knights Islands Marine Reserve was established in 1981 with the aim of protecting reef fish. However, with the exception of two small no-take areas, restricted recreational fishing was allowed around the majority of the island group up until October 1998 when the area became fully no-take. Since no-take protection was implemented in 1998 there has been a large and rapid increase in the abundance of snapper *Pagrus auratus* (Denny et al., 2003; Denny & Shears, 2004; Denny et al., 2004), the most heavily targeted recreational and commercial fish species throughout northeastern New Zealand. The abundance of other species has been variable since no-take protection was initiated and in some cases declines in a number of non-target species may be related to climatic effects, or possibly due to competitive or predatory interactions with snapper (Denny & Shears, 2004). To date the response of other communities or habitats to no-take protection at the Poor Knights have not been investigated.

Shallow subtidal reef communities at the Poor Knights are typical of offshore islands in northeastern New Zealand, being dominated by Laminarian (e.g., *Ecklonia radiata* and *Lessonia variegata*) and Fucalean algae (e.g., *Carpophyllum* spp., *Landsburgia quercifolia* and *Sargassum sinclairii*), with the sea urchin *Evechinus chloroticus* also being common (Choat & Schiel, 1982; Schiel, 1984; Shears & Babcock, 2004b). The subtropical sea urchin *Centrostephanus rodgersii* is also common at this offshore location (Shears & Babcock, 2004b). A comparison between subtidal reef communities at the Poor Knights and the fully-fished Mokohinau Island's in 1999 found higher *Ecklonia* biomass and lower densities of exposed *Evechinus* at the Poor Knights (Shears & Babcock, 2004a). While these differences were consistent with a trophic cascade effect, whereby potentially higher predator abundances at the Poor Knights could have suppressed *Evechinus* numbers allowing an increase in *Ecklonia* biomass, the Poor Knights had only been no-take for less than one year and such effects have been shown to take greater than 15 years (Shears & Babcock, 2003). Instead, Shears & Babcock (2004a) suggested that these differences were most likely due to variation in the environmental conditions and ecology of the two areas, and further monitoring was needed to better understand how reef communities would respond to no-take protection at the Poor Knights.

In the present study the sites at the Poor Knights Islands Marine Reserve, surveyed by Shears & Babcock (2004a, b), were resurveyed to investigate changes in subtidal reef communities and key species (e.g., *Ecklonia* and *Evechinus*) between 1999 and 2006. Data were also compared with analogous time series data from monitoring sites at Leigh (reserve and non-reserve sites) and the Mokohinau Islands (Fig. 1) to assess whether potential changes reflect region wide variation over this time period, or alternatively are consistent with the increased numbers of predators (primarily snapper) at the Poor Knights after 8 years of no-take protection.

2. Methods

2.1 SAMPLING PROCEDURE

The nine sites sampled at the Poor Knights in June 1999 (Fig. 1) were resurveyed in June 2006 using the exact same sampling procedures (described in detail in Shears & Babcock, 2004b). In summary, the depth distribution of habitat types (as defined by Shears et al., 2004) were recorded at 5 m intervals along a line transect run perpendicular to the shore at each site, and benthic communities were quantified using five haphazardly placed 1m^2 quadrats within each of four depth ranges (0-2, 4-6, 7-9 and 10-12 m). Within each quadrat all large brown macroalgae were counted and measured, while the percent cover of smaller algal species was estimated. Red algal species less than 5 cm in height or length were divided into the following groups: crustose corallines, coralline turf, red encrusting algae, and red turfing algae. The percent cover of sediment, bare rock and other sessile forms (e.g., sponges, bryozoans, hydroids, ascidians and anemones) were also estimated in each quadrat. Counts and measurements of all mobile macroinvertebrates species (e.g., *Evechinus* and *Centrostephanus*) were also made.

Site positions and descriptions are given in Shears & Babcock (2004b) and a pdf file including photos of the sites and diagrams of exact site positions is available from the Department of Conservation’s Whangarei Area Office or from the author.

2.2 MULTIVARIATE ANALYSES

2.2.1 Macroalgal assemblages

Analysis on macroalgal community data was carried out separately on (1) presence-absence data to investigate variation in species composition, and (2) on fourth-root transformed biomass data to investigate variation in community structure. Biomass was calculated for each species or group using length-weight relationships for large brown algae and percent cover-weight relationships for smaller species and groups as in Shears & Babcock (2004b).

Variation in macroalgal species composition and structure among sites and between years was investigated using principal coordinates analysis based on Bray-Curtis similarities (using the PCO program, Anderson, 2003). The original species variables were also correlated with principal coordinates axes, and the correlation coefficients plotted as bi-plots, to give an indication of the relationship between individual species and the multivariate patterns. Differences in algal communities between years and sites were then tested using non-parametric multivariate analysis of variance (NP-MANOVA) (Anderson, 2001) based on Bray-Curtis similarities. Year was treated as a fixed factor and Site as a random effect.

2.2.1 Sessile benthic assemblages

Differences between sites and years in sessile benthic assemblages were investigated using the same procedure as for macroalgae (PCO and NP-MANOVA). Fourth-root transformed percent cover data for 19 sessile benthic groups were used in this analysis. Macroalgae species made up eleven of these groups, along with six encrusting invertebrate groups (sponges, bryozoans, hydroids, ascidians, cup corals and anemones) and two physical groups (sediment and bare rock).

2.3 UNIVARIATE ANALYSES

Differences in key macroalgal and macroinvertebrate species, and dominant sessile groups, were investigated between years, depths and sites with mixed model analysis using the GLMMIX macro in SAS (Littell et al., 1996). Year and Depth range were treated as fixed factors and Site as a random factor. Models were back-fitted by sequentially removing non-significant interaction terms. In some cases, Depth range was removed from the analysis as models would not converge for species with highly restricted depth distributions, e.g., *Carpophyllum angustifolium*. Count and biomass data were modelled using a Poisson distribution, while percent cover data were modelled using a binomial distribution. Ratios of effect sizes were calculated from the model along with 95% confidence limits (Note: confidence limits are asymmetrical as they are calculated on the log-scale).

2.4 REGIONAL ANALYSES

Patterns in *Ecklonia* biomass and *Evechinus* abundance at the Poor Knights were compared with data from four monitoring sites inside and outside the Cape Rodney to Okakari Point Marine Reserve at Leigh (Shears & Babcock, 2003), and four sites at the Mokohinau Is (Lighthouse Point, Lizard Is, Southeast Bay and Sentinel South; Shears & Babcock 2004a). Sampling in these locations was carried out in 1999 and in 2006, with some intermittent sampling between these years. The same methods were used in each location however sampling at Leigh was restricted to the 4-6 m depth stratum, while at the Mokohinau Islands sampling was carried out at 4-6 and 7-9 m. Mixed model analysis (GLMMIX) was carried out separately for each depth range to test for differences in *Ecklonia* biomass and *Evechinus* abundance between Area's (Poor Knights, Mokohinau's, Leigh Reserve (4-6 m only), Leigh Non-reserve(4-6 m only)) and Year's (1999 and 2006), while Site (Area x Year) was treated as a random effect.

3. Results

3.1 EXTENT OF HABITAT TYPES

The distribution of habitat types was highly patchy and varied down the depth gradient at each site (Appendix 1). *Ecklonia* forest was the dominant habitat type (covering ~35% of the reef, Fig. 2) and typically dominated at depths greater than 8 m, while a variety of other habitat types (e.g., Shallow *Carpophyllum*, Mixed algal habitat, Red foliose algal habitat, Turfing algal habitat, and Urchin barrens) dominated at shallower depths

(Appendix 1). At the more sheltered sites (e.g., Skull Bay, Nursery Cove) *Ecklonia* forest extended up into 3-5 m of water.

The overall extent of each habitat type remained relatively stable between the two surveys (Fig. 2), with the exception of turfing algal habitat which was more extensive in 1999 and urchin barrens which were higher in 2006. The increase in urchin barrens was most apparent at Bartles Bay over a large area of reef (6-10 m depth) that was predominantly classified as turfing algae in 1999 (Appendix 1). At Frasers and Cleanerfish there was an increase in the extent of barrens at 10-12 m, in areas that were classified as *Ecklonia* forest in 1999. These barrens areas, however, were solely associated with the sea urchin *Centrostephanus rodgersii* rather than *Evechinus*.

3.2 MACROALGAE ASSEMBLAGES

3.2.1 Macroalgal community analysis

A total of 44 macroalgal taxa were recorded during benthic monitoring at the Poor Knights in 1999 and 2006 (Table 1). The total biomass of macroalgae appeared to increase between 1999 and 2006 (Table 1), but this increase appeared largely due to an increase in the biomass of the stipitate kelp *Ecklonia radiata* (Section 3.2.2). *Ecklonia* was the dominant macroalgal species in both years, typically accounting for over half of the total macroalgal biomass. *Carpophyllum angustifolium* was the second greatest contributor to overall macroalgal biomass, while other large brown algae such as *Lessonia variegata*, *C. maschalocarpum*, *Xiphophora chondrophylla*, *C. plumosum*, *Landsburgia quercifolia* and *Sargassum sinclairii* were common in both surveys but each made up less than 5% of the total biomass. The large brown alga *Carpophyllum flexuosum* was relatively common in 1999, occurring in ~8% of the quadrats sampled, but rare in 2006 (<2%).

Red turfing algae (<5 cm in height), such as *Gigartina macrocarpa* and *Champia novaezealandiaea*, were very common in both surveys, but their average biomass and incidence, appeared to decline between 1999 and 2006 (Table 1). Coralline turf and crustose corallines were also highly common in both surveys and were important contributors to macroalgal biomass. A number of red foliose algal species were also common in both surveys, e.g., *Osmundaria colensoi, Pterocladia lucida, Nesophila hoggardii, Pachymenia crassa, Curdiea coriacea, Euptilota formosissima*, *Plocamium* sp. and an undescribed species of *Rhodymenia* (previously only recorded at the Three Kings Island's; W. Nelson pers. comm.). *Ulva* sp. was the most common green alga recorded however the mean biomass of this species was considerably lower in 2006. The green algae *Caulerpa flexilis* and *Codium convolutum* were also common in both surveys.

There was a general gradient in both macroalgal species composition and community structure among sites which appeared to be associated with the spatial distribution of sites (Fig. 3). Sites located on the more sheltered western side of the island were clustered on the left of the ordination and sites on the more wave-exposed eastern side on the right. The correlations between species and PC1 reflected this gradient, with species such as *C. plumosum*, *Distromium scottsbergii*, *Phascelocarpus labillardieri*, *Rhodymenia* sp., *Delisea compressa*, *Euptilota*, *Codium cranwelliaea* being more typical of western sites, while *C. angustifolium*, *Xiphophora*, *Landsburgia*, *P. crassa*, and *Caulerpa geminata* were more characteristic of eastern sites. There was also a separation between northern (Cleanerfish, Skull, Light and Rocklily) and southern (Nursery, Labrid, Frasers, Matts and Bartles) sites along PC2 based on macroalgal community structure (Fig. 3).

The spatial variation in algal species composition (presence-absence) and community structure (fourth-root transformed biomass) among sites appeared consistent between both surveys (Fig. 3), and no significant difference was found between years (Table 2). There was, however, a highly significant difference between sites and a significant interaction between year and site, indicating that the effect of year varied among sites. This was reflected by pair-wise tests which revealed significant differences between the two years for a number of sites (species composition: Nursery, Rocklily and Skull, community structure: Nursery, Rocklily, Skull, Labrid and Light).

3.2.2 Dominant macroalgal species and groups

Ecklonia radiata was the dominant large brown algae across all sites, however, there was considerable variation in the depth distribution in *Ecklonia* biomass among sites (Fig. 4, Table 3(a)). This variation appeared to be related to wave exposure, with *Ecklonia* occurring across all depths at sheltered sites, particularly Skull and Nursery, but generally being restricted to deeper water at exposed eastern sites (e.g., Matts, Bartles, Rocklily and Light) (Fig. 4). *Ecklonia* biomass was 2.3 (95% confidence limits (CL_{95}) = 1.9, 2.8) times higher in 2006, and this effect was consistent across all sites and depths (Table 3(a)). Analysis of *Ecklonia* count data revealed the same patterns, but the overall difference between years was not as great with a 1.7 (CL_{95} = 1.4, 2.0) fold increase in abundance (Table 3(a)). This increase in *Ecklonia* abundance was apparent across the whole size range of *Ecklonia* (Appendix 2). However, the greater magnitude of increase in biomass compared to counts could be attributed to an increase in the numbers of large *Ecklonia* plants (>60 cm total length) at a number of sites, e.g., Matts, Rocklily, Light and Labrid.

Carpophyllum angustifolium was generally restricted to the shallow depth stratum (Fig. 4), which meant the effect of depth could not be tested (Table 3(a)). The biomass of *C. angustifolium* was lowest at the most sheltered sites, however the effect of site was only marginally significant (p=0.059). There was also a marginally significant effect of Year (p=0.074) on *C. angustifolium* biomass, however, count data suggested a 1.6 (CL_{95} = 1.1, 2.5) fold increase between years (Table 3(a)). The biomass and abundance of *C. maschalocarpum* also increased between years by ~1.5 (CL_{95} = 1.2, 1.9) times. *C. maschalocarpum* only occurred in the shallow depth stratum at sheltered sites, but was more common in deeper strata at more exposed sites (Fig. 4). *Lessonia* exhibited similar patterns with depth and wave exposure, but was highly variable among sites and the effects of depth could not be tested. There was no difference in *Lessonia* biomass or counts between years (Table 3(a)).

The biomass of the four most common red foliose algal species among sites and depths is given in Fig. 5. *Osmundaria* and *Nesophila* were found across all depths, while

Pterocladia and *Rhodymenia* sp. (Three Kings) were generally restricted to the shallow stratum and the effect of depth could not be tested. A deeper water variety of *Pterocladia lucida* was common but occurred in low biomass at 10-12 m at some sites. All species were highly variable among sites and depths and either had a significant Site effect or Site x Depth range interaction (Table 3(a), Fig. 5). Both *Nesophila* and *Rhodymenia* increased significantly between 1999 and 2006, *Nesophila* by 6.5 (CL_{95} = 3.4, 12.2) times, and *Rhodymenia* by 1.9 (CL_{95} = 1.1, 3.3) times. The effect of Year varied with Depth range for *Nesophila* (Table 3(a)), which was apparent by the large increase in biomass between years in the 10-12 m depth stratum (Fig. 5). On average, for all red foliose algae there was a 2.2 (CL_{95} = 1.4, 3.3) fold increase in biomass between 1999 and 2006, and this effect varied with depth (Table 3(a)).

Among the smaller algal groups, red turfing algae, coralline turf, crustose corallines and *Ulva* sp. were the greatest contributors to overall algal biomass (Table 1, Fig. 6). Each of these groups were found across all depths, had a significant Site x Depth range interaction, and varied significantly between years (Table 3(a)). Red turfing algae, coralline turf, and *Ulva* sp. exhibited similar patterns across sites, having high biomasses in shallow strata at sheltered sites, and deeper strata at more exposed sites, while crustose corallines were ubiquitous across all depths at all sites (Fig. 6). Both crustose corallines and *Ulva* had a significant three-way interaction between Year, Depth and Site, however, on average the biomass of crustose corallines increased between years, and *Ulva* declined by 4.0 (CL_{95} = 1.4, 11.7) times (Fig. 6). The biomass of red turfing algae declined by 2.1 (CL_{95} = 1.4, 3.1) times and coralline turf by 1.3 (CL_{95} = 1.1, 1.5) times.

3.3 SESSILE BENTHIC ASSEMBLAGES

3.3.1 Benthic community analysis

Sessile benthic forms recorded during quadrat sampling were grouped into 19 structural groups (Table 4). Crustose coralline algae (CCA) were clearly the dominant structural form, found in all quadrats and on average covering greater than 40% of the reef. The cover of CCA increased between 1999 and 2006 (Table 4) and as seen above this resulted in a significant increase in CCA biomass (Table 3 (a)). Red turfing algae, coralline turf and *Ulva* sp. were also dominant forms, but their incidence, cover and biomass declined between years (Table 3(a) and 4). In contrast the cover and incidence of a number of sessile invertebrate groups appeared to increase between years, e.g., sponges, bryozoans, hydroids and anemones (these patterns are tested in Section 3.3.2).

Sessile benthic assemblages did not exhibit a clear spatial gradient among sites, as seen for macroalgal communities (Fig. 7). Instead, the variation along PC1 appeared to reflect a shift in the assemblages for most sites between 1999 and 2006. This shift from the right to left of the ordination was reflected by the correlations between structural group variables and the principal coordinates axes (Fig. 7). Structural groups positively correlated with PC1 were generally more common in 1999, e.g., coralline turf, red turfing algae and *Ulva*, while groups negatively correlated tended to have higher covers in 2006, e.g., anemones, cup corals (*Monomyces rubra*), brown encrusting algae, sponges, bryozoans and hydroids (Fig. 7). Despite the apparent differences in benthic assemblages between years (Fig. 7), there was only a marginally significant difference between years (p=0.09). There was, however, a highly significant interaction between Year and Site (Table 2(c)), indicating that sites varied differently among years.

3.3.2 Dominant sessile groups

Macroalgal groups were typically the dominant primary substratum cover (Table 4), and variation among sites and depths for these groups is shown in (Fig 6) and was tested in Section 3.2.2 (Table 3(a)). Sponges, hydroids, ascidians and bryozoans were also important substratum covers, and were found at all sites across all depths (Fig. 8). There was a significant Site x Depth range interaction for hydroids and bryozoans (Table 3(b). Hydroids were generally more common in the shallow stratum at sheltered sites, but most common in the 4-6 m stratum at the more exposed sites. Bryozoans, however, had the greatest cover in the deeper strata at sheltered sites (Fig. 8). There was no clear variation in the cover of sponges or ascidians among sites with depth.

Sponges and bryozoans increased significantly between years (Fig. 8, Table 3(b)), while hydroids had a significant Year x Site interaction, indicating the effect of Year varied among sites. In general, hydroids appeared to increase at all sites except Light (Fig. 8). There was a significant Year x Depth range interaction for ascidians, and the cover of this group appeared to decline in the shallow stratum and increase in the deeper strata between years (Fig. 8). The cover of anemones also increased significantly between 1999 and 2006 (Table 3(a)), but data are not presented.

Sediment was also an important component of the benthos (Table 4) and increased in coverage with depth across all sites (Fig. 9). There was clear variation between sheltered (high sediment) and exposed (low sediment) sites and subsequently a significant Site effect (Table 3(b)). There was no overall effect of year on sediment cover, but a significant interaction between Year and Depth range. The cover of sediment appeared to decline at 4-6 m and increase in coverage at 7-9 and 10-12 m between years (Fig. 9).

3.4 MOBILE MACRO-INVERTEBRATES

Twenty-one species of mobile macro-invertebrates were recorded during the 1999 and 2006 (Table 5). However, with the exception of the sea urchins *Evechinus chloroticus* and *Centrostephanus rodgersii*, the total numbers of other mobile macroinvertebrate species were very low (Table 5) preventing community analysis or tests of differences between years for those species.

Evechinus was clearly the dominant mobile macroinvertebrate species at the Poor Knights, making up ~90% of the total counts for all macroinvertebrate species in both years (Table 5). Total *Evechinus* abundance was variable across sites, depths and between years (Table 3(c)). In general, *Evechinus* were more abundant in deeper strata at exposed sites, while at more sheltered sites they were restricted to the shallow stratum (Fig. 10). This variation in depth distribution among sites was reflected by the significant interaction between Site and Depth range (Table 3(c)). Overall there was no change in *Evechinus* abundance between 1999 and 2006. When analyses were carried out separately for exposed and cryptic *Evechinus*, the results were broadly consistent with a highly significant interaction between Site and Depth range (Table 3(c)). There was, however, weak evidence for an increase in cryptic *Evechinus* ($p=0.078$) between years.

The size distribution of *Evechinus* populations also remained relatively stable across all sites between 1999 and 2006 (Appendix 3). However, the relative proportions of cryptic and exposed urchins appeared to change at some sites, e.g., the number of cryptic urchins recorded increased across most size-classes at Matts and Rocklily.

Centrostephanus rodgersii was recorded in comparatively low numbers compared to *Evechinus* (Fig. 10). The highest abundances were recorded in the 7-9 and 10-12 m strata but the low numbers recorded in shallow strata prevented analysis of a depth effect. No clearly significant difference in *Centrostephanus* abundance was detected between sites, or between years (Table 3(c)). However, almost double the numbers of *Centrostephanus* were recorded in 2006 than in 1999 (Table 5).

3.5 TEMPORAL VARIATION IN *ECKLONIA* AND *EVECHINUS* AT A REGIONAL SCALE

Data on *Ecklonia* biomass and *Evechinus* abundance from the Poor Knights are compared with data collected from Leigh (Reserve and Non-reserve) and the Mokohinau Island's over the same time period in Fig. 11. On average *Ecklonia* biomass increased by 5.7 (CL_{95} = 1.6, 20.1) times in the 4-6 m depth stratum between the 1999 and 2006 surveys across all areas (Fig. 11(a), Table 6(a)). There was also a significant difference between area's, with *Ecklonia* biomass at the Poor Knights being comparable to that found in the Leigh Reserve area (p=0.329), but significantly higher than *Ecklonia* biomass at the Mokohinau Is (p=0.011) and Leigh Non-reserve area (p=0.032). At 7-9 m there was no difference between the Poor Knights and the Mokohinau Is, and only weak evidence (p=0.08) for an increase in *Ecklonia* biomass between 1999 and 2006 (Fig. 11(b), Table 6(b)). In general *Ecklonia* biomass was highly variable in 2006 but the time-series data from the Mokohinau Is suggested and increasing trend in biomass prior to this.

The abundance of *Evechinus* at 4-6 m also varied between the 1999 and 2006 surveys, increasing by 1.7 (CL_{95} = 1.6, 20.1) times across all areas (Fig. 11(a), Table 6(a)). *Evechinus* abundance also differed between areas; there was no difference in abundance between the Poor Knights and Leigh Reserve (p=0.549), but abundances were significantly lower at the Poor Knights than the Mokohinau's (p=0.002) and Leigh Non-reserve (p=0.033). In the 7-9 m stratum, no significant difference was detected in *Evechinus* abundance between 1999 and 2006 or between Areas (Table 6(b)), although the densities appeared higher at the Mokohinau Is sites (Fig. 11(b)). There was no difference in the abundance of exposed *Evechinus* between 1999 and 2006 for both depths, but there was a significant difference between areas for the 4-6 m. On average, the abundance of exposed *Evechinus* at Leigh Non-reserve and the Mokohinau Islands were 4.9 (CL_{95} = 1.8, 13.3) and 4.7 (CL_{95} = 1.7, 12.9) times higher than at the Poor Knight, while there was no difference between the Poor Knights and the Leigh Reserve.

4. Discussion

4.1 VARIATION IN REEF COMMUNITIES BETWEEN 1999 AND 2006

The Poor Knights Islands Marine Reserve became completely no-take in 1998, which has resulted in a dramatic change in reef fish assemblages (Denny et al., 2003), in particular resulting in a large and rapid increase in the abundance of the predatory fish snapper (Denny et al., 2004). In contrast, there appears to have been comparatively less change in shallow subtidal reef communities after 8 years of no-take protection. Overall, there was no significant variation in macroalgal species composition (presence-absence 44 species groups), macroalgal community structure (fourth-root transformed biomass off 44 species groups), and sessile benthic assemblages (percent cover of 19 sessile groups) between June 1999 (8 months after implementation of no-take status) and June 2006. There was however high variation among sites, and in some cases sites varied between the two surveys (as indicated by a significant site and year interaction). The greatest variation in benthic communities appeared to be related to differences in wave exposure among sites, in particular differences between the exposed eastern and sheltered western side of the island. Based on comparisons of algal community structure with other northeastern New Zealand sites, Shears & Babcock (2004b) divided the nine Poor Knights sites into three groups; a moderately exposed group (Skull, Nursery, Labrid and Frasers); an exposed group (Light, Rocklily, Bartles and Matts); and Cleanerfish Bay which formed its own group. This spatial variation in communities, in relation to wave exposure around the

Poor Knights, remained consistent between 1999 and 2006. Similarly, there was also considerable variation among sites in the abundance and/or biomass of key species that appeared to be strongly related to wave exposure, e.g., *Ecklonia radiata*, *Carpophyllum angustifolium*, *C. mascahlocarpum*, *Lessonia variegata*, and also the sea urchin *Evechinus chloroticus*. For most of these species this was reflected by a significant site x depth interaction, whereby the depth distribution of these species varied with wave exposure. These broad patterns in the abundance and/or biomass of key species with depth and among sites also remained consistent between years.

While overall assemblages were generally stable between surveys, there was some variation in the abundance and biomass of key macroalgal species and groups, and also some sessile benthic forms, between surveys. Overall macroalgal biomass increased greatly between the two surveys, and this was largely due to a doubling in biomass of the kelp *Ecklonia*, the dominant macroalgal species in both surveys. Despite this increase in biomass, the overall extent of *Ecklonia* forest did not vary between the two surveys and the increase in biomass appeared to be due to increases in the size and density of plants. The biomass of *C. angustifoium* which is highly abundant in the shallow subtidal fringe at most sites also increased between the two surveys. The increase in these two canopy-forming species may explain some of the changes seen in other algal groups and sessile invertebrates groups. For example, the increase in cover of encrusting corallines, and decline in turfing and ephemeral species (e.g., Ulva sp), between surveys may be due to reduced light levels under the canopy (Connell, 2003b). Furthermore, this may in turn have facilitated the increase in cover of sessile invertebrates such as sponges, bryozoans and hydroids between surveys. However, these effects are likely to be depth specific as physical abrasion by the macroalgae canopy may also affect understorey communities (Connell, 2003a). This was reflected in the depth distribution of bryozoans (predominantly highly branched species such as *Bugula dentata*) which exhibited the largest increase in cover in the deeper strata at the most sheltered sites. It was at these sites and depths where *Ecklonia* was typically tall (>1 m total length) and exhibited the greatest increase in biomass between years. Further analysis of change in the depth distribution of different morphological forms of sessile invertebrates may further explain these patterns. The red foliose species *Euptilota formosissima* and *Phascelocarpus labillardieri* were also more common in 2006 and these species are generally found beneath *Ecklonia* canopies at depths greater than 10 m at the Poor Knights (N.S. unpubl. data). These results suggest that the increase in the biomass of macroalgal canopy species, predominantly *Ecklonia*, has resulted in changes in the understorey assemblages at the Poor Knights since 1999.

The potential mechanism for the large increase in *Ecklonia* biomass at the Poor Knights between 1999 and 2006 is not known. Sea urchins are known to have an important influence on *Ecklonia* biomass in northeastern New Zealand (Andrew & Choat, 1982), however, their abundance and size distribution, remained constant between years. Comparisons with analogous monitoring data from sites at Leigh and the Mokohinau Islands demonstrate that this increase in *Ecklonia* biomass has occurred at a regional scale. This suggests that climatic or oceanographic variation (e.g., water temperature, storm intensity) over the sampling period may be important in explaining this change, rather than any local-scale ecological (e.g., grazing) or environmental (e.g., sedimentation) factors operating at the Poor Knights. Furthermore, the offshore nature of the Poor Knights and Mokohinau Islands mean the likelihood of any land-based activities influencing the communities is minimal. In general, the increase in numbers of plants across the full size range of *Ecklonia* suggest continued growth and recruitment between 1999 and 2006, and an absence of periodic die-off events that are known to effect *Ecklonia* populations in northeastern New Zealand (e.g., Cole & Babcock, 1996; Haggitt & Babcock, 2003; Haggitt, 2004).

Despite the widespread increase in *Ecklonia* biomass, populations of the sea urchin *Evechinus* appear to have remained stable at the Poor Knights between years, and in some cases, the extent of barrens has increased, e.g., a large area of reef at Bartles Bay has changed from turfing algae in 1999 to barrens in 2006. In other cases, however, an increase in barrens could be attributed the subtropical sea urchin *Centrostephanus rodgersii*. For example, at Cleanerfish and Fraser's Bay *Centrostephanus* was found in patches of barrens up to c.10m^2 in amongst the *Ecklonia* forest at 10-12 m depth. Such areas were not observed in 1999 and may be a result of increased *Centrostephanus* abundance. However, despite almost twice the number of *Centrostephanus* recorded during quadrat sampling in 2006, there was no significant difference between surveys. Due to the currently low density and spatially aggregated nature of this large sea urchin, the methods used in this study are probably not appropriate for continued monitoring of this species over time. Increases in *Centrostephanus* abundance and the extent of urchin barrens have been recorded along the east coast of Tasmania and attributed to warming sea conditions (Edgar et al., 2005). This species is abundant in New South Wales (Andrew & Underwood, 1989) and is believed to be transported via the East Auckland Current to Tasmania and New Zealand. Therefore changing oceanographic conditions and warming sea surface temperatures may see an increase in this species in northeastern New Zealand, as seen in Tasmania where the absence of natural predators through overfishing appears to have facilitated this expansion (S. Ling, University of Tasmania, unpubl. data). The present study provides some evidence for an increase in *Centrostephanus* abundance at the Poor Knights over the last 7 years and it is therefore recommended that a dedicated sampling program be implemented to monitor this species and determine whether it is in fact increasing in abundance.

4.2 EFFECTS OF PROTECTION ON REEF COMMUNITIES

Based on the current literature on the effects of no-take marine reserves on temperate rocky reef ecosystems, there is a general expectation for a recovery of predatory species to result in a decline in sea urchins and increase in kelp (Shears & Babcock, 2002; Lafferty, 2004; Guidetti et al., 2005; Micheli et al., 2005). After eight years of no-take protection at the Poor Knights there has been an increase in snapper, no change in sea urchins, and an increase in kelp. However, this increase in kelp appears to have occurred across a large portion of the northeastern region and the relative difference among locations has remained constant between 1999 and 2006. On average, *Ecklonia* biomass at the Poor Knights (4-6 m depth) was considerably higher than at the Mokohinau Is and non-reserve sites at Leigh, but no different to the reserve sites at Leigh. Similarly the abundance of exposed *Evechinus* was c.5 times higher at Mokohinau Is and Leigh non-reserve sites, compared to the Poor Knights and the Leigh reserve. This is a considerably larger difference than reported by Shears & Babcock (2004a) who found the density of exposed sea urchins to be twice as high at the Mokohinau Is. The difference in magnitude of this effect is most probably due to different sites and depths being compared between the two studies. In the present study comparisons were made between nine sites surrounding the Poor Knights and four moderately exposed to exposed sites at the Mokohinaus, whereas Shears & Babcock (2004a) compared the nine Poor Knights sites with nine sites surrounding the Mokohinaus. These differences do not effect the main conclusions drawn from these analyses in that the difference in exposed *Evechinus* abundance (and *Ecklonia* biomass) among areas remained constant between surveys. However, it does reiterate the importance of sampling sites with similar environmental conditions when comparing between two areas or inside and outside reserves.

The differences in *Ecklonia* biomass and exposed *Evechinus* abundance between reserve and non-reserve sites at Leigh have been conclusively attributed to the higher abundances of predators in the reserve, and higher levels of predation on *Evechinus* (Babcock et al., 1999; Shears & Babcock, 2002; 2003). The time-series data presented in the present study demonstrate that these contrasting states between reserve and non-reserve sites have persisted since 1999, despite short-term variations in *Evechinus* numbers (declines at Leigh non-reserve sites) and the regional-scale increases in the biomass of *Ecklonia*. Therefore, this provides continued support for the importance of top-down factors in controlling kelp forest communities at Leigh. However, the contrasting patterns in *Ecklonia* and *Evechinus* abundance between the Poor Knights and the Mokohinau Islands cannot be attributed to similar top-down mechanisms for a number of reasons (Shears & Babcock, 2004a). Primarily, these patterns were apparent less than one year after no-take protection was implemented, suggesting fundamental differences in the environmental conditions and/or ecology of shallow reefs in these two areas, which are located approximately 50 km apart. The higher algal biomass across all depths at the Poor Knights, and higher proportion of cryptic sea urchins, suggest higher algal productivity than at the Mokohinau's (Shears & Babcock, 2004a). This may be explained by a stronger influence of the East Auckland Current at the Poor Knights Is than at Mokohinau Is (Stanton et al., 1997) or greater influence of a number of other oceanographic features such as upwelling (Black et al., 2000) and internal waves (Stewart, 2001) which may be important mechanisms for driving nutrient and larval supply at the Poor Knights.

In general it appears that strong bottom-up processes result in high algal recruitment and growth at the Poor Knights, allowing sea urchins to lead a more cryptic lifestyle (cf. Harrold & Reed, 1985). However, both *Evechinus* and *Centrostephanus* openly graze the substratum and form urchin barrens habitat at some sites and the potential remains for predators to have an important top-down effect on shallow reef communities over time. It took >15 years before any habitat-level effects of protection were detected in the Leigh Marine Reserve (Babcock et al., 1999; Shears & Babcock, 2003). The decline in *Evechinus* at Leigh was attributed to predation by both snapper and the spiny lobster *Jasus edwardsii* (Shears & Babcock, 2002). However, despite spiny lobster being protected at the Poor Knights since 1981 under the restricted fishing regulations there is little evidence to suggest this species has recovered (MacDiarmid & Breen, 1993). *J. edwardsii* is known to prey on large *Evechinus* (Shears & Babcock, 2002) and *Centrostephanus* (S. Ling, University of Tasmania, unpubl. data), while snapper typically feed on smaller *Evechinus* (Shears & Babcock, 2002). Therefore, with comparatively low numbers of lobster and the dominance of large sea urchins (>70 mm test diameter), potential effects of predators (primarily snapper) on urchin populations may take longer to be manifested at the Poor Knights than was recorded at Leigh. In general the effect of snapper populations on *Evechinus* populations as well as other organisms at the Poor Knights is unknown. Further research into the diet and general ecology of snapper at the Poor Knights is necessary to determine what resources they are utilising (e.g., reef associated, soft-sediment, pelagic) and better understand any potential community-level effects associated with the large increase in this predatory species at the Poor Knights.

Establishment and monitoring of new marine reserves throughout New Zealand provides a unique opportunity to better understand the ecology of New Zealand’s marine ecosystems and the impacts of fishing on these communities. While limited conclusions can be drawn from spatial comparisons between isolated reserve and non-reserve areas (e.g., Poor Knights and Mokohinaus) we have seen that dominant components of community structure (e.g., *Ecklonia* biomass) vary across regional-scales. Therefore, following the trajectories of community change across a range of reserve and non-reserve locations will be highly informative in determining the effects of marine reserve protection and their generality. The proposed marine reserves at Mimiwhangata and Great Barrier Island, along with existing reserves in northeastern New Zealand, provide an unprecedented spatial framework to achieve this.

4.3 CONCLUSIONS

There appears to have been no change in shallow subtidal reef communities at the Poor Knights Islands Marine Reserve after 8 years of no-take protection that could be attributed to this increased numbers of predators, despite the large increase in snapper populations. Benthic assemblages have generally remained stable between 1999 and 2006, however, there has been some changes in the abundance and/or biomass of key species. In particular, there was a doubling in biomass of the dominant kelp *Ecklonia* which coincided with a decline in a number of smaller algal groups (e.g., coralline turf, red turfing algae and *Ulva* sp.) and an increase in shade-tolerant groups (e.g., crustose corallines, sponges, bryozoans and hydroids). This increase in *Ecklonia* biomass was also apparent at Leigh and the Mokohinau Is and appears to reflect regional variation over this time period associated with optimum climatic and oceanographic conditions, rather than any local scale effects.

The abundance or size distribution of the dominant sea urchin *Evechinus chloroticus* remained stable after eight years of no-take protection, however, there was some evidence for an increase in populations of the subtropical sea urchin *Centrostephanus rodgersii*. These patterns broadly suggest that the increase in predators at the Poor Knights has not had a noticeable top-down effect on sea urchin populations over this time period. However, a more convincing assessment of this hypothesis will only be possible with continued monitoring over sufficient time periods to allow potential trophic cascade effects to manifest at the Poor Knights.

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Table 1. Mean biomass (g dry-weight m^{-2}) of macroalgal taxa, percent contribution to total macroalgal biomass, and percent occurrence (n=180 quadrats) of taxa at the Poor Knights in 1999 and 2006. Species listed according to ranked dominance in 1999.

Rank	Species	Code	1999	2006	%Biom 1999	%Biom 2006	%Occ. 1999	%Occ. 2006
1	*Ecklonia radiata*	Eckl	251.17	583.01	47.413	64.531	66.67	64.44
2	*Carpophyllum angustifolium*	Angu	79.38	119.67	14.985	13.246	20.00	21.11
3	Red turfing	Rtur	34.06	19.75	6.430	2.186	91.11	70.00
4	*Lessonia variegata*	Less	27.09	26.66	5.113	2.951	20.00	15.00
5	Coralline turf	Ctur	24.69	18.49	4.661	2.046	79.44	73.89
6	*Osmundaria colensoi*	Osmu	16.92	17.86	3.193	1.977	32.78	38.33
7	Crustose coralline	CCA	14.58	16.31	2.753	1.805	100.00	100.00
8	*Carpophyllum maschalocarpum*	Mash	13.15	19.82	2.481	2.194	18.33	17.78
9	*Xiphophora chondrophylla*	Xiph	12.42	21.61	2.344	2.392	23.89	27.22
10	*Pterocladia lucida*	Pter	10.47	9.21	1.977	1.019	25.56	22.22
11	*Ulva* sp.	Ulva	8.11	2.04	1.530	0.226	58.89	47.78
12	*Caulerpa flexilis*	Cfle	4.22	4.71	0.797	0.522	7.22	8.33
13	*Carpophyllum plumosum*	Plum	3.66	7.14	0.691	0.790	8.89	10.56
14	*Nesophila hoggardii*	Neso	3.58	6.80	0.676	0.752	39.44	30.56
15	*Rhodymenia* sp. (Three Kings)	Rho3	3.58	6.87	0.676	0.760	13.89	20.56
16	*Codium convolutum*	Ccon	3.07	1.59	0.579	0.176	42.78	30.56
17	*Pachymenia crassa*	Pcra	3.00	3.95	0.566	0.437	16.11	22.22
18	*Curdiea coriacea*	Ccor	2.67	1.17	0.503	0.130	21.11	12.22
19	*Euptilota formosissima*	Eupt	2.42	6.83	0.456	0.756	21.67	34.44
20	*Plocamium* sp.	Ploc	2.17	1.17	0.409	0.129	25.00	15.00
21	*Zonaria turneriana*	Zona	1.60	0.81	0.302	0.090	24.44	15.00
22	*Placentophora colensoi*	Plac	1.00	0.36	0.189	0.040	10.56	4.44
23	*Distromium scottsbergii*	Dist	0.90	0.15	0.170	0.016	4.44	1.11
24	*Caulerpa geminata*	Cgem	0.84	0.26	0.159	0.029	7.22	7.78
25	*Carpophyllum flexuosum*	Flex	0.78	0.08	0.147	0.009	7.78	1.67
26	Red encrusting	Renc	0.63	0.58	0.118	0.064	46.67	30.00
27	*Rhodymenia* sp.	Rhod	0.61	0.36	0.115	0.040	8.33	3.89
28	*Codium cranwelliaea*	Ccra	0.59	0.19	0.111	0.021	8.89	6.11
29	*Delisea compressa*	Deli	0.42	0.11	0.079	0.012	8.33	1.67
30	*Melanthalia abscissa*	Mela	0.42	1.77	0.079	0.196	6.11	9.44
31	*Landsburgia quercifolia*	Land	0.28	0.55	0.053	0.061	5.56	5.56
32	*Sargassum sinclairii*	Sarg	0.26	0.24	0.049	0.027	16.67	15.56
33	*Taylorophycus filiformis*	Tayl	0.22	0.42	0.042	0.047	1.67	2.78
34	*Halopteris* spp.	Halo	0.18	0.81	0.034	0.089	2.78	5.56
35	*Phascelocarpus labillardieri*	Phac	0.17	0.75	0.031	0.083	2.78	6.11
36	*Carpomitra costata*	Carp	0.13	0.21	0.024	0.023	4.44	5.56
37	*Curdiea codioides*	Ccod	0.12	0.04	0.022	0.005	7.22	2.78
38	*Kallymenia berggenii*	Kall	0.08	0.00	0.016	0.000	1.67	0.00
39	*Colpomenia sinuosa*	Colp	0.06	0.00	0.010	0.000	1.67	0.00
40	*Plocamium costatum*	Pcos	0.06	0.86	0.010	0.095	1.11	4.44
41	*Callophyllis* sp.	Call	0.02	0.03	0.003	0.004	1.67	2.78
42	*Pedobesia clavaeformis*	Pedo	0.01	0.01	0.002	0.001	1.11	0.56
43	*Dictyota* sp.	Dict	0.00	0.08	0.000	0.009	0.00	3.33
44	*Perithalia capillaris*	Peri	0.00	0.14	0.000	0.015	0.00	0.56
	Mean total biomass (m^{-2})		529.76	903.47				

Table 2. Results from NPMANOVA investigating the effect of Year and Site on (a) macroalgal species composition (presence-absence), (b) macroalgal community structure (fourth-root transformed biomass) and (c) sessile benthic assemblages (fourth-root transformed percent cover).

	df	MS	*F*	p
(a)				
Year	1	7470.8	3.54	0.211
Site	8	11755.7	9.09	0.001
Year x Site	8	2113.3	1.63	0.010
(b)				
Year	1	11218.7	4.91	0.170
Site	8	14353.2	9.56	0.001
Year x Site	8	2286.0	1.52	0.024
(c)				
Year	1	10517.0	8.12	0.090
Site	8	40031.8	7.79	<0.001
Year x Site	8	10358.5	2.02	<0.001

Table 3. Results from mixed model analysis on dominant macroalgal species and groups (a), sessile benthic forms (b), and mobile macroinvertebrates (c) from quadrat sampling in 1999 and 2006. Model back-fitted by removing non-significant interaction terms (as indicated by ns). C=counts, B=Biomass, %=Percent cover, X=factor could not be tested. Bold values indicate significant tests (p<0.05).

		Fixed			Random			
(a) Macroalgae		Year	Depth range	Year x Depth range	Site	Year x Site	Site x Depth range	Year x Site x Depth range
Ecklonia	C	**$F_{1,323}$=33.83, *p*=<0.001**	**$F_{3,24}$=18.42, *p*=<0.001**	ns	Z=1.48, *p*=0.069	ns	**Z=2.32, *p*=<0.010**	ns
	B	**$F_{1,323}$=76.77, *p*=<0.001**	**$F_{3,24}$=17.82, *p*=<0.001**	ns	Z=1.61, *p*=0.054	ns	**Z=2.33, *p*=0.010**	ns
C. angustifolium	C	**$F_{1,350}$=4.54, *p*=0.034**	X	X	Z=1.56, *p*=0.059	ns	X	X
	B	$F_{1,350}$=3.21, *p*=0.074	X	X	Z=1.56, *p*=0.059	ns	X	X
C. maschalocarpum	C	**$F_{1,322}$=14.34, *p*=<0.001**	$F_{3,25}$=1.69, *p*=0.195	ns	Z=1.30, *p*=0.097	ns	**Z=2.36, *p*=0.009**	ns
	B	**$F_{1,323}$=11.62, *p*=<0.001**	$F_{3,24}$=1.57, *p*=0.223	ns	Z=1.19, *p*=0.117	ns	**Z=2.39, *p*=0.009**	ns
Lessonia	C	$F_{1,350}$=0.31, *p*=0.581	X	X	Z=1.31, *p*=0.096	ns	X	X
	B	$F_{1,350}$=0.00, *p*=0.970	X	X	Z=1.10, *p*=0.137	ns	X	X
Osmundaria	B	$F_{1,323}$=0.16, *p*=0.691	$F_{3,24}$=1.40, *p*=0.268	ns	Z=1.33, *p*=0.092	ns	**Z=2.38, *p*=0.009**	ns
Pterocladia	B	$F_{1,350}$=0.28, *p*=0.600	X	X	Z=1.66, *p*=0.049	ns	X	X
Rhodymenia	B	**$F_{1,350}$=5.54, *p*=0.019**	X	X	Z=1.46, *p*=0.072	ns	X	X
Nesophila	B	**$F_{1,320}$=4.21, *p*=0.041**	$F_{3,24}$=2.77, *p*=0.064	**$F_{3,320}$=8.73, *p*=<0.001**	Z=1.22, *p*=0.112	ns	**Z=2.29, *p*=0.011**	ns
Red foliose	B	**$F_{1,320}$=7.13, *p*=0.008**	**$F_{3,24}$=3.49, *p*=0.031**	**$F_{3,320}$=3.08, *p*=0.028**	Z=1.23, *p*=0.110	ns	**Z=2.87, *p*=0.002**	ns
Red turfing	B	**$F_{1,8}$=14.38, *p*=0.005**	**$F_{3,24}$=3.19, *p*=0.042**	ns	Z=0.80, *p*=0.212	**Z=1.66, *p*=0.049**	**Z=2.93, *p*=0.002**	ns
Coralline turf	B	**$F_{1,323}$=13.65, *p*=<0.001**	**$F_{3,24}$=8.44, *p*=<0.001**	ns	Z=0.64, *p*=0.262	ns	**Z=2.70, *p*=0.003**	ns
Crustose corallines	B	**$F_{1,8}$=7.45, *p*=0.026**	$F_{3,24}$=1.15, *p*=0.351	$F_{3,24}$=1.13, *p*=0.356	Z=0.11, *p*=0.133	Z=1.00, *p*=0.999	**Z=1.78, *p*=0.037**	**Z=2.09, *p*=0.018**
Ulva sp.	B	**$F_{1,8}$=9.21, *p*=0.016**	$F_{3,24}$=0.13, *p*=0.942	$F_{3,24}$=0.51, *p*=0.682	Z=0.80, *p*=0.211	Z=1.01, *p*=0.156	**Z=1.72, *p*=0.043**	**Z=1.88, *p*=0.030**
(b) Sessile benthic forms		Year	Depth range	Year x Depth range	Site	Year x Site	Site x Depth range	Year x Site x Depth range
Sponges	%	**$F_{1,347}$=8.82, *p*=0.003**	$F_{3,347}$=0.49, *p*=0.687	ns	Z=1.33, *p*=0.091	ns	ns	ns
Hydroids	%	$F_{1,8}$=3.07, *p*=0.118	$F_{3,24}$=1.28, *p*=0.303	ns	Z=1.00, *p*=0.999	**Z=2.13, *p*=0.017**	**Z=2.82, *p*=0.002**	ns
Ascidians	%	$F_{1,344}$=0.03, *p*=0.859	**$F_{3,344}$=3.39, *p*=0.018**	**$F_{3,344}$=4.34, *p*=0.005**	Z=0.97, *p*=0.165	ns	ns	ns
Bryozoans	%	**$F_{1,8}$=8.46, *p*=0.020**	$F_{3,24}$=2.20, *p*=0.114	**$F_{3,312}$=3.38, *p*=0.019**	Z=1.00, *p*=0.999	**Z=1.80, *p*=0.036**	**Z=2.75, *p*=0.003**	ns
Anemones	%	**$F_{1,323}$=40.53, *p*=<0.001**	$F_{3,24}$=2.29, *p*=0.104	ns	Z=0.03, *p*=0.490	ns	**Z=2.57, *p*=0.005**	ns
Sediment (excl. 0-2 m)	%	$F_{1,255}$=0.29, *p*=0.589	**$F_{2,255}$=50.46, *p*=<0.001**	**$F_{2,255}$=4.43, *p*=0.013**	**Z=1.77, *p*=0.038**	ns	ns	ns

Table 3 (Continued)

(c) Mobile invertebrates		Year	Depth range	Year x Depth range	Site	Year x Site	Site x Depth range	Year x Site x Depth range
Evechinus – all	C	$F_{1,8}=1.95$, $p=0.199$	$F_{3,24}=2.48$, $p=0.086$	$F_{3,24}=0.09$, $p=0.963$	$Z=0.83$, $p=0.204$	$Z=0.20$, $p=0.420$	**$Z=2.54$, $p=0.006$**	**$Z=1.73$, $p=0.042$**
Evechinus - exposed	C	$F_{1,323}=1.14$, $p=0.288$	$F_{3,24}=0.63$, $p=0.605$	ns	$Z=0.78$, $p=0.217$	ns	**$Z=2.63$, $p=0.004$**	ns
Evechinus - cryptic	C	$F_{1,323}=3.13$, $p=0.078$	**$F_{3,24}=3.25$, $p=0.039$**	ns	$Z=0.89$, $p=0.187$	ns	**$Z=2.43$, $p=0.008$**	ns
Centrostephanus	C	$F_{1,350}=2.37$, $p=0.125$	X	X	$Z=1.48$, $p=0.070$	ns	X	X

Table 4. The mean percent cover and occurrence (n=180 quadrats) of sessile benthic groups used in analyses of sessile benthic communities. Groups are ranked according to dominance in 1999.

Rank	Group	Phyla	Dominant species	%Cover 1999	%Cover 2006	%Occ. 1999	%Occ. 2006
1	CCA	Rhodophyta	Unknown	41.67	46.36	100.0	100.0
2	Red turf	Rhodophyta	*Gigartina* spp. *Champia novaezealandiae*	17.08	9.74	91.7	71.7
3	Coralline turf	Rhodophyta	*Corallina officinalis,* *Arthrocardia corymbosa,* *Amphiroa anceps* *Haliptilon roseum*	16.46	11.61	79.4	73.9
4	Red foliose	Rhodophyta	See Fig. 5	4.77	6.19	88.9	87.8
5	Large browns	Phaeophyta	See Fig. 4	4.75	5.05	91.1	88.9
6	Ulva	Chlorophyta	*Ulva* sp.	4.05	0.80	58.9	47.8
7	Sediment	-	-	4.05	5.11	32.8	34.4
8	Red encrusting	Phaeophyta	*Hildenbrandia* sp	1.79	1.65	46.7	30.6
9	Sponge	Porifera	*Cliona celata* *Ciocalypta*, *Polymastia* and *Tethya* spp. *Ancorina elata*	1.41	2.28	56.7	67.2
10	Caulerpa	Chlorophyta	*Caulerpa flexilis* *Caulerpa geminata*	1.15	0.87	14.4	15.0
11	Hydroid	Hydrozoa	Unknown short turfing forms (<10 cm height)	1.00	1.88	37.8	47.8
12	Ascidian	Chordata	*Pseudodistoma* spp. *Didemnum* spp.	0.95	1.00	53.9	44.4
13	Other green	Chlorophyta	*Codium convolutum* *Codium convolutum* *Pedobesia clavaeformis*	0.92	0.42	50.0	35.6
14	Bryozoan	Bryozoa	*Bugula dentata* *Steganoporella neozelanica*	0.73	2.28	25.6	51.7
15	Small brown	Phaeophyta	*Zonaria turnieriana* *Distromium scottsbergii* *Carpomitra costata*	0.57	0.47	32.2	24.4
16	Anemone	Cnidaria	*Anthothoe albocincta* *Corynactis australis*	0.23	0.81	11.1	34.4
17	Bare	-	-	0.01	0.44	0.6	4.4
18	Brown encrusting	Phaeophyta	*Ralfsia* spp.	0.00	0.09	0.0	5.6
19	Cup coral	Cnidaria	*Monomyces rubrum* *Culicea rubeola*	0.00	0.02	0.0	3.3

Table 5. Total count and percent occurrence (n=180 quadrats) of mobile macroinvertebrate species in 1999 and 2006.

Rank	Species	Count 1999	Count 2006	%Occ. 1999	%Occ. 2006
1	*Evechinus chloroticus*	478	520	40.00	51.67
2	*Centrostephanus rodgersii*	16	29	4.44	10.00
3	*Cookia sulcata*	5	0	2.78	0.00
4	*Eudoxochiton nobilis*	4	1	2.22	0.56
5	*Ceratosoma amoena*	3	17	1.67	7.78
6	*Dicathais orbita*	3	1	1.67	0.56
7	*Buccinulum lineum*	2	0	1.11	0.00
8	*Cabestana spenglerii*	2	3	1.11	1.11
9	*Calliostoma punctulatum*	2	1	1.11	0.56
10	*Muricopsis sp.*	2	0	0.56	0.00
11	*Cantharidus purpureus*	1	0	0.56	0.00
12	*Charonia lampax*	1	0	0.56	0.00
13	*Modelia granosus*	1	0	0.56	0.00
14	*Trochus viridis*	1	0	1.67	0.00
15	*Tambja* sp.	0	3	0.00	0.56
16	*Cellana stellifera*	0	3	0.00	0.56
17	*Coscinasterias muricata*	0	1	0.00	0.56
18	*Haliotis australis*	0	2	0.00	0.56
19	*Heliocidaris tuberculata*	0	4	0.00	2.22
20	*Haliotis iris*	0	1	0.00	0.56
21	*Calliostoma tigris*	0	1	0.00	0.56

Table 6. Results from mixed model analysis on *Ecklonia* biomass and *Evechinus* abundance (all and exposed urchins) from quadrat sampling at 4-6 m (a) and 7-9 m (b) depth at Poor Knights, Mokohinau, Leigh reserve and Leigh non-reserve (Area) in 1999 and 2006 (Year). Model back-fitted by removing non-significant interaction terms (ns). Bold values indicate significant tests ($p<0.05$). Note: Comparisons only made between Poor Knights and Mokohinau Island's at 7-9 m (b).

	Fixed			Random
(a) 4-6 m	Area	Year	Area x Year	Site(Area x Year)
Ecklonia biomass	**$F_{3,37}$=4.82, *p*=0.006**	**$F_{1,37}$=7.14, *p*=0.011**	ns	**Z=3.32, *p*=<0.001**
Evechinus-all	**$F_{3,37}$=4.39, *p*=0.010**	**$F_{1,37}$=5.35, *p*=0.026**	ns	**Z=2.90, *p*=0.002**
Evechinus-exp	**$F_{3,37}$=6.58, *p*=0.001**	$F_{1,37}$=1.23, *p*=0.274	ns	**Z=3.02, *p*=0.001**
(b) 7-9 m	Area	Year	Area x Year	Site(Area x Year)
Ecklonia biomass	$F_{1,23}$=1.00, *p*=0.328	$F_{1,23}$=3.22, *p*=0.086	ns	**Z=2.49, *p*=0.006**
Evechinus-all	$F_{1,23}$=2.05, *p*=0.166	$F_{1,23}$=0.27, *p*=0.610	ns	**Z=2.57, *p*=0.005**
Evechinus-exp	$F_{1,23}$=2.78, *p*=0.109	$F_{1,23}$=0.00, *p*=0.968	ns	**Z=2.62, *p*=0.004**

Fig. 1. Location of Poor Knights Islands (PKI), Mokohinau Islands (MOK) and Leigh (LEI) in northeastern New Zealand. Inset map shows position of Poor Knights monitoring sites (CLN, Cleanerfish Bay; SKB, Skull Bay; LHB, Lighthouse Bay; RLI, Rocklily Inlet; NUR, Nursery Cove; BAR, Bartles Bay; MTC, Matt's Crack; FRA, Frasers Bay; LAB, Labrid Channel).

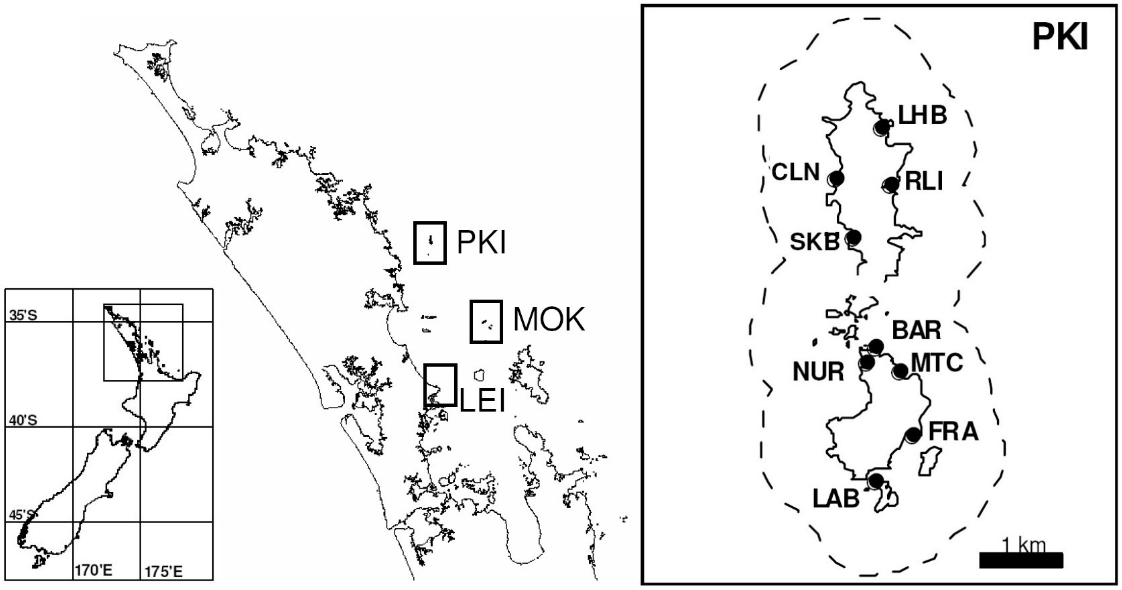


Fig. 2. Mean extent of dominant subtidal reef habitat types at the Poor Knights in 1999 and 2006 from line transect sampling. See Appendix 1 for depth distribution of habitats at each site and Shears et al. (2004) for habitat descriptions).

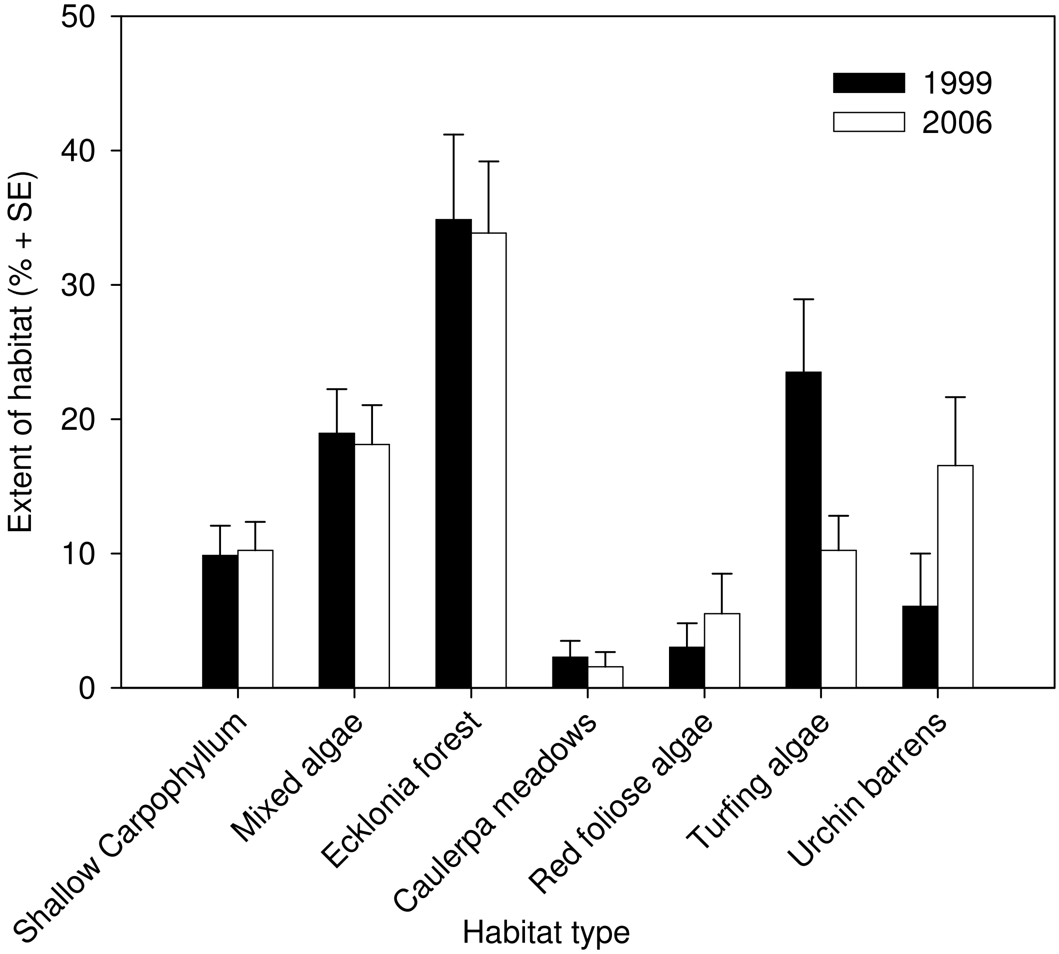
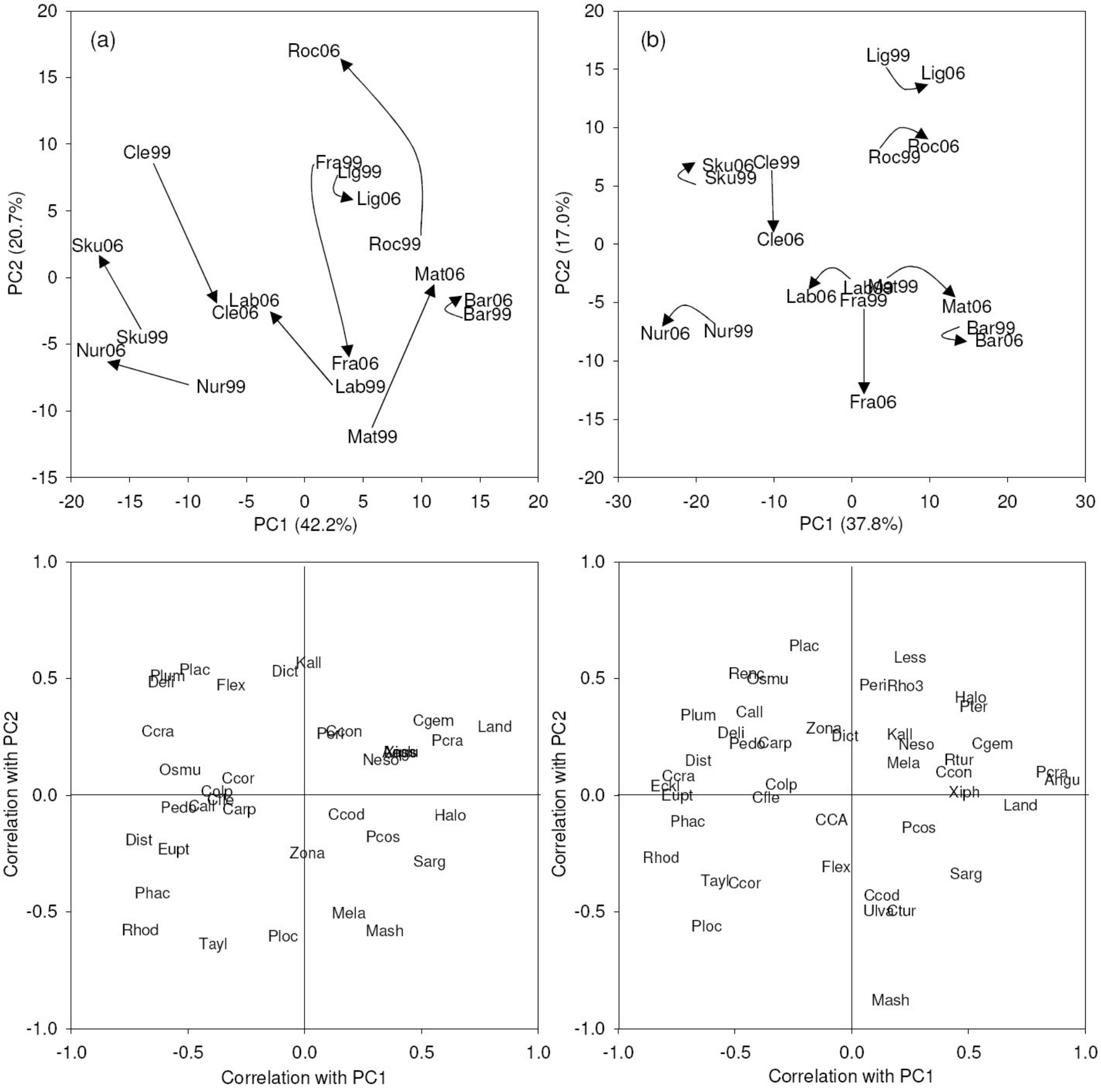


Fig. 3. Principal coordinates analysis of (a) macroalgal species composition (presence-absence) and (b) macroalgal community structure (fourth root transformed biomass) for Poor Knights monitoring sites in 1999 and 2006. Bi-plot shows correlation species variables and principal coordinate axes. See Table 1 for species abbreviations.



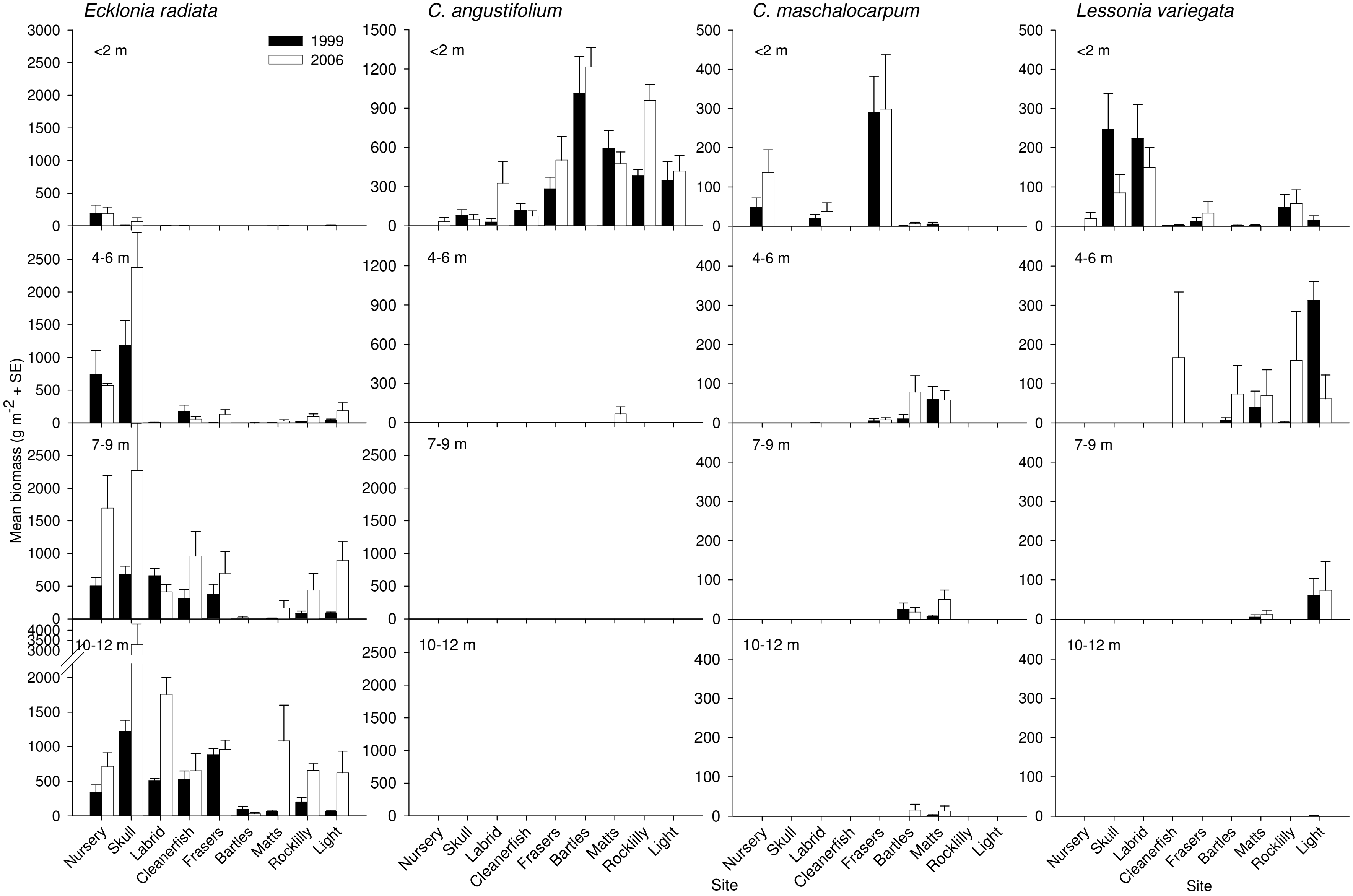


Fig. 4. Mean biomass of the four dominant large brown algal species at each site in 1999 and 2006. Note: sites are arranged from most sheltered (left) to most wave exposed (right), as estimated from total wind fetch (Shears & Babcock, 2004b).

Fig. 5. Mean biomass of the four dominant red foliose algal species at each site in 1999 and 2006. Note: sites are arranged from most sheltered (left) to most wave exposed (right), as estimated from total wind fetch (Shears & Babcock, 2004b).

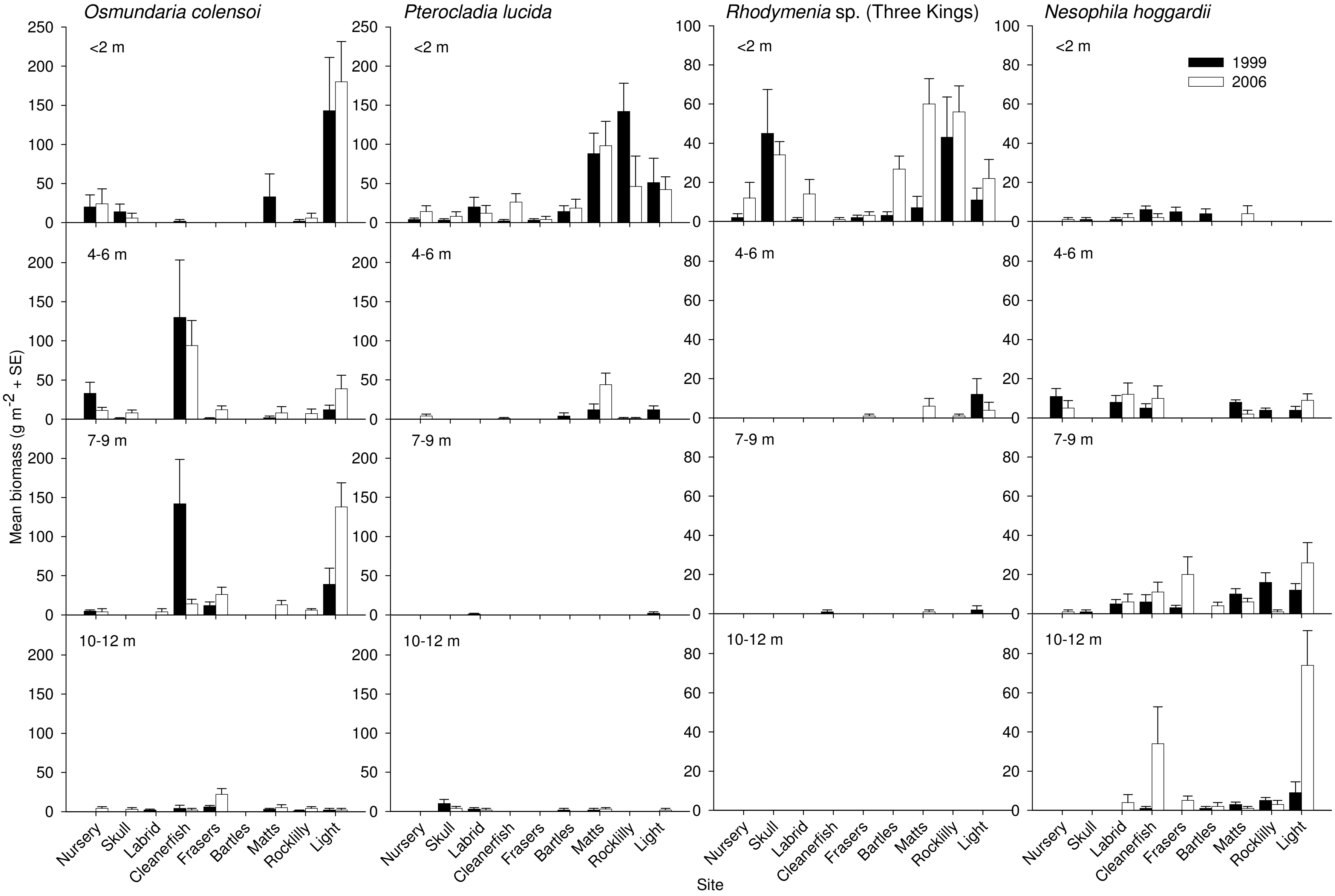


Fig. 6. Mean biomass of red turfing algae, coralline turf, crustose coralline algae (CCA) and *Ulva* sp. at each site in 1999 and 2006. Note: sites are arranged from most sheltered (left) to most wave exposed (right), as estimated from total wind fetch (Shears & Babcock, 2004b).

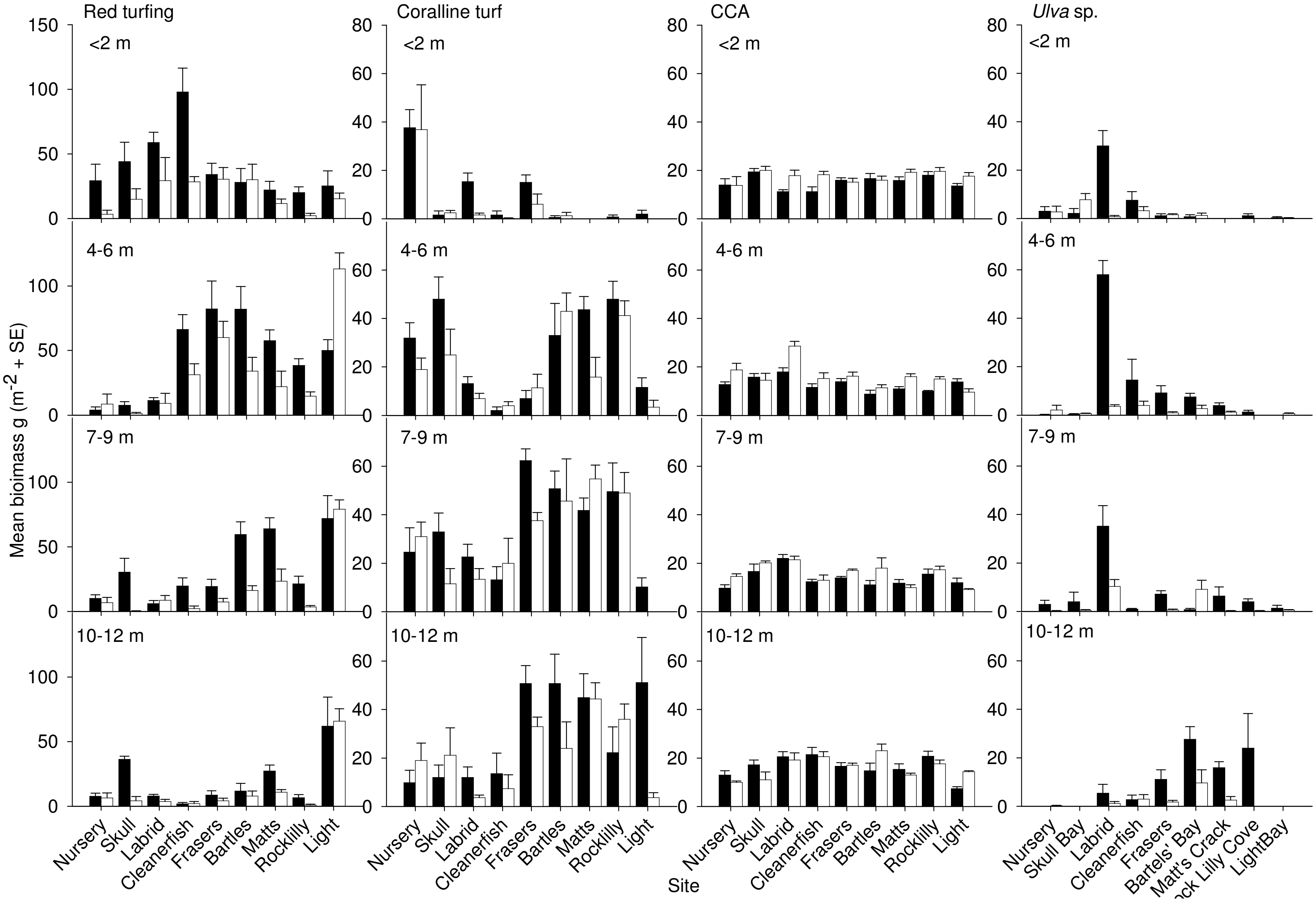
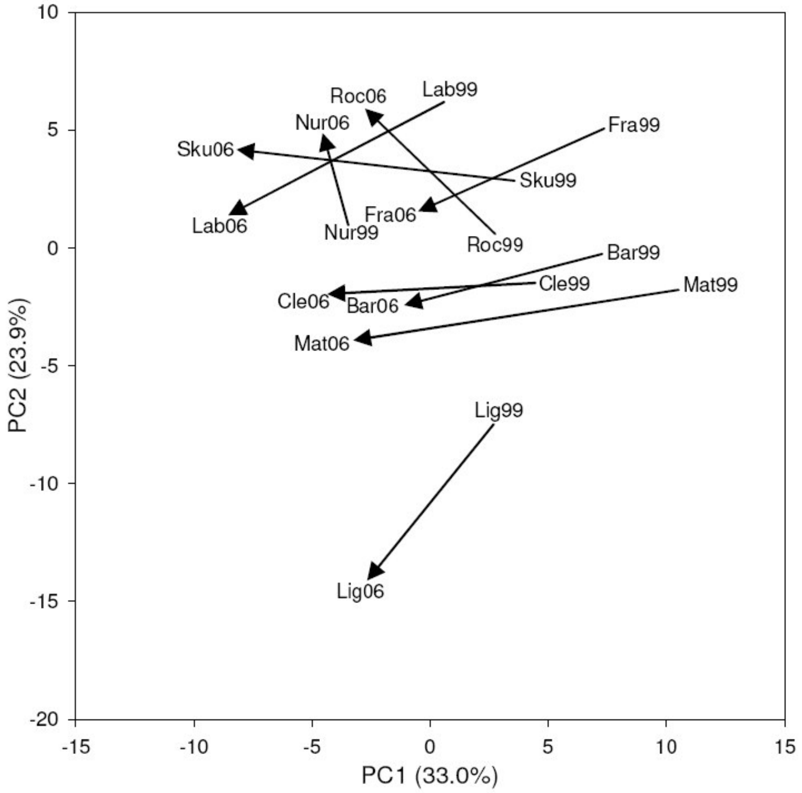


Fig. 7. Principal coordinates analysis of sessile benthic assemblages (fourth-root transformed percent cover data) for Poor Knights monitoring sites in 1999 and 2006. Bi-plot shows correlation between sessile benthic group variables and principal coordinate axes.



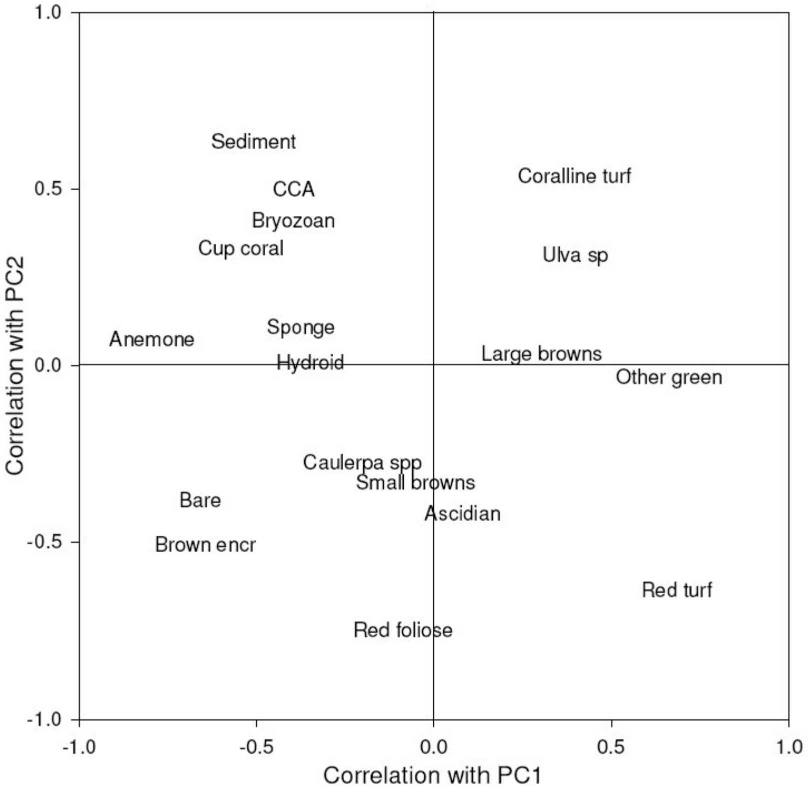


Fig. 8. Mean percent cover of dominant sessile invertebrate groups at each site in 1999 and 2006. Note: sites are arranged from most sheltered (left) to most wave exposed (right), as estimated from total wind fetch (Shears & Babcock, 2004b).

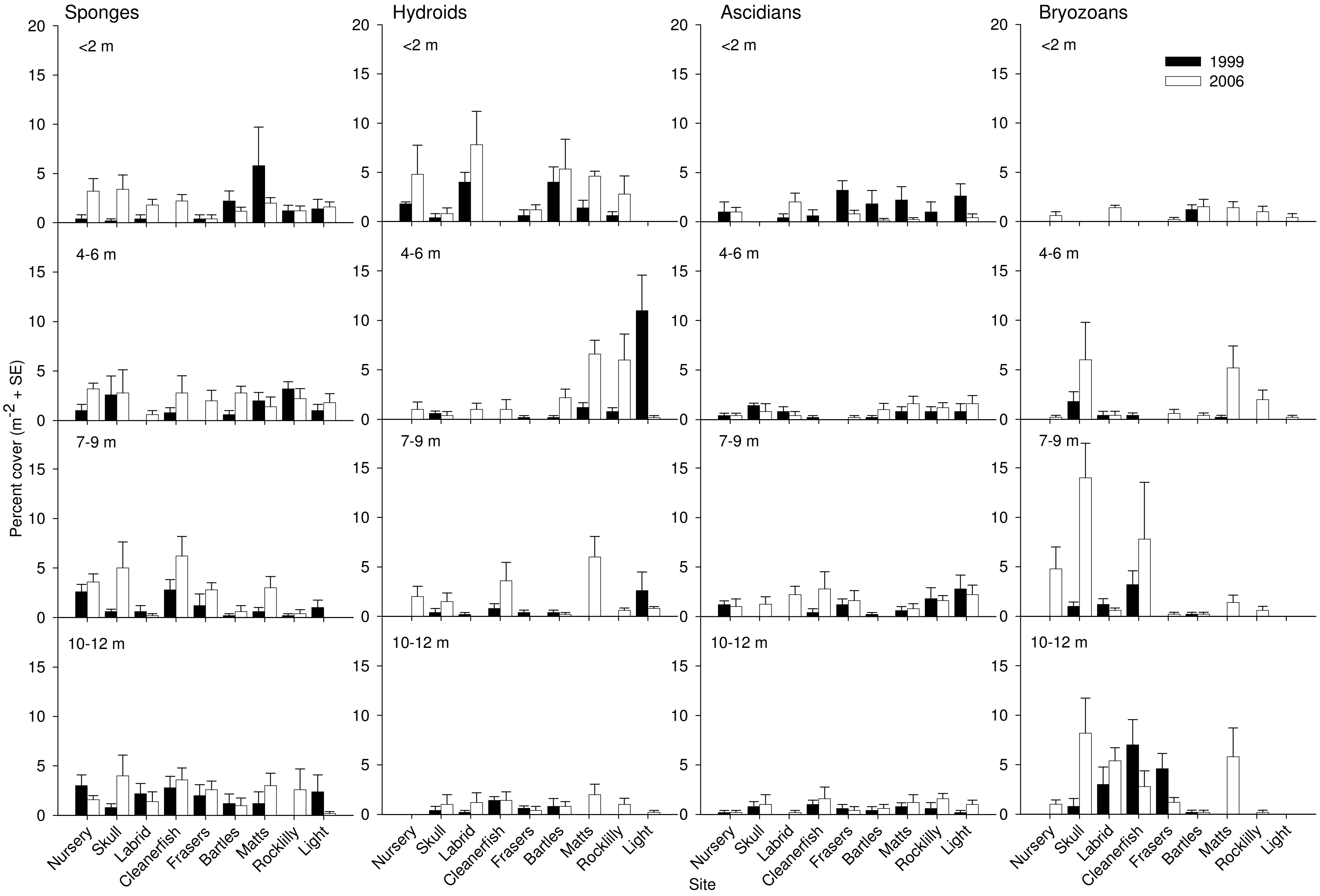


Fig. 9. Mean percent cover of sediment at each site in 1999 and 2006. Note: sites are arranged from most sheltered (left) to most wave exposed (right), as estimated from total wind fetch (Shears & Babcock, 2004b).

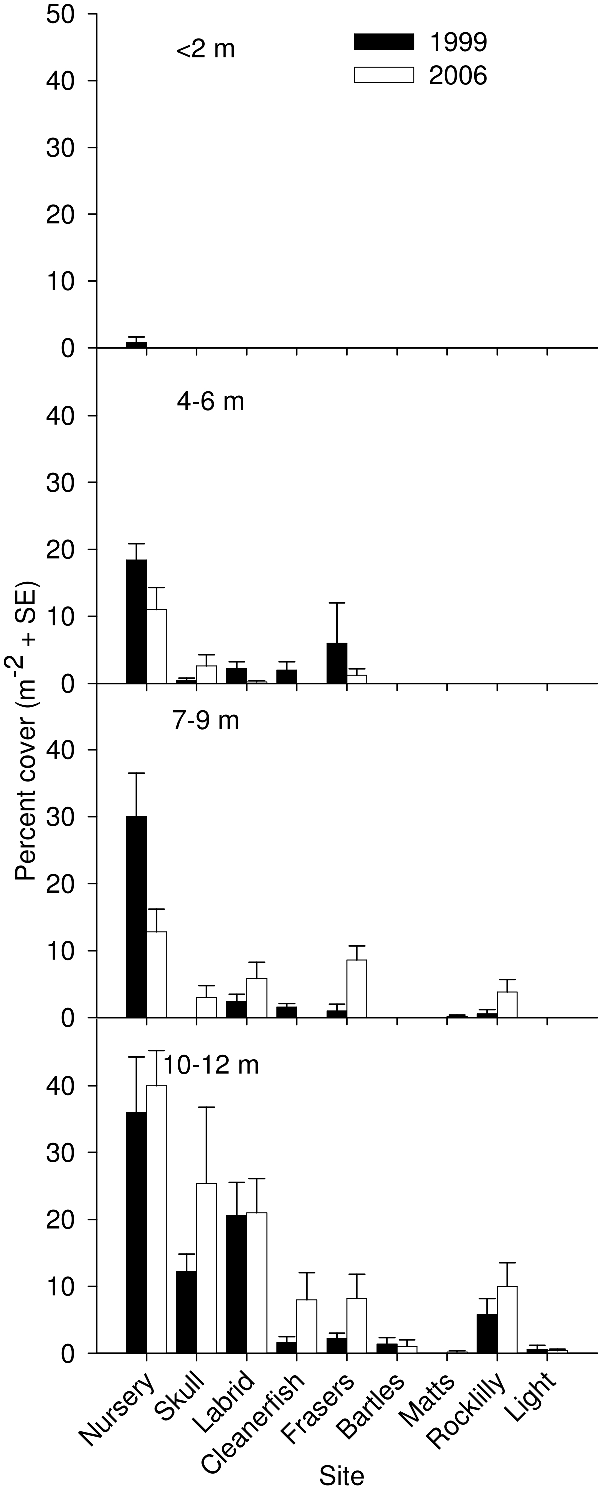


Fig. 10. Mean abundance of *Evechinus chloroticus* and *Centrostephanus rodgersii* in 1999 and 2006. Sites arranged from most sheltered on the left to most wave exposed on the right.

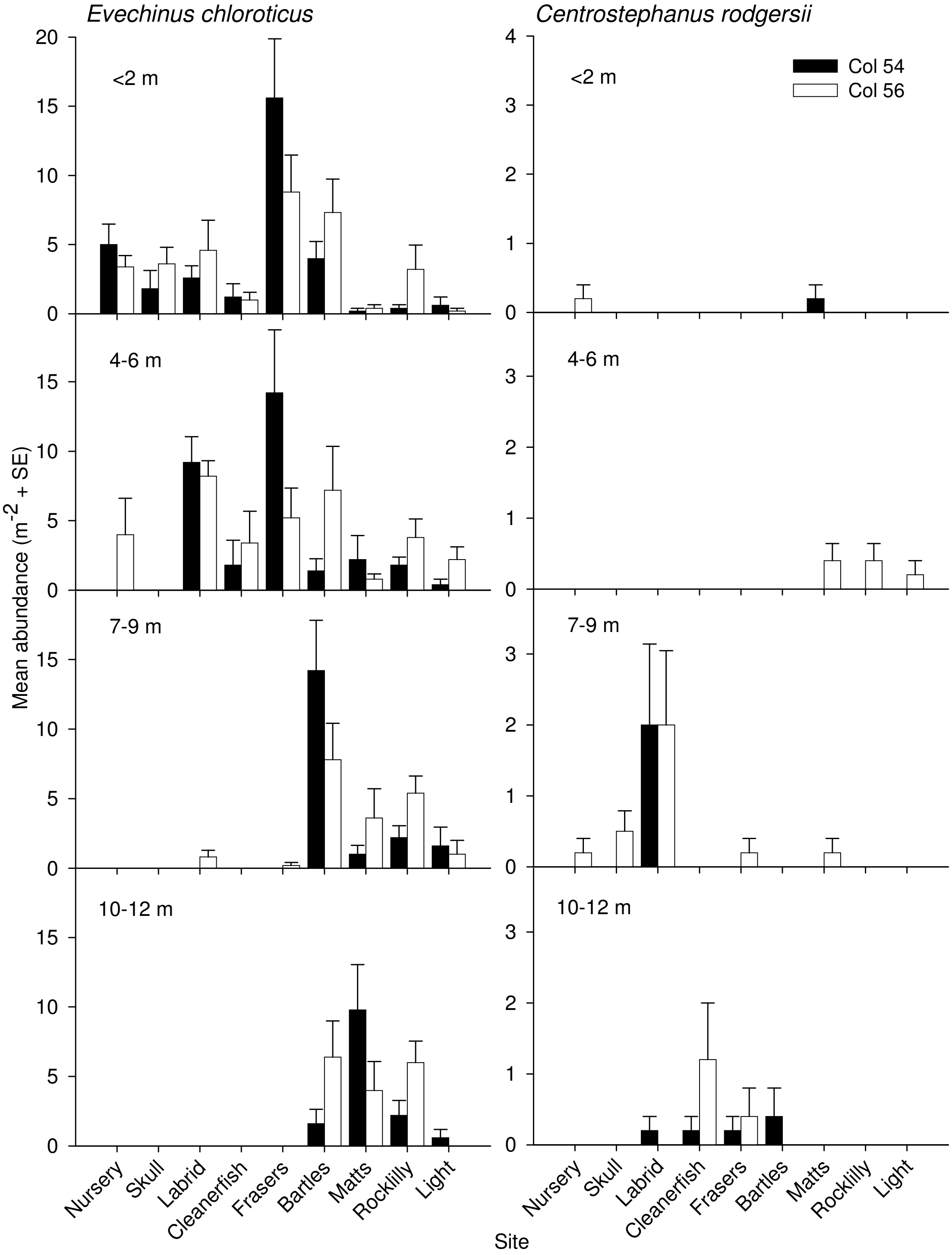
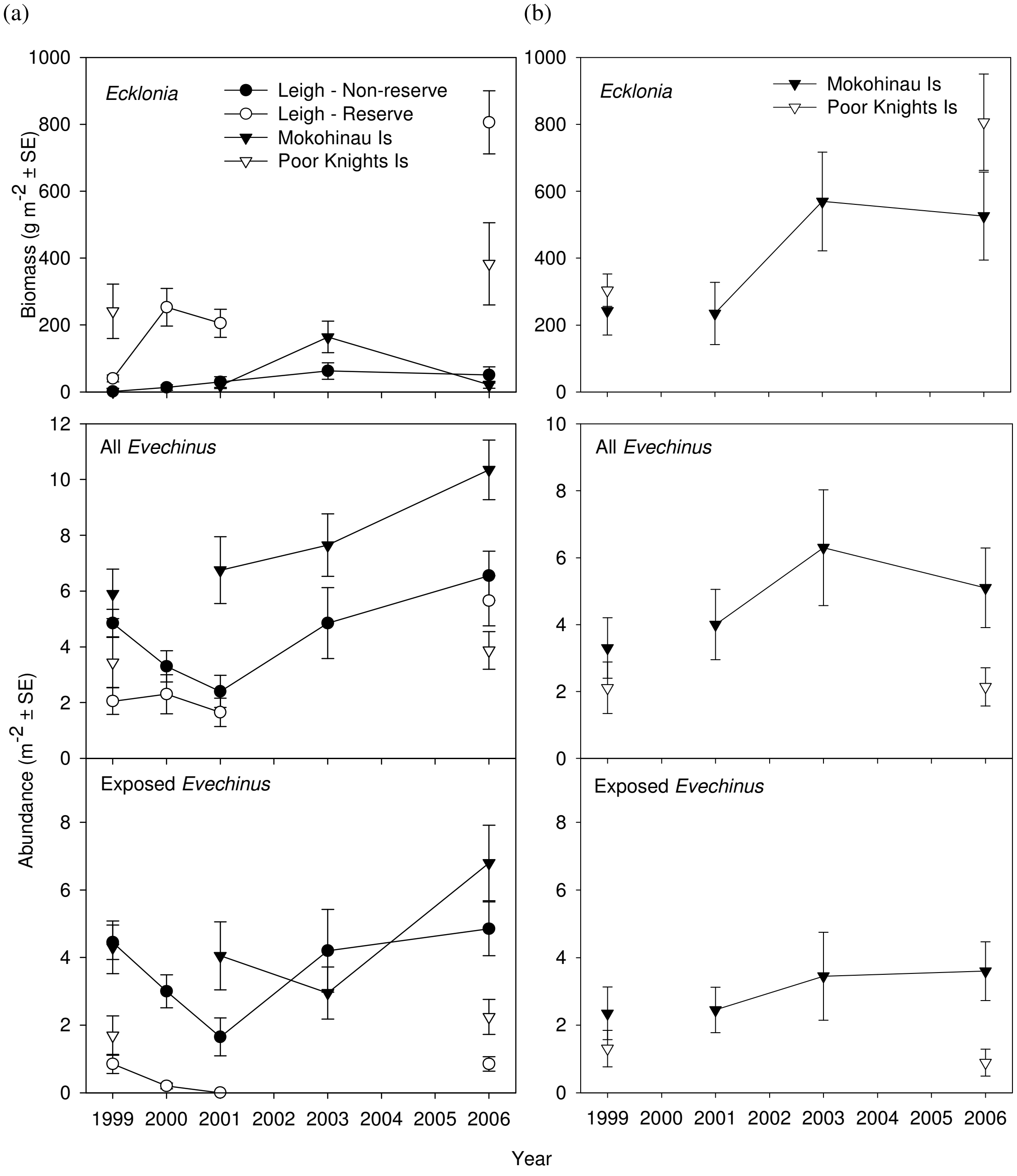
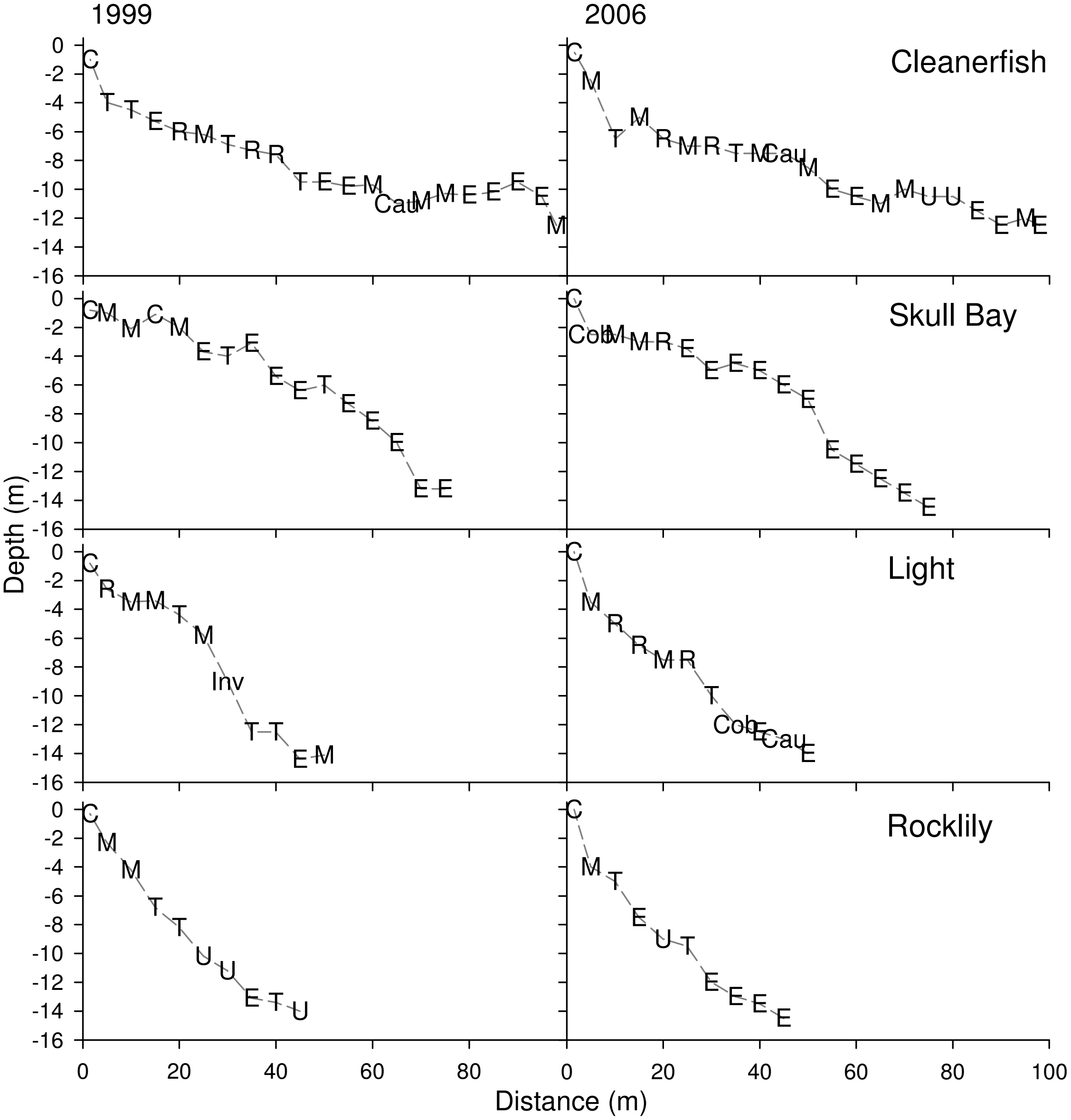


Fig. 11. Regional comparison of *Ecklonia* biomass and *Evechinus* abundance (all and exposed urchins) between 1999 and 2006 in two depth ranges: 4-6 m (a) and 7-9 m (b).



Appendix 1

Depth distribution of habitat types at each site in 1999 and 2006. Habitat types: C= Shallow *Carpophyllum*, M=Mixed algal habitat, E=*Ecklonia* forest, R=Red foliose algal habitat, T=Turfing algal habitat, Cau=*Caulerpa* meadows, U=Urchin barrens, Inv=Encrusting invertebrates, Cob=Cobbles and S=Sand.



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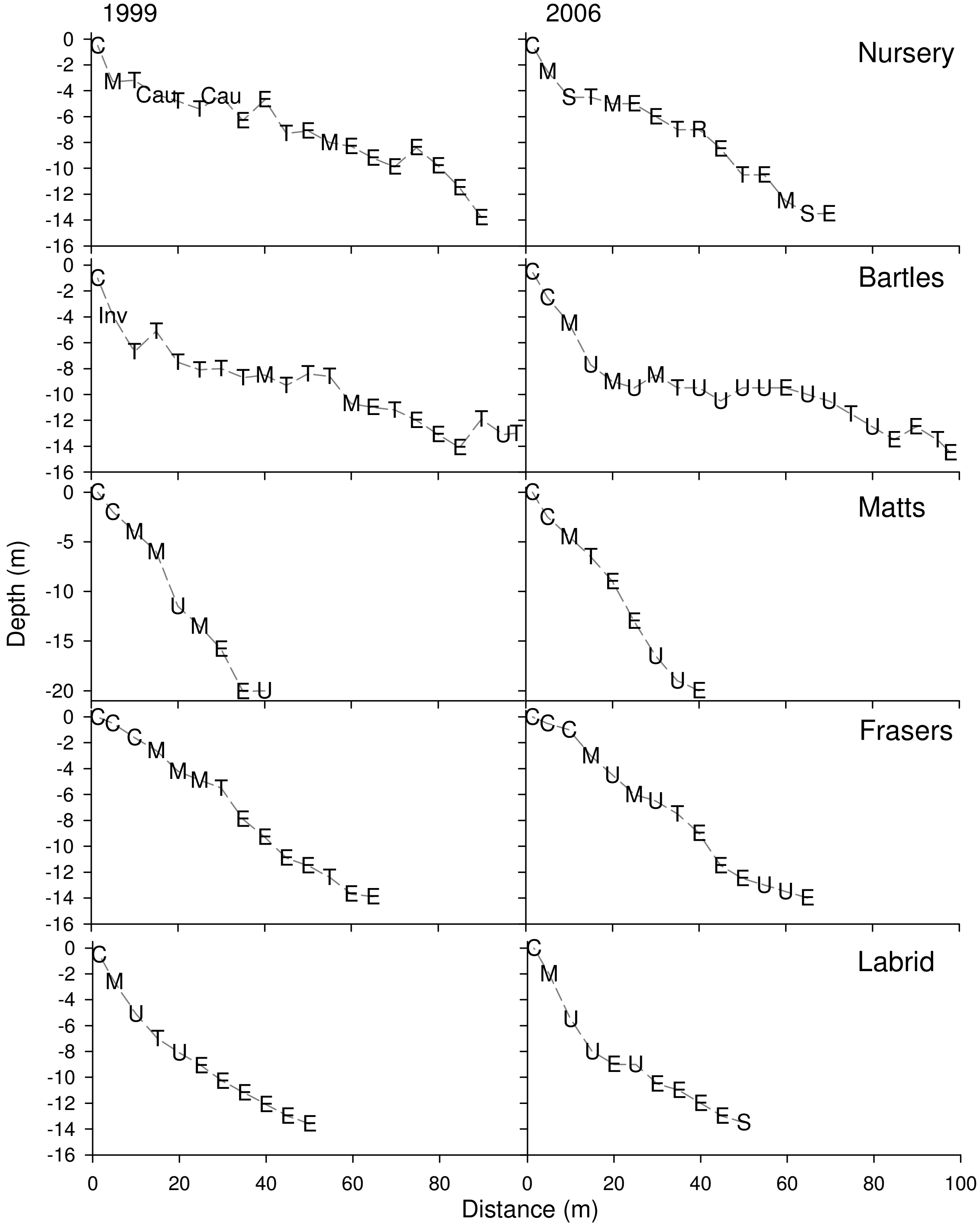
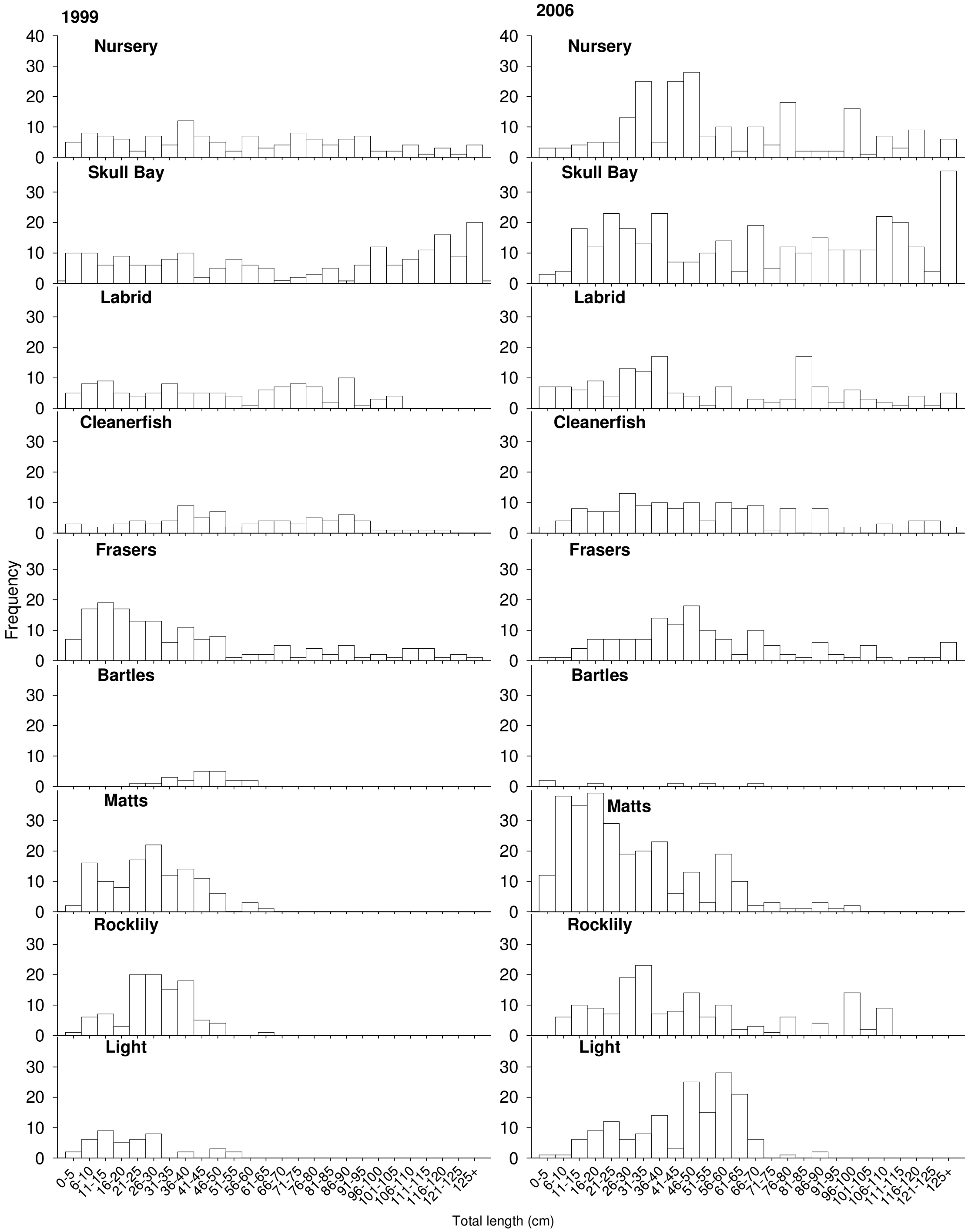


Appendix 2

Ecklonia radiata size frequency distribution (total length) at each site (n=20 quadrats) in 1999 and 2006.



Appendix 3

Evechinus chloroticus size frequency distribution (test diameter) at each site (n=20 quadrats) in 1999 and 2006.