Figure 9. Structural patterns in reef communities among all locations from principal coordinates analysis based on fourth-root transformed AFDW of 29 algal and invertebrate structural groups (A) (see Fig. 1 for location codes and Table 2 for structural group codes). Centroids are plotted for each location; standard error bars indicate the variation among sites at each location. Shaded symbols indicate bioregions in the Southern Province and open symbols indicate bioregions in the Northern Province. Bi-plots give correlations between principal coordinates axes and environmental variables (B) and structural group variables (C). * Long Bay is distinguished from other Northeastern locations as it was not included in biogeographic analyses (Shears et al. in press).
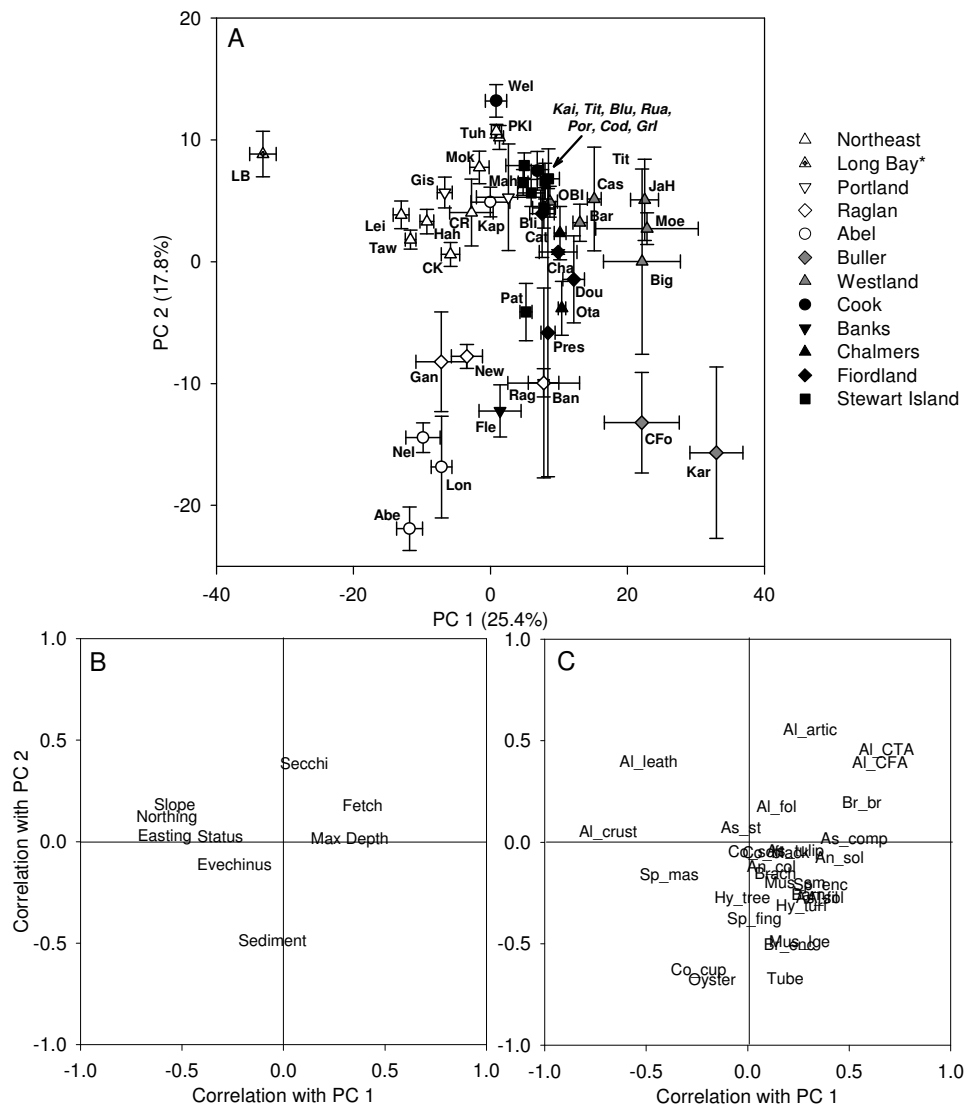
more dominant, to more oceanic locations (top portion of ordination) with clearer water that are dominated by macroalgal groups.

The amount of variation explained by environmental variables (Table 9) tended to increase with decreasing spatial scale, explaining the most variation at the bioregional level (predominantly Secchi, Fetch and Evechinus). At the national level, Slope explained the greatest variation (8%), but at the provincial level Secchi (Northern: 12%) and Fetch (Southern 8%) explained the most variaiton. The abundance of *Evechinus chloroticus* was significantly related to benthic community structure at all spatial scales, accounting for only a small proportion of the variation at the national scale (3%), but 9–18% of the variation at the bioregional scale.

3.3.2   National patterns in dominant structural groups

Leathery macrophytes made up 67% of the total biomass across all sites (Table 8) and dominated at all bioregions except Buller and Westland on the West Coast (Figs 10 and 11). In general, the biomass of leathery macrophytes was low at most west coast sites compared with sites on the east coast (Fig. 11A). The contribution

of other structural groups was relatively small in Northern bioregions, with sponges, crustose algae and corticated terete algae being the largest contributors after leathery macrophytes. Overall, Southern bioregions tended to have a lower biomass of leathery macrophytes and a larger contribution from other groups such as corticated algae (Figs 10A and 11A) as well as mussels, solitary ascidians, other ascidians, sponges, and bryozoans (Fig. 10B). For the Buller bioregion, total biomass of algal groups was low and the structure of benthic communities was dominated by encrusting invertebrates (mussels, ascidians and sponges).

Among the encrusting invertebrate groups, sponges were the largest contributor to total biomass (9%; Table 8), particularly at Raglan and Chalmers locations (Figs 10B and 11B). Mussels were also a dominant structural component of benthic communities at Banks and Buller. Large mussels such as *Perna canaliculus* and *Mytilus* spp. were important at several locations (Raglan, Karamea, Banks Peninsula North, and those in Fiordland), whereas small mussels (*Xenostrobus pulex*) were an important component of the benthic communities at Cape Foulwind and Raglan. Solitary ascidians accounted for only 1% of the total biomass but were a major component of the benthic community at highly turbid locations where leathery macrophytes were reduced or restricted to shallow water, e.g. Buller, Westland and Banks locations (Figs 10B and 11B). Branching bryozoans were typically more abundant at Southern locations, whereas encrusting bryozoans were locally abundant at Cape Foulwind, Karamea, Abel Tasman, Nelson and New Plymouth. Cup corals (predominantly *Culicia rubeola*) were also locally abundant at Long Island and Abel Tasman (data not presented).

TABLE 9. RESULTS OF NON-PARAMETRIC MULTIVARIATE REGRESSION OF BENTHIC COMMUNITY STRUCTURE DATA (FOURTH-ROOT TRANSFORMED BIOMASS OF 29 STRUCTURAL GROUPS), AND ENVIRONMENTAL AND SPATIAL VARIABLES AT DIFFERING BIOGEOGRAPHIC SCALES. THE PERCENTAGE VARIANCE EXPLAINED BY EACH VARIABLE IS GIVEN (ns = NOT SIGNIFICANT), ALONG WITH CUMULATIVE FREQUENCY EXPLAINED FOLLOWING FORWARD SELECTION OF FACTORS (THE SIGNIFICANT FACTORS FROM THIS PROCEDURE ARE LISTED IN DESCENDING ORDER OF VARIATION EXPLAINED).

		BIOGEOGRAPHIC PROVINCES		BIOREGIONS		
				NORTHEASTERN	ABEL	STEWARTI
	NZ	NORTHERN	SOUTHERN			
n	247	135	112	81	37	42
Local variables						
Fetch	5.5	5.1	7.5	9.8	14.9	14.8
Status	2.9	1.5	5.4	ns	ns	-
Slope	8.3	7.6	3.9	16.0	5.4(0.08)	ns
MaxDepth	4.2	9.4	3.5	29.0	5.8(0.06)	4.9
Secchi	5.2	11.9	6.3	27.8	18.2	5.7
Evechinus	2.7	1.6	2.5	12.2	8.5	17.9
Sediment	5.6	9.1	6.1	5.9	14.6	13.0
Cumulative %	**27.6**	**32.0**	**35.7**	**43.9**	**39.0**	**31.0**
Significant factors	All	All, excl. Status	All	MaxDepth, Secchi, Fetch, Slope	Secchi, Fetch, MaxDepth	Evechinus, Fetch, Secchi
Spatial—Northing and Easting						
	14.8	21.9	20.3	43.9	34.1	17.5

Figure 10. Mean biomass of benthic structural groups (macroalgal groups, A, and other groups, B) for all bioregions. Dashed line indicates division between the Northern and Southern Provinces.
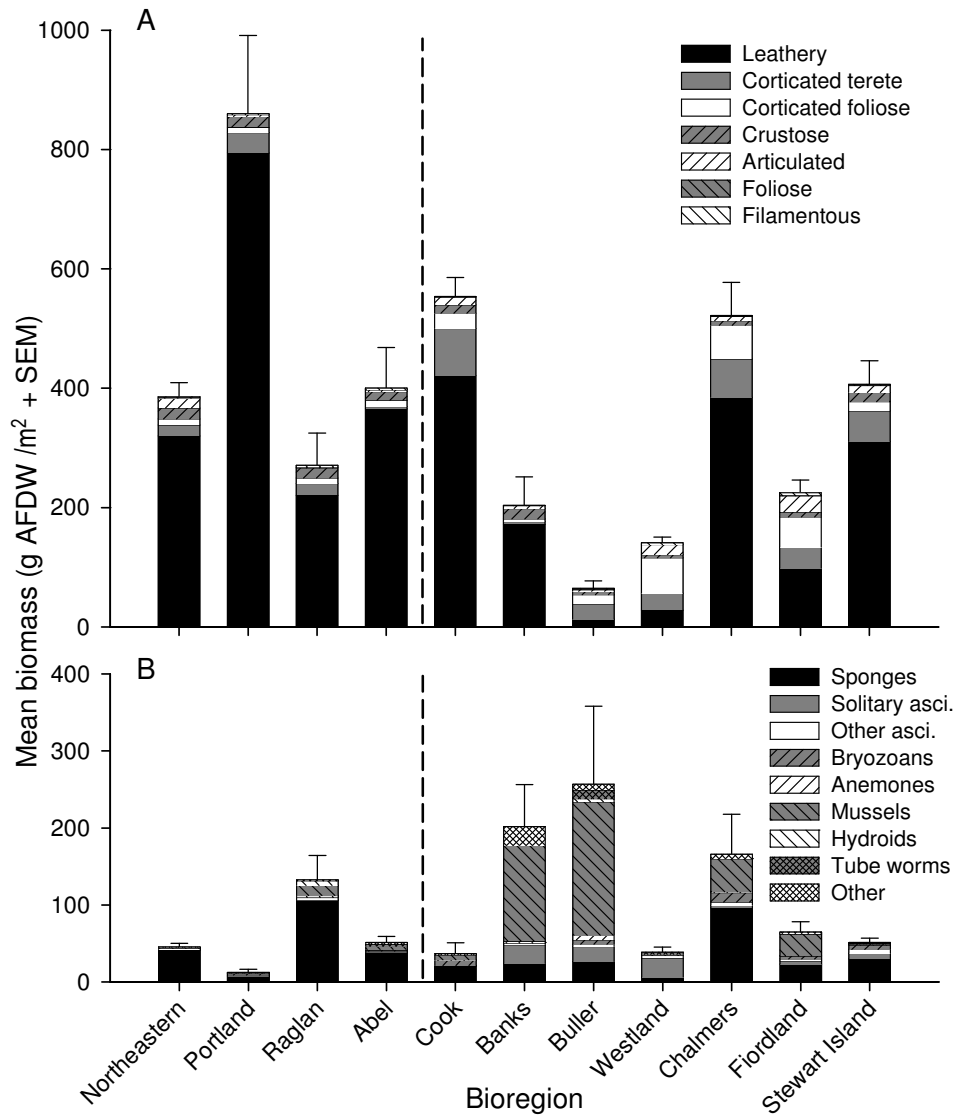
Other structural groups were locally abundant at specific locations, e.g. black coral at Fiordland locations; sea tulips at Banks Peninsula and Chalmers locations (data not presented).

3.4 BIOREGIONAL PATTERNS IN BENTHIC COMMUNITIES

3.4.1 Northeastern bioregion

There was large variation in algal community structure among sites within and between locations in the Northeastern bioregion (Fig. 12). However, consistent patterns were apparent among sites in relation to the environmental variables which explained 39% of the variation (Table 4). Hierarchical cluster analysis divided Northeastern sites into five groups at the 70% similarity level that broadly corresponded to large-scale differences in wave exposure (Fetch) among sites (Fig. 12A). PC1 was strongly correlated with several environmental variables (Fig. 12B) and reflected a gradient in algal community structure from exposed
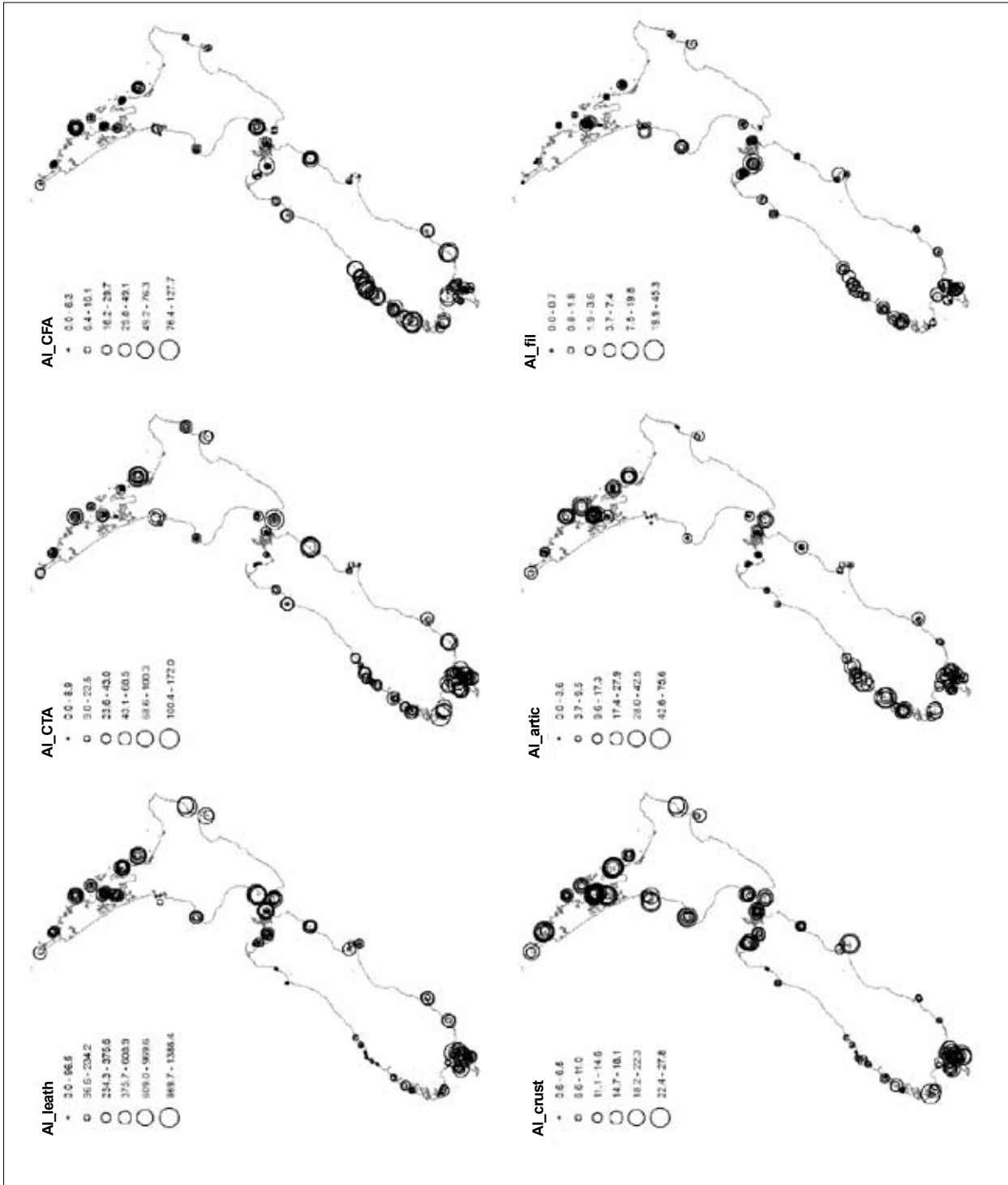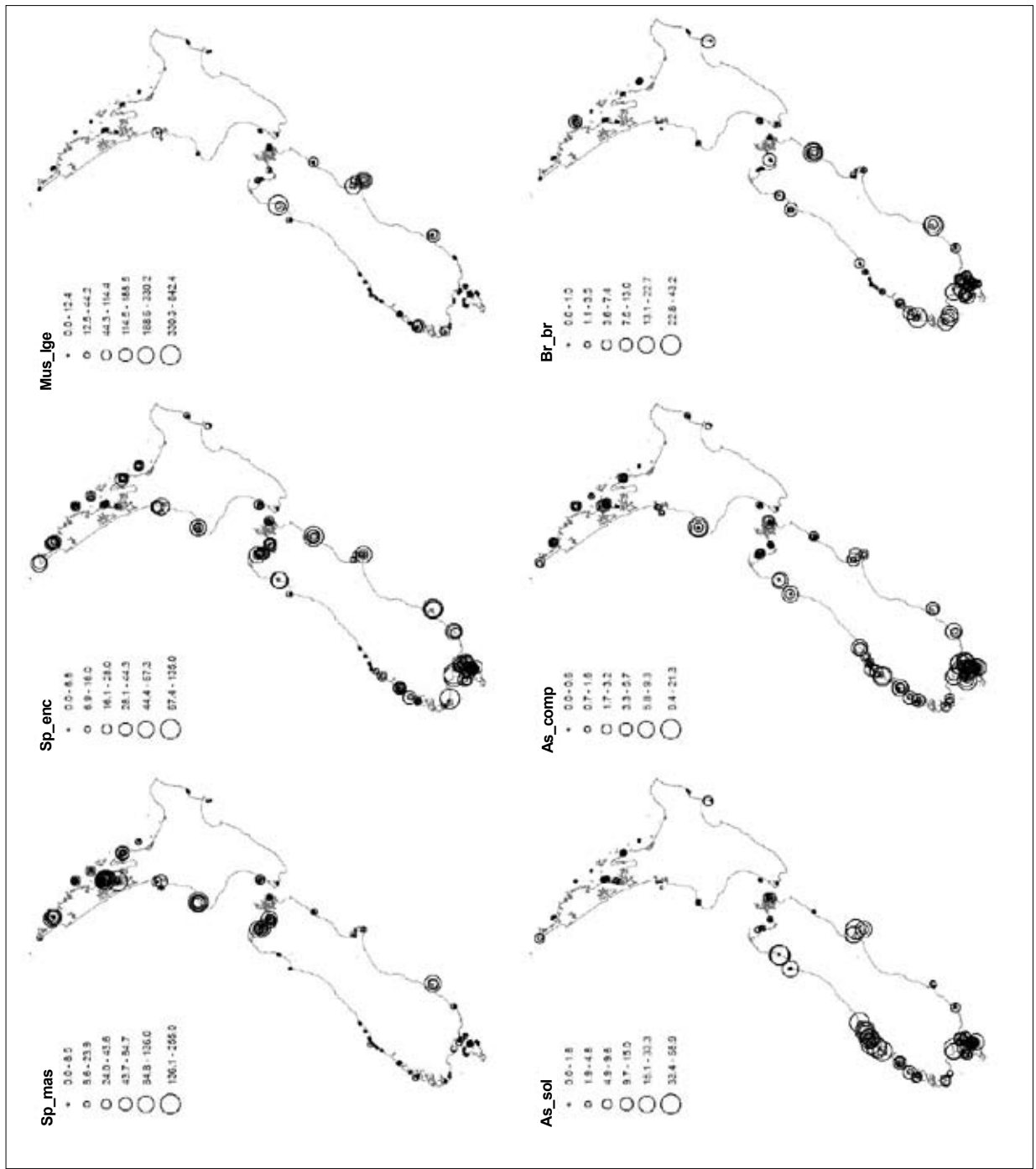
Figure 11A. Biomass of dominant structural groups (g AFDW/m^2) at all sites: algal groups. See Table 2 for structural group codes.

Figure 11B. Biomass of dominant structural groups (g AFDW/m²) at all sites: sessile invertebrate groups. See Table 2 for structural group codes.

and offshore sites with steeply sloping reefs and clear water to more gradually sloping, sheltered coastal sites with high turbidity and a high percentage cover of sediment (e.g. Long Bay). Evechinus was also negatively correlated with PC1 and tended to be more common at exposed locations. There was a clear gradient in the organisation of algal communities across this large environmental gradient. *Carpophyllum flexuosum* was positively correlated with PC1 and was most abundant at sheltered sites, whereas *Lessonia variegata*, red turfing algae, coralline turf and green algae (e.g. *Ulva* spp.) were negatively correlated and were more characteristic of exposed and/or offshore sites (Fig. 12C). Similar groupings of Northeastern sites in relation to wave exposure were identified and described for each location in Shears & Babcock (2004b). Therefore, overall patterns in reef communities for each exposure group (Fig. 12) are summarised below for all locations combined.

Sheltered group

This group included all Long Bay sites and the most sheltered site from Hahei (Mussel Rock) (Fig. 12A). The shallow stratum (< 2 m) was characterised by high biomasses of *Carpophyllum maschalocarpum* and to a lesser extent *Ecklonia radiata* (Fig. 13A), while the 4–6 m depth range was dominated by *C. flexuosum*. A number of other brown algal species were also common at these sites, e.g. *C. plumosum*, *Cystophora retroflexa*, *Sargassum sinclairii* and *Zonaria* spp.

Figure 12. Principal coordinates analysis of sites sampled in the Northeastern bioregion, based on fourth-root transformed biomass of 23 macroalgal groups (A). Bi-plots give correlations between principal coordinates axes and environmental variables (B) and original macroalgal species groups (C) (see Table 1 for macroalgal group codes). Sites shaded according to groupings identified at the 70% similarity level. White = sheltered, grey = moderately exposed, black = exposed-offshore, LT = Lighthouse, PP and TP = P-Point and Ti Point, respectively.
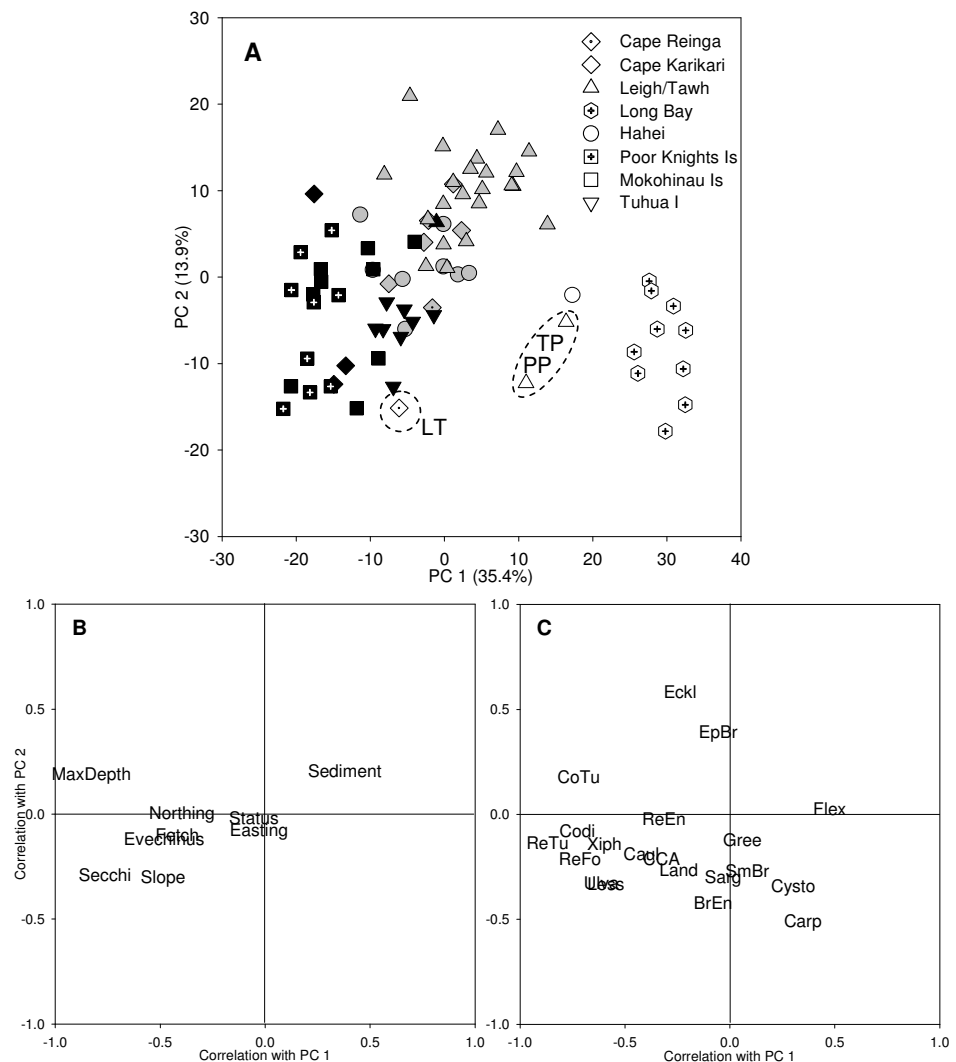
(data not presented). Red foliose and turfing algae were rare across both depths. *Evechinus chloroticus* was rare at all sites, *Turbo smaragdus* occurred at high densities in the < 2 m stratum, and *Trochus viridis* was abundant at 4–6 m (Fig. 13B). Crustose coralline algae ('CCA') were the dominant substratum cover (> 70%), but sediment also covered a considerable proportion of reef (10–20%) (Fig. 13C).

Ti Point and P-Point

These two sites at Leigh and Tawharanui formed their own group at the 70% similarity level (Fig. 12A). Unlike other sites at these locations, the reef at both sites was inundated with sand at c. 5 m of depth. *Carpophyllum maschalocarpum* dominated the shallow stratum (< 2 m), whereas the reef at 4–6 m was relatively devoid of large brown macroalgae and sea urchins were common (Fig. 13A). Moderate numbers of *Turbo smaragdus* were recorded in the shallow stratum, whereas *Trochus viridis* and *Cellana stellifera* were most abundant at 4–6 m (Fig. 13B). Crustose coralline algae were the dominant substratum cover, but sediment covered a considerable proportion of reef at 4–6 m, and turfing and foliose algae were rare (Fig. 13C).

Moderately exposed group

The moderately exposed group included the remaining coastal sites, excluding Sunburn Point, Takini South and Pihoaka Point at Cape Karikari, Cape Rodney at Leigh and Tapotupotu at Cape Reinga, which were grouped in the Exposed-offshore group, as well as the highly exposed Lighthouse site (Cape Reinga), which formed its own group (Fig. 12A). Algal communities at these sites had a bimodal depth distribution with *Evechinus chloroticus* abundant in the 4–6 m depth stratum and peaks in algal biomass in the shallow (< 2 m) and deeper (7–9 m and 10–12 m) strata (Fig. 13A). *Carpophyllum maschalocarpum* dominated the < 2 m stratum, although *C. plumosum*, *Ecklonia radiata*, coralline turf, red turfing and red foliose algae were also abundant in the shallow stratum at some sites. *Carpophyllum angustifolium* and *Lessonia variegata* were common components of this shallow stratum at some of the more exposed sites in this group; however, *C. angustifolium* was not recorded at Cape Karikari or Cape Reinga. At some sites (e.g. sites in the following reserves: Cape Rodney-Okakari Point Marine Reserve, Tawharanui Marine Park, Te Whanagnui-a-Hei (Cathedral Cove) Marine Reserve), the 4–6 m depth stratum was dominated by a mixture of *E. radiata*, *C. maschalocarpum* and *C. flexuosum*. At Koware South (Cape Karikari), *C. flexuosum* (sheltered morphology) dominated the 4–6 m stratum. For the remaining sites, *Evechinus chloroticus* was common and macroalgal biomass reduced at this depth. *Evechinus chloroticus* was rare in the deeper strata (7–9 m, 10–12 m) across all sites in this group and forests of *Ecklonia radiata* dominated. The understorey was dominated by crustose coralline algae, coralline turf, and to a lesser extent sponges, ascidians and small brown algae such as *Zonaria* spp. and *Distromium scottsbergii* (Fig. 13C). The percentage cover of sediment tended to increase with depth, on average covering c. 30% of the substratum at 10–12 m. Herbivorous gastropods occurred at relatively high densities at sites within this group (Fig. 13B). *Cookia sulcata* was the most abundant in the 0–2 m and 4–6 m strata, whereas *Trochus viridis* and *Cantharidus purpureus* were most abundant in the deeper strata and associated with *E. radiata*. *Cellana stellifera* was most abundant at 4–6 m and associated with *Evechinus chloroticus*, whereas the predatory gastropod *Dicathais orbita* occurred across all depths.

Figure 13. Depth-related patterns in biomass (g AFDW/m²) of dominant macroalgal groups and density of *Evechinus chloroticus* (A), density of common mobile invertebrates (B) and cover of common encrusting forms (C) for site groups within the Northeastern bioregion. See Shears & Babcock (2004b) for description of groups within each location for the Northeastern bioregion.
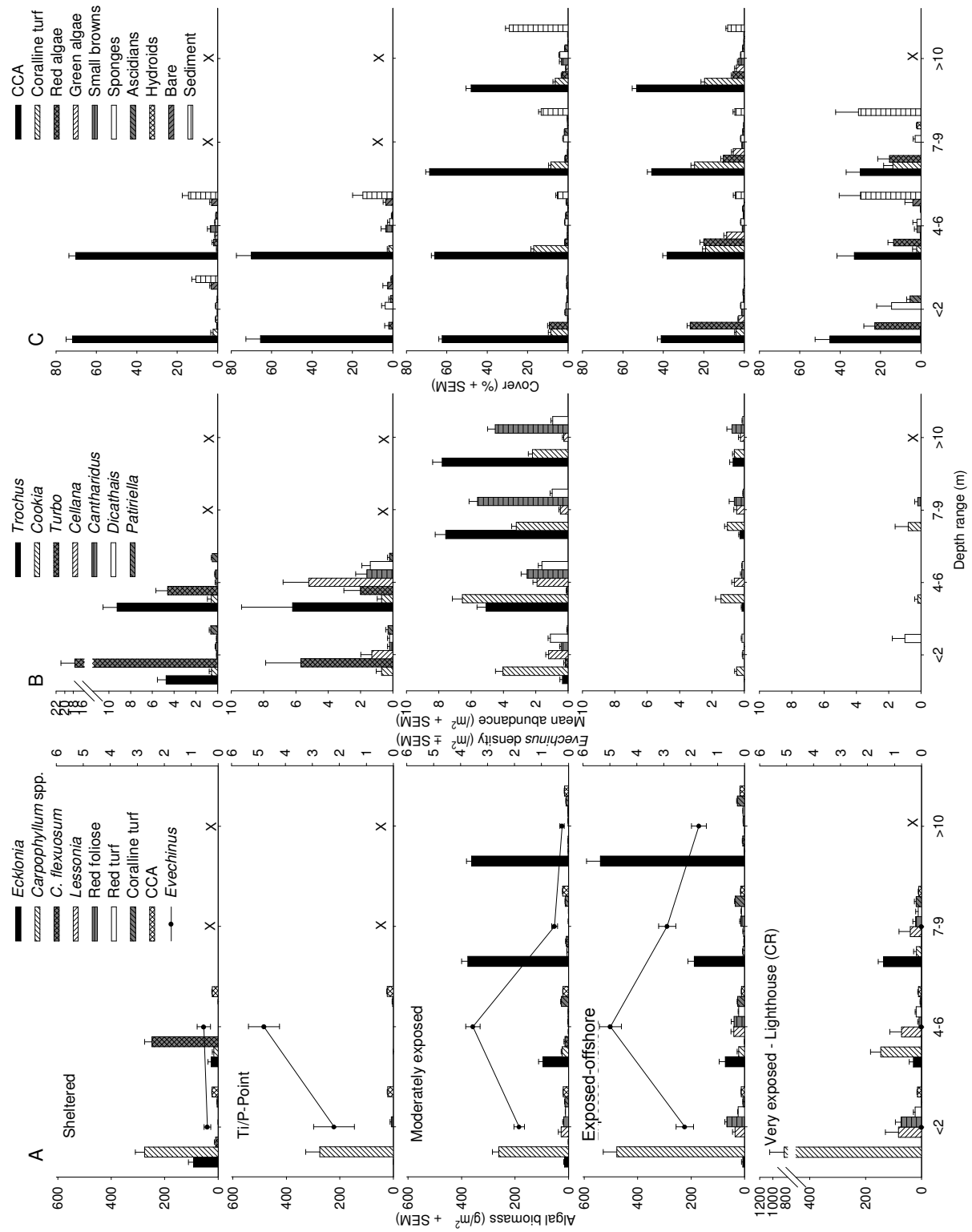
Exposed-offshore group

This group included all offshore island sites, and four of the most exposed coastal sites (Sunburn Point, Takini South, Pihoaka Point and Cape Rodney) (Fig. 12A). Algal community structure at sites in the exposed-offshore group also had a bimodal depth distribution, although sea urchins were abundant to depths of c. 8 m and the biomass of *Ecklonia radiata* was generally reduced (Fig. 13A). The shallow stratum (< 2 m) was dominated by *Carpophyllum angustifolium* and/or *C. maschalocarpum* with *Lessonia variegata*, red foliose and red turfing algae also common. The mid-depth ranges (4–6 m and 7–9 m) were characterised by mixed large brown algae (*L. variegata*, *C. maschalocarpum* and *E. radiata*) interspersed with sea urchins, and patches of coralline turf, red turf, red foliose algae and green algae, mainly *Ulva* spp. and *Caulerpa flexilis*. *Ecklonia radiata* dominated the 10–12 m stratum at most sites in this group, although at some sites sea urchins were abundant and macroalgal biomass reduced to depths of c. 12 m. Crustose coralline algae were the dominant cover at all depths, however, coralline turf, red foliose algae and green algae covered a considerable proportion of the reef at all depths (Fig. 13C). Herbivorous gastropods occurred in only low numbers (Fig. 13B), with *Cookia sulcata*, *Trochus viridis* and *Cellana stellifera* being the most common. The sea urchin *Centrostephanus rodgersii* and herbivorous gastropod *Modelia granosa* were also common in the deeper strata (7–9 m and 10–12 m) at some sites (data not presented).

Very exposed: Lighthouse (Cape Reinga)

The organisation of algal communities at this site was considerably different to that of the other Northeastern bioregion sites. Lighthouse was the most exposed Northeastern site (based on fetch estimates), but the reef was relatively gradually sloping and inundated by sand at c. 9 m. *Evechinus chloroticus* was rare and restricted to crevices at all depths, and algal biomass tended to decline with depth (Fig. 13A). *Carpophyllum maschalocarpum* dominated the immediate subtidal, whereas at greater depths mixed stands of large brown algae (e.g. *C. maschalocarpum*, *Lessonia variegata*, *Ecklonia radiata*, *C. plumosum*, *Landsburgia quercifolia*) and patches of red foliose algae (e.g. *Osmundaria colensoi*, *Pterocladia lucida*) occurred. All gastropod species were rare (Fig. 13B). Crustose coralline algae were the dominant cover at shallow depths but there was a high percentage cover of sediment (mainly coarse sand) in the deepest strata (Fig. 13C).

3.4.2 Portland bioregion

Sites from Gisborne and Mahia were clustered among Northeastern localities for all datasets (Figs 2, 6 and 9), and their algal communities were typically dominated by the same few species (*Ecklonia radiata*, *Carpophyllum maschalocarpum*, *C. flexuosum*). Algal community structure was relatively similar between sites from Gisborne and Mahia (Fig. 14), with sites from the two locations being separated at only the 77% similarity level. The correlation between environmental variables and principal coordinates axes (Fig. 14B) gives some indication of factors that may explain the differences between these locations. Sites from Gisborne and Mahia were separated along PC1 (Fig. 14A), which was strongly correlated with Secchi, MaxDepth and Slope (Fig. 14B). Gisborne sites were more turbid, had shallower, more gradually sloping reefs, and a higher biomass of *C. flexuosum*

(Figs 14C and 15A). In contrast, Mahia had clearer water and a greater biomass of coralline turf, red turf and red foliose algae (Figs 14C and 15C). All the sites sampled in this bioregion were highly exposed compared to most Northeastern locations, with similar wave exposure estimates to the Cape Reinga sites. Fetch was negatively correlated with PC2, and the biomass of *E. radiata* was positively correlated with it, with the most wave-exposed sites (Portland Island, Pouawa Reef North and Pouawa Reef South) having reduced biomass of *E. radiata*.

Algal biomass declined with depth at Gisborne and Mahia, and *Evechinus chloroticus* was rare at all depths (Fig. 15A). *Carpophyllum maschalocarpum* dominated shallow depths down to c. 6 m at Gisborne, and to c. 9 m at the more exposed Mahia sites. *Ecklonia radiata* dominated the deepest stratum at Mahia, but was mixed with *C. flexuosum* and the green algae *Caulerpa articulata* at Gisborne sites. *Landsburgia quercifolia*, *Lessonia variegata* and *Cystophora* spp. were not recorded at any of the sampling sites in this region. *Durvillaea antarctica* was common in the intertidal at both Mahia and Gisborne and in some cases small plants did extend into the shallow subtidal. The small brown algal species *Zonaria* spp. and *Carpomitra costata* were common at Gisborne, whereas *Halopteris* spp. were also common at Mahia (Appendix 5: Table A5.1). Several red foliose algal species were found in both areas, but were more common at Mahia, e.g. *Osmundaria colensoi*, *Pterocladia*

Figure 14. Principal coordinates analysis of sites sampled in the Portland bioregion, based on fourth-root transformed biomass of 23 macroalgal groups (A). Bi-plots give correlations between principal coordinates axes and environmental variables (B) and original macroalgal species groups (C) (see Table 1 for macroalgal group codes). Sites shaded according to grouping at 77% similarity level.
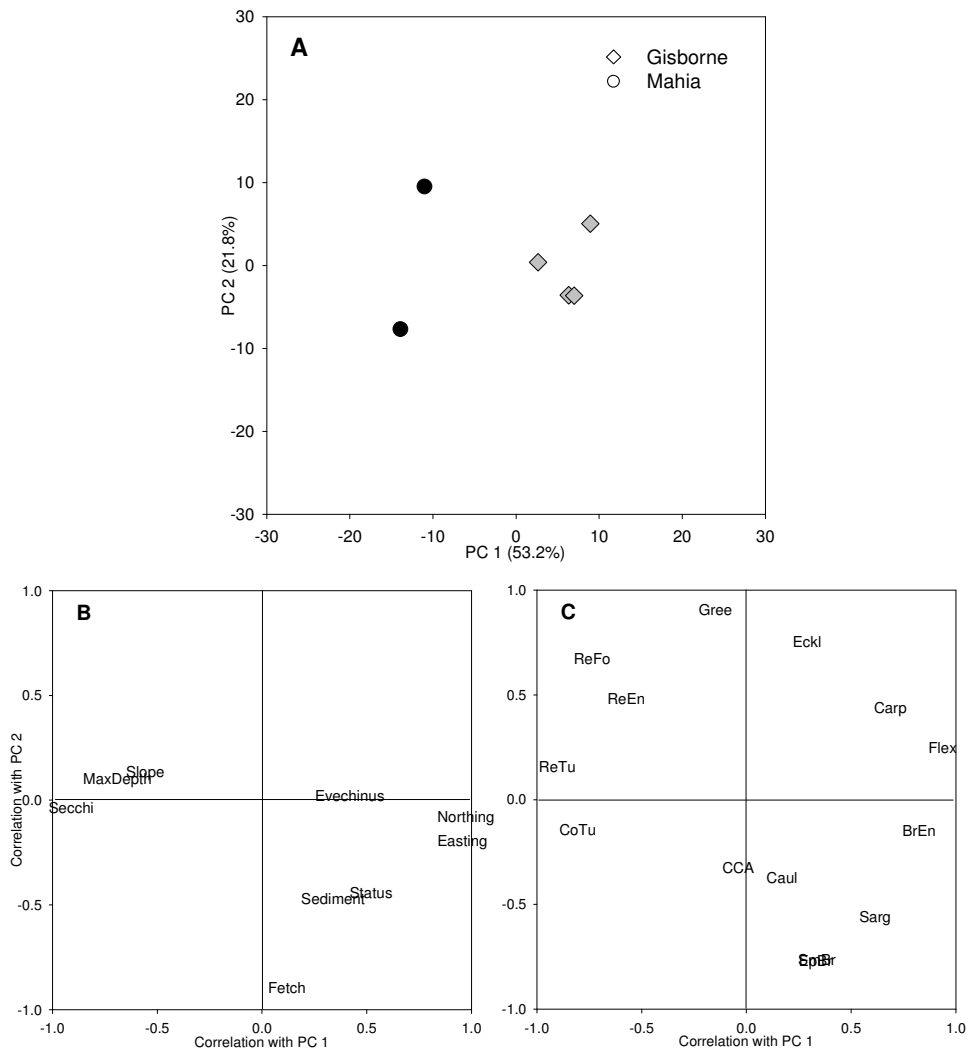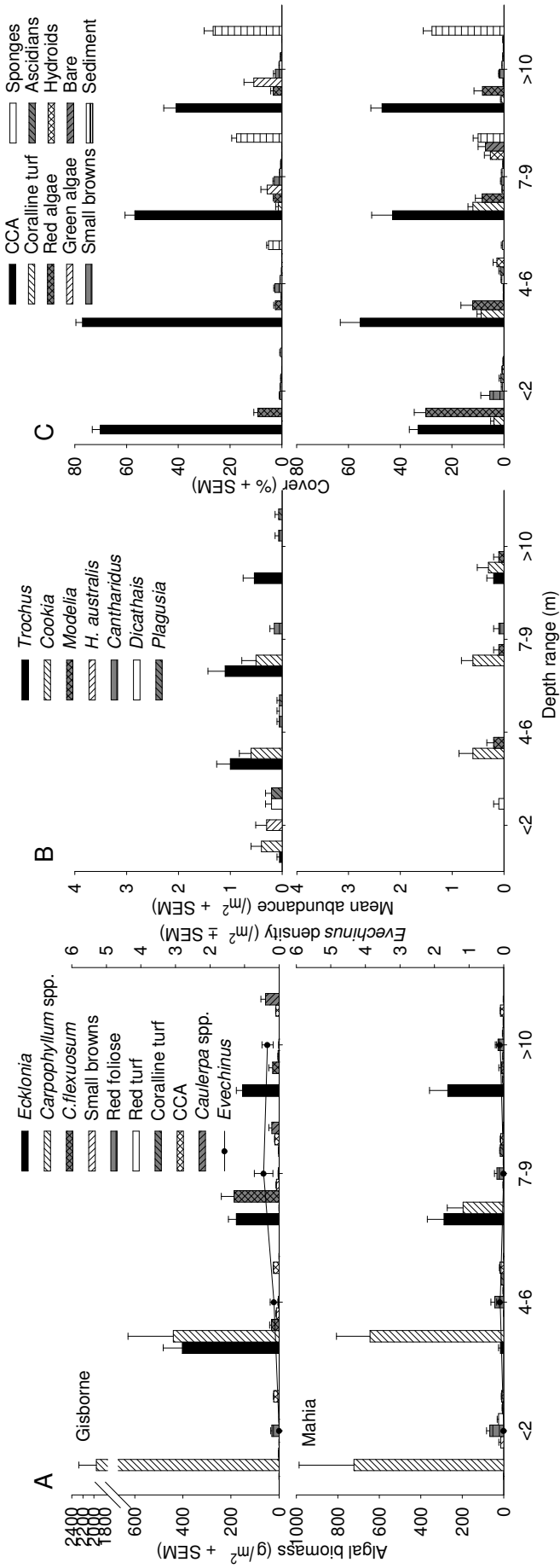
Figure 15.   Depth-related patterns in biomass (g AFDW/m²) of dominant macroalgal groups and density of *Evechinus chloroticus* (A), density of common mobile invertebrates (B) and cover of common encrusting forms (C) for site groups within the Portland bioregion.