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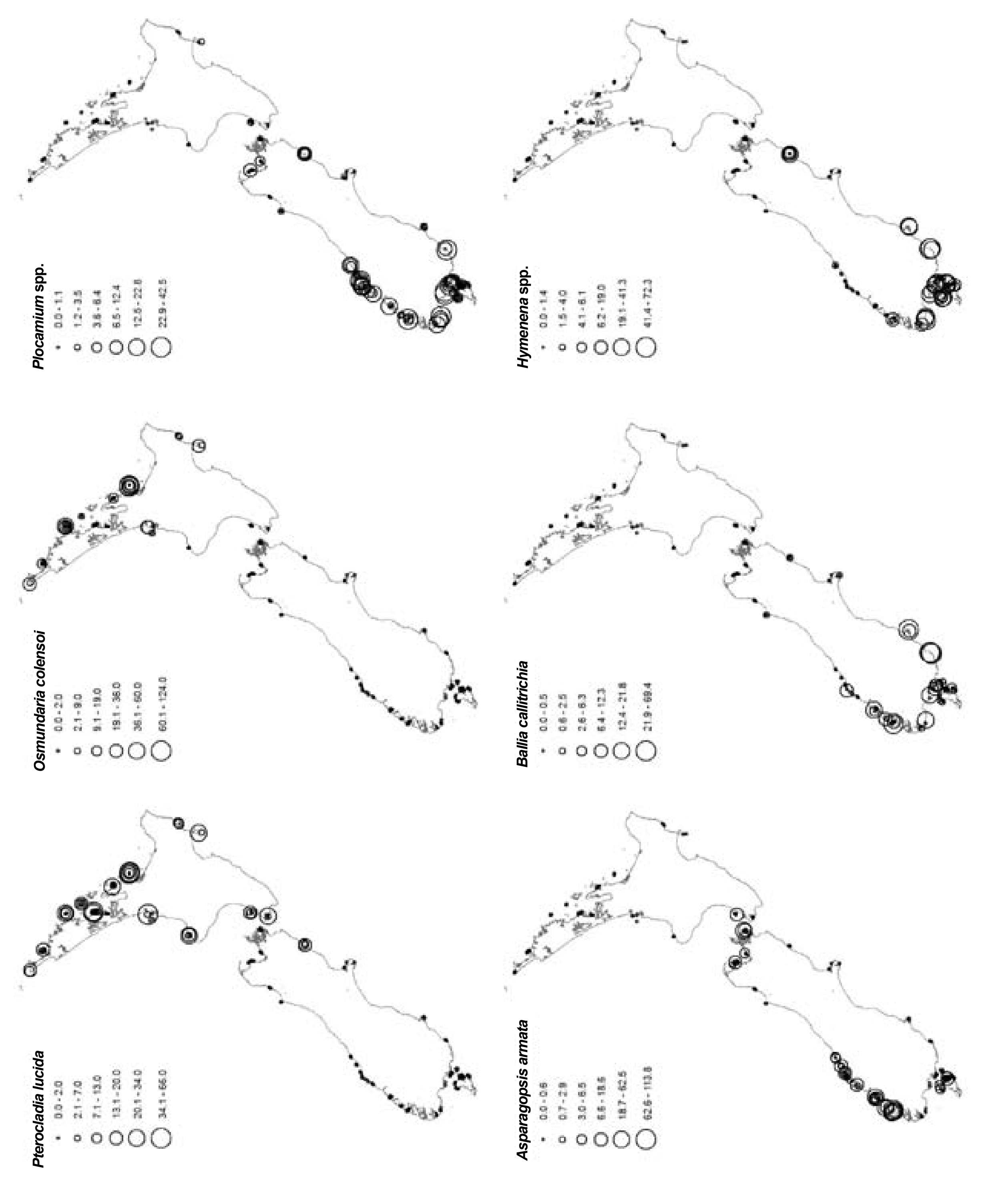


Figure 4C. Mean biomass (g AFDW/m^2) of dominant red macroalgal species at all sites, averaged across all depths sampled.

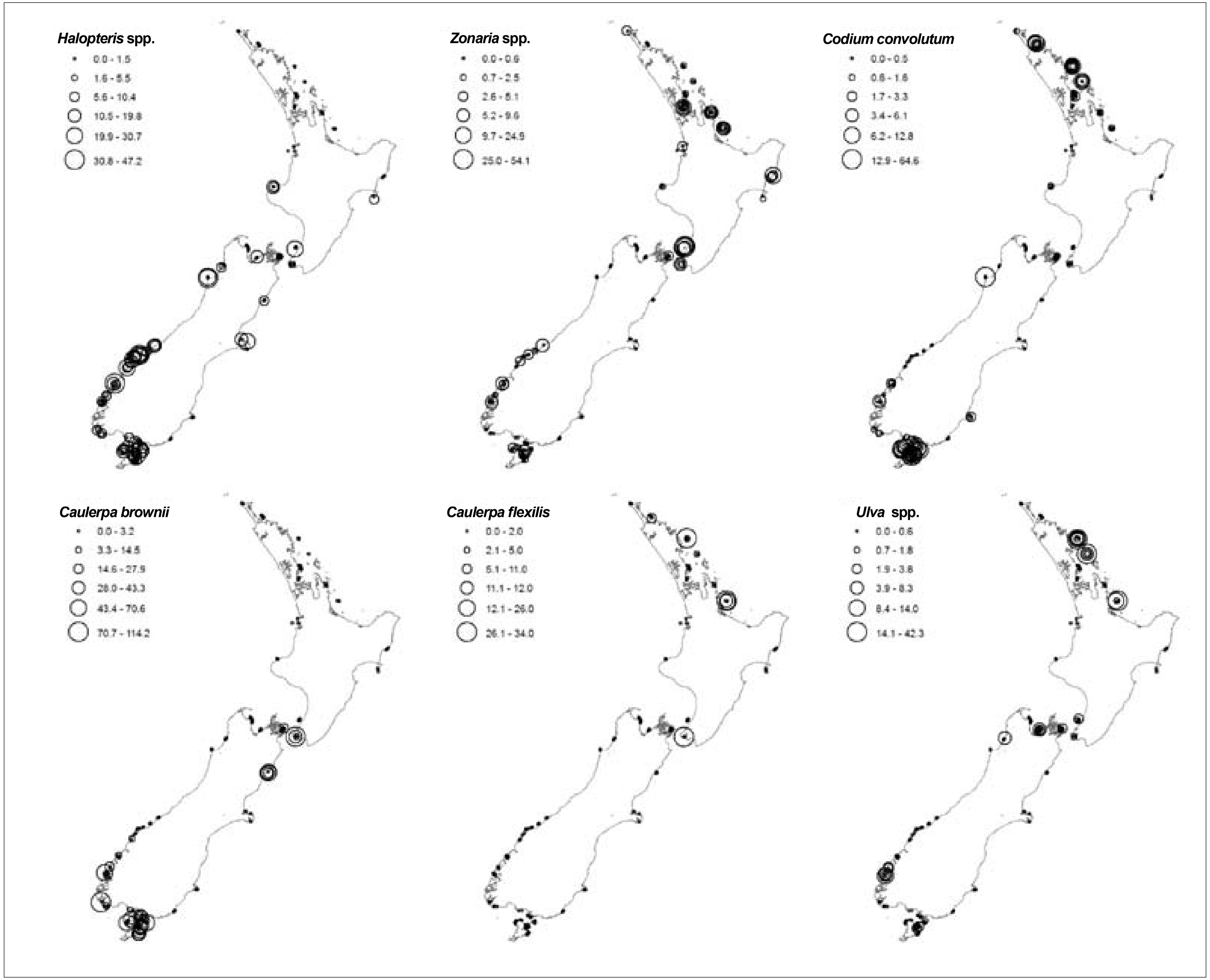


Figure 4D. Mean biomass (g AFDW/m^2) of dominant small brown and green macroalgal species at all sites, averaged across all depths sampled.

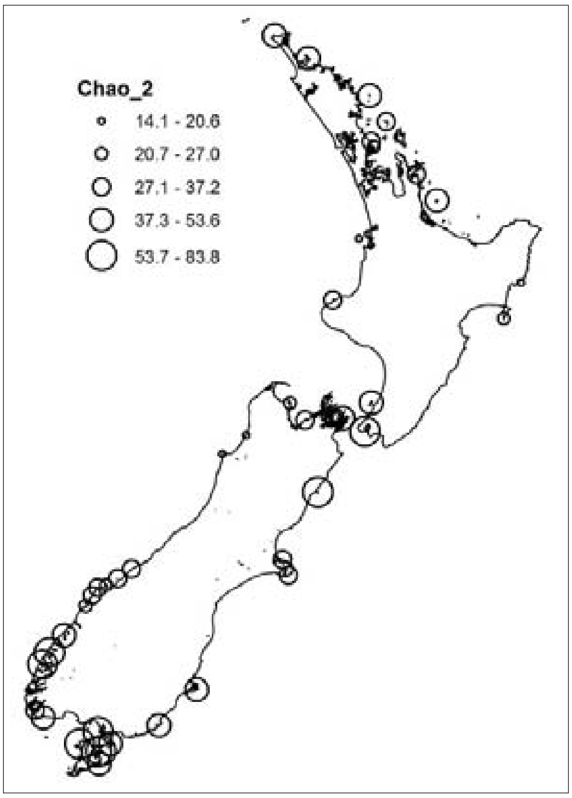
Red foliose algae were most abundant in the Cook, Chalmers and Stewart Island bioregions (Fig. 3B). Among the red foliose algae two Northern species were the greatest contributors to total algal biomass (*Pterocladia lucida* and *Osmundaria colensoi*) whereas a variety of red foliose algal species were important contributors at Southern locations, e.g. *Plocamium* spp., *Asparagopsis armata*, *Ballia callitrichia* and *Hymenena* spp (Table 3, Fig. 4C).

A variety of smaller brown algal species were found at low biomasses across all bioregions (Fig. 3B). Of these *Halopteris* spp. was the most abundant, particularly at Southern locations (Fig. 4D). *Zonaria* spp. were also common across many bioregions, but notably absent from Buller, Banks and Chalmers. Among the green algal species, *Caulerpa brownii* was the greatest contributor to overall biomass (1.2%), and was most common in Southern locations, particularly Wellington and Kaikoura. In contrast, *C. flexilis* was only found at North Island locations (Fig. 4D). Other green algal species such as *Ulva* spp. and *Codium convolutum* were common and found throughout New Zealand but were only small contributors to total algal biomass (Table 3).

3.1.3 Macroalgal species richness

There was a general trend of increasing macroalgal species richness (Chao 2 estimator, Estimate-S, Colwell & Coddington 1994) with latitude, with the highest algal diversity occurring at Southern locations (Fig. 5). There were, however, some Northern locations that had relatively high algal diversity, e.g. Cape Karikari and Northeastern offshore islands, and overall algal species richness was weakly correlated with northing ($r = -0.46$). Algal species richness was weakly positively correlated with water clarity (Secchi 0.37) and most of the locations with low species diversity were relatively turbid, e.g. Long Bay, Gisborne, Raglan, Cape Foulwind and Karamea.

Figure 5. Predicted macroalgal species richness among locations (Chao 2 estimator, Estimate-S) (Colwell & Coddington 1994).



3.2 MOBILE MACROINVERTEBRATE ASSEMBLAGES

3.2.1 National variation in mobile macroinvertebrate assemblages

The number of mobile macroinvertebrate species (Table 5) was considerably lower than the number of macroalgal species recorded in this study. Despite notable variation in macroinvertebrate assemblages among locations within bioregions (e.g. Northeastern and Stewart Island), and among sites within locations (e.g. Open Bay Islands, Raglan and Mahia), there was a general north–south gradient in macroinvertebrate assemblages along PC1 (Fig. 6A). This was reflected by the strong correlation between PC1 and the spatial variables (Fig. 6B). As for macroalgal community structure, Banks Peninsula locations were most closely clustered with Northern locations, whereas Raglan and Kapiti were more similar to Southern locations. There was a particularly high level of variation among the two Preservation Inlet sites.

Several species were negatively correlated with PC1 and are generally more abundant at Northern locations, e.g. *Evechinus chloroticus*, *Trochus viridis*, *Cookia sulcata*, *Cantharidus purpureus* and *Dicathais orbita*, whereas the

Figure 6. Mobile macroinvertebrate assemblages among sites from principal coordinates analysis based on fourth-root transformed count data of 47 species (A) (see Fig. 1 for location codes and Table 5 for species 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 original species (C). * Long Bay is distinguished from other Northeastern locations as it was not included in biogeographic analyses (Shears et al. in press).

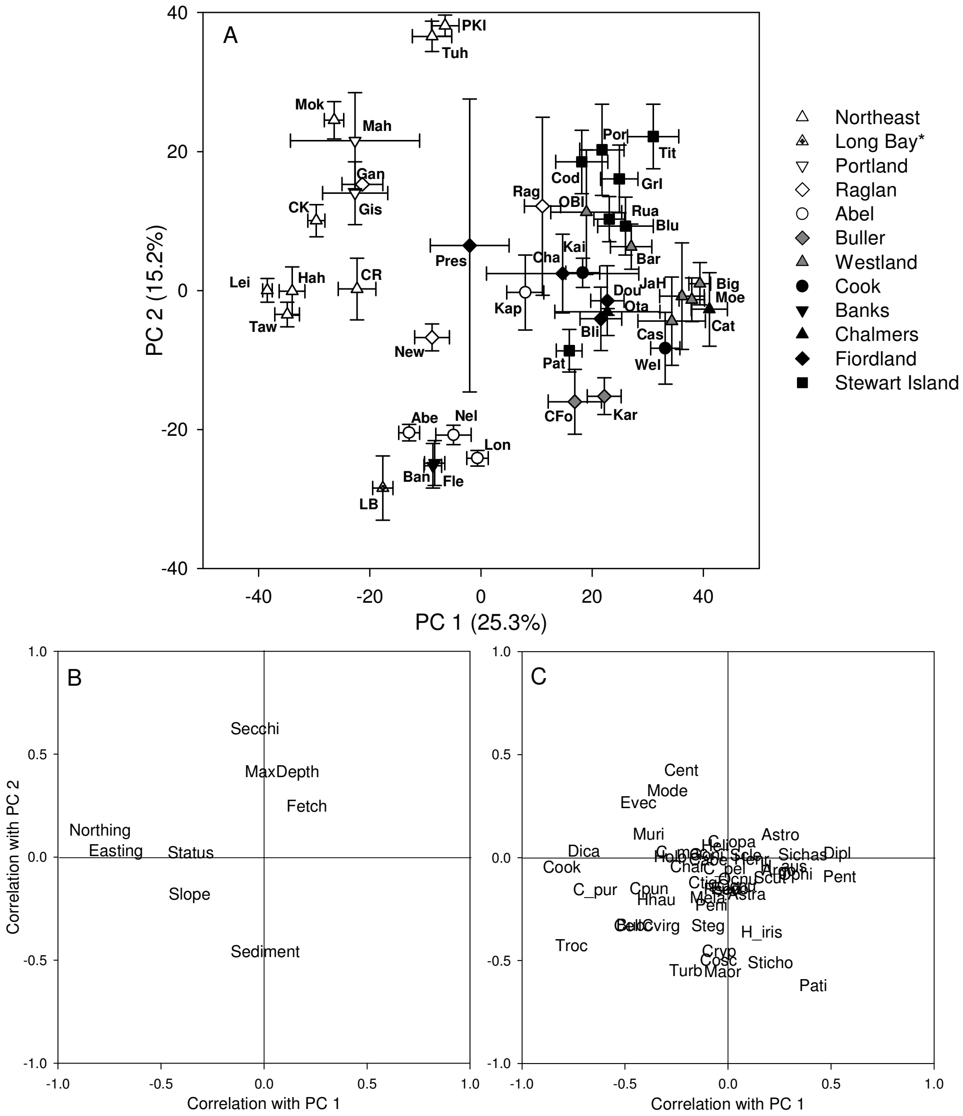


TABLE 5. MEAN ABUNDANCE OF MOBILE MACROINVERTEBRATE SPECIES RECORDED. THE DISTRIBUTIONAL PATTERNS IN ABUNDANCE OF THE DOMINANT SPECIES ARE GIVEN IN FIG. 8. CODE INDICATES SPECIES ABBREVIATIONS USED IN FIG. 6.

NO.	SPECIES	CODE	CLASS	% OCC.	MEAN	%MEAN
1	*Evechinus chloroticus*	Evec	Echinoidea	85.02	1.341	17.59
2	*Trochus viridis*	Troc	Gastropoda	56.68	1.307	17.14
3	*Cookia sulcata*	Cook	Gastropoda	59.51	0.967	12.68
4	*Turbo smaragdus*	Turb	Gastropoda	21.05	0.881	11.55
5	*Cantharidus purpureus*	C_pur	Gastropoda	32.79	0.548	7.18
6	*Cellana stellifera*	Cell	Gastropoda	54.25	0.514	6.74
7	*Patiriella* spp.*	Pati	Asteroidea	54.25	0.464	6.09
8	*Maoricolpus roseus*	Maor	Gastropoda	23.48	0.370	4.85
9	*Dicathais orbita*	Dica	Gastropoda	34.41	0.211	2.76
10	*Stichopus mollis*	Sticho	Holothuroidea	38.06	0.124	1.63
11	*Ophiopsammus maculata*	Ophi	Ophiuroidea	29.15	0.118	1.55
12	*Haliotis australis*	H_aus	Gastropoda	46.96	0.082	1.08
13	*Cominella virgata*	Cvirg	Gastropoda	12.55	0.077	1.01
14	*Modelia granosa*	Mode	Gastropoda	29.15	0.077	1.01
15	*Stichaster australis*	Sichas	Asteroidea	19.84	0.063	0.82
16	*Haliotis iris*	H_iris	Gastropoda	19.84	0.060	0.78
17	*Buccinulum lineum*	Bucc	Gastropoda	27.53	0.054	0.71
18	*Pentagonaster pulchellus*	Pent	Asteroidea	37.25	0.052	0.68
19	*Calliostoma punctulatum*	Cpun	Gastropoda	24.29	0.047	0.61
20	*Eudoxochiton nobilis*	Eudo	Polyplacophora	36.44	0.040	0.52
21	*Cryptoconchus porosus*	Cryp	Polyplacophora	22.67	0.032	0.41
22	*Coscinasterias muricata*	Cosc	Asteroidea	21.86	0.029	0.38
23	*Diplodontias* spp.	Dipl	Asteroidea	20.24	0.025	0.33
24	*Haustrum haustorium*	Hhau	Gastropoda	14.17	0.022	0.29
25	*Astraea heliotropium*	Astra	Gastropoda	8.10	0.013	0.18
26	*Centrostephanus rodgersii*	Cent	Echinoidea	8.10	0.013	0.17
27	*Stegnaster inflatus*	Steg	Asteroidea	8.50	0.012	0.16
28	*Cantharidus opalas*	C_opa	Gastropoda	13.77	0.011	0.14
29	*Melagraphia aethiops*	Mela	Gastropoda	3.64	0.009	0.11
30	*Calliostoma tigris*	Ctig	Gastropoda	7.69	0.008	0.11
31	*Ocnus brevidentis*	O_brev	Holothuroidea	1.62	0.008	0.10
32	*Scutus breviculus*	Scut	Gastropoda	6.88	0.006	0.08
33	*Muricopsis* sp.	Muri	Gastropoda	8.10	0.006	0.08
34	*Pseudechinus* sp.	Pseu	Echinoidea	1.21	0.006	0.08
35	*Penion* sp.	Peni	Gastropoda	4.86	0.006	0.07
36	*Astrostole scabra*	Astro	Asteroidea	6.48	0.004	0.06
37	*Ocnus* sp. (white)	Ocnu	Holothuroidea	1.62	0.004	0.05
38	*Holopneustes* sp.	Holo	Echinoidea	4.45	0.004	0.05
39	*Cabestana spengleri*	Cabe	Gastropoda	5.67	0.004	0.05
40	*Argobuccinulum pustulosum*	Argo	Gastropoda	4.86	0.003	0.05
41	*Charonia lampas*	Char	Gastropoda	2.83	0.002	0.02
42	*Cominella maculosa*	C_mac	Gastropoda	2.43	0.001	0.02
43	*Goniocidaris tubaria*	Goni	Echinoidea	0.40	0.001	0.01
44	*Henricia* sp.	Henr	Echinoidea	1.21	0.001	0.01
45	*Sclerasterias mollis*	Scle	Echinoidea	0.40	0.001	0.01
46	*Calliostoma pellucida*	C_pel	Gastropoda	0.81	0.001	0.01
47	*Heliocidaris tuberculata*	Heli	Echinoidea	0.40	0.001	0.01

* Recorded as *Patiriella regularis* and was not distinquished from the new species of *Patiriella* described by O'Loughlin et al. (2002).

starfishes *Diplodontias* spp., *Pentagonaster pulchellus* and *Patiriella* spp. were positively correlated with PC1 and more typical of Southern bioregions (Figs 6C and 7). Secchi and Sediment were both correlated with PC2 (Fig. 6B), and this axis appeared to reflect an environmental gradient from more oceanic locations (e.g. Titi Islands and Northeastern offshore islands) to more sheltered and/or turbid coastal locations, such as the locations Long Bay, Abel Tasman, Nelson, Long Island and Banks Peninsula. Several species were correlated to PC2 and reflected this gradient; the sea urchin *Centrostephanus rodgersii* was positively correlated and only found at Northeastern offshore locations and Cape Karikari, whereas the sea cucumber *Stichopus mollis*, starfish *Patiriella* spp., and the gastropods *Turbo smaragdus*, *Trochus viridis* and *Maoricolpus roseus* were negatively correlated and more common at the more turbid coastal locations (Figs 6C and 8).

Environmental variables explained 24% of the variation in macroinvertebrate species composition at the national level (Table 6), with Secchi being the most strongly associated (7%). The relationship between explanatory variables and species composition varied with spatial scale and among bioregions (Table 6).

Figure 7. Mean abundance of the most common mobile macroinvertebrate species (gastropods, A, and echinoderms, B) for all bioregions. Dashed line indicates division between the Northern and Southern Provinces.

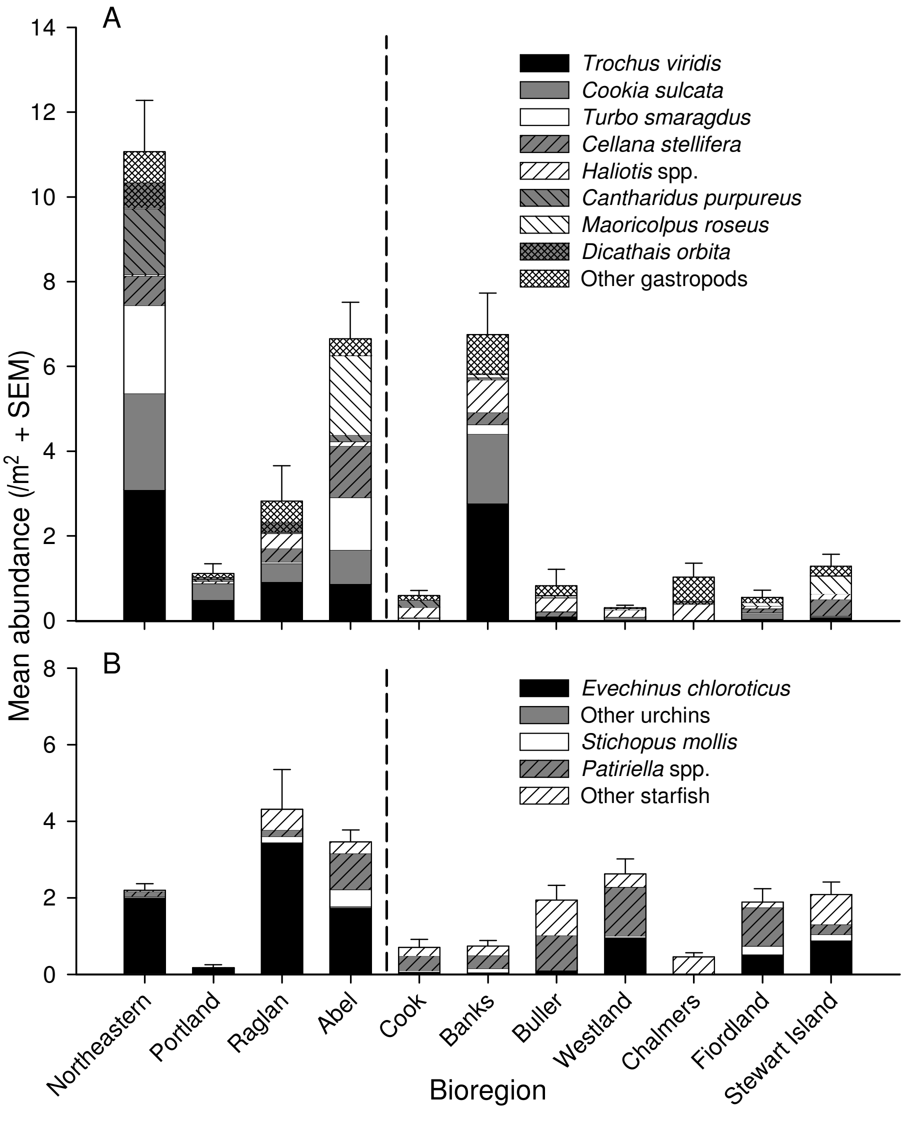


TABLE 6. RESULTS OF NON-PARAMETRIC MULTIVARIATE REGRESSION OF MOBILE MACROINVERTEBRATE ASSEMBLAGES (FOURTH-ROOT TRANSFORMED COUNT DATA), AND ENVIRONMENTAL AND SPATIAL VARIABLES AT DIFFERING BIOGEOGRAPHIC SCALES. THE PERCENTAGE VARIANCE EXPLAINED FOR EACH VARIABLE IS GIVEN (ns = NOT SIGNIFICANT), ALONG WITH THE CUMULATIVE FREQUENCY EXPLAINED FOLLOWING FORWARD SELECTION OF FACTORS (THE SIGNIFICANT FACTORS FROM THIS PROCEDURE ARE LISTED IN DESCENDING AMOUNT OF VARIATION EXPLAINED).

		BIOGEOGRAPHIC PROVINCES		BIOREGIONS		
	NZ	NORTHERN	SOUTHERN	NORTHEASTERN	ABEL	STEWARTI
n	247	135	112	81	37	42
Local variables						
Fetch	5.9	5.9	11.8	6.6	9.3	20.0
Status	3.6	ns	3.3	3.5	ns	-
Slope	4.9	4.5	1.8	12.1	5.8	ns
MaxDepth	4.5	8.5	3.7	21.6	ns	5.7
Secchi	7.3	16.4	6.3	31.3	23.4	6.0
Sediment	4.0	8.0	4.6	4.8	12.1	19.7
Cumulative %	**24.0**	**30.6**	**28.7**	**48.2**	**36.7**	**31.1**
Significant factors	All	All	All	All, excl. Slope	Secchi, Fetch, Slope	Fetch. Sediment, MaxDepth
Spatial—Northing and Easting	19.3	20.8	18.7	30.7	31.3	16.8

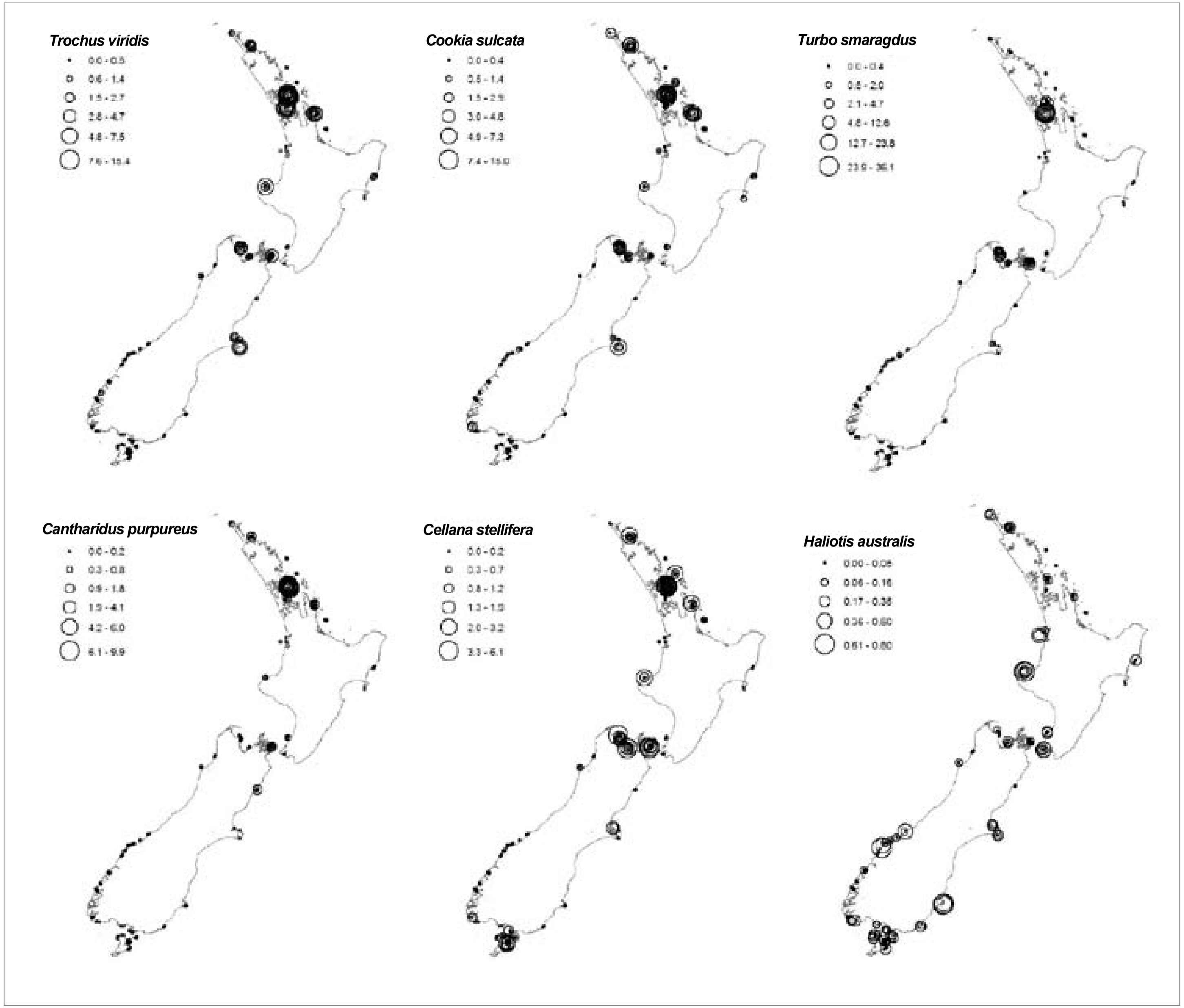
Secchi explained the greatest variation for the Northeastern and Abel bioregions, while Fetch and Sediment were most important in the Stewart Island bioregion. The proportion of variation explained by environmental variables tended to increase with decreasing spatial scale.

3.2.2 National patterns in dominant mobile macroinvertebrate species

There was large variation in the total number of mobile invertebrates among bioregions (Fig. 7) and also among sites and locations within each bioregion (section 3.4). Total numbers were low (< $2/m^2$) at Portland, Cook and Chalmers, whereas at Northeastern, Abel and Banks, herbivorous gastropods such as *Trochus viridis*, *Cookia sulcata* and *Turbo smaragdus* were common and total numbers exceeded $8/m^2$ (Figs 7A and 8A).

Evechinus chloroticus was the most commonly recorded mobile macroinvertebrate (Table 5), and was recorded at all locations except Karamea, Flea Bay and Catlins (Figs 7B and 8B). It was also particularly rare at several locations, e.g. Mahia, Kaikoura and Otago Peninsula. The abundance of *E. chloroticus* was generally highest in Northern bioregions (Fig. 7B) and, overall, was positively correlated with the Northing variable ($r = 0.36$). At the national level, Secchi explained the greatest variation (15%) in the abundance of *E. chloroticus* (Table 7) and was positively correlated across all sites ($r = 0.39$). Secchi also explained the greatest variation among sites in the Northeastern bioregion (28.5%), where *E. chloroticus* are rare at sheltered and turbid coastal sites (see section 3.4.1). In contrast, within the Abel bioregion, MaxDepth (23%) was found to be the

Figure 8A. Mean abundance (per m^2) of dominant mobile macroinvertebrates at all sampling sites: herbivorous gastropods.



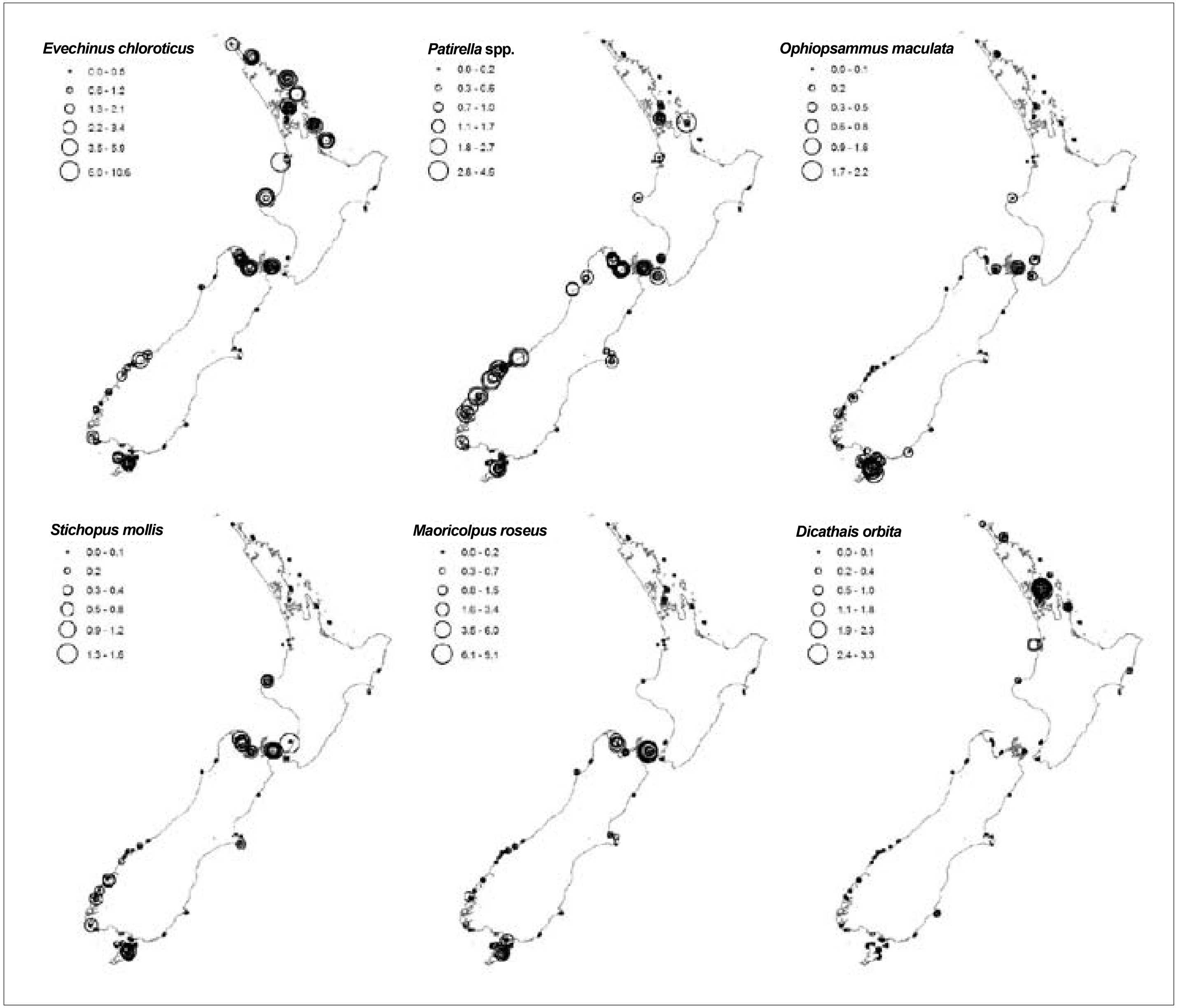


Figure 8B. Mean abundance (per m^2) of dominant mobile macroinvertebrates at all sampling sites: echinoderms and other gastropods.

most important variable (Table 7). This was due to a few sites with shallow reefs (< 9 m depth) having high urchin densities. Fetch explained the greatest variation in the abundance of *E. chloroticus* among sites in the Stewart Island bioregion as the highest densities were recorded at sheltered sites in Paterson Inlet. For both Abel and Stewart Island there was no clear gradient in water clarity among sites or locations.

The size distributions of populations of *E. chloroticus* among the locations sampled exhibited some clear biogeographic patterns (Appendix 6). In most Northern bioregions, there were relatively high numbers of juveniles, most urchins were less than 100 mm TD, and the maximum size was c. 125 mm TD. One exception was Portland, where urchins occurred at low numbers and the population structure resembled Southern bioregions, with urchins generally larger than 100 mm TD and juveniles rare. At Open Bay Islands, Preservation Inlet and Paterson Inlet, where *E. chloroticus* was abundant, few individuals with a TD of less than 70 mm were recorded. Overall, *E. chloroticus* reached much greater sizes in Southern locations, with the maximum size recorded being 190 mm TD at Edwards Island (Titi Islands).

Trochus viridis and *C. sulcata* were the most common and abundant herbivorous gastropods nationwide (Table 5). Both species had similar distributions, being most abundant at locations in Northeastern, Abel and Banks bioregions (Fig. 8A). *Turbo smaragdus* was also one of the most abundant gastropods, but this was largely due to high densities at a number of sheltered locations, e.g. Nelson, Long Island and Long Bay. The limpet *Cellana stellifera* was generally most abundant in locations with high urchin abundances such as Northeastern and Abel locations, as well as New Plymouth and Paterson Inlet. The abalone *Haliotis australis* was also relatively common, but found at relatively low numbers throughout the country. A number of echinoderm species such as *Patiriella* spp., *Ophiopsammus maculata* and *Stichopus mollis* were found throughout the country, but tended to be more abundant on shallow reefs in southern regions (Figs 7B and 8B).

TABLE 7. RESULTS OF STEP-WISE MULTIVARIATE REGRESSION OF THE ABUNDANCE OF *Evechinus chloroticus*, AND ENVIRONMENTAL AND SPATIAL VARIABLES, AT DIFFERING BIOGEOGRAPHIC SCALES. THE *F*-VALUE AND PERCENTAGE VARIANCE EXPLAINED FOR EACH VARIABLE SELECTED FOR THE MODEL IS GIVEN. STATISTICALLY SIGNIFICANT VARIABLES ARE INDICATED BY: * = $P < 0.05$, ** = $P < 0.01$ AND *** = $P < 0.001$). THE R-SQUARED VALUE FOR EACH TEST IS ALSO GIVEN.

NZ			NORTHEASTERN			ABEL			STEWART I		
VARIABLE	*F*	%	VARIABLE	*F*	%	VARIABLE	*F*	%	VARIABLE	*F*	%
Local											
(R^2 = 0.17)			(R^2 = 0.33)			(R^2 = 0.33)			(R^2 = 0.40)		
Secchi	43.1***	15.0	Secchi	33.0***	28.5	MaxDepth	11.6**	23.0	Fetch	27.0***	40.3
Fetch	10.7**	4.2	Fetch	4.2*	5.0	Secchi	4.9*	9.7			
Spatial—Northing and Easting											
	19.4***	13.7		14.9***	27.7		12.0***	41.4		6.3**	24.3

3.3 BENTHIC COMMUNITY STRUCTURE

3.3.1 National variation in benthic community structure

There was a general gradient in the structure of benthic communities (biomass of algae and sessile invertebrates combined; Table 8) between Northern and Southern locations along PC1 (Fig. 9A). However, this axis of greatest variation (PC1) also appeared to more strongly reflect a gradient from sheltered Northern locations (Long Bay) to highly exposed West Coast locations at Buller and Westland. This was reflected by the correlation between PC1 and Fetch (Fig. 9B). Benthic community structure changed along this axis from being dominated by crustose and leathery algae to domination by corticated terete and corticated foliose algae, as indicated by the correlations between these groups and PC1 (Fig. 9C). PC2 was correlated with Secchi and Sediment. Therefore, it appears that PC2 reflects a gradient in community structure from turbid sites (bottom portion of ordination, Fig. 9A), where invertebrates (e.g. encrusting bryozoans, solitary ascidians, serpulid tube worms, mussels, oysters and cup corals) were

TABLE 8. CONTRIBUTION OF 29 STRUCTURAL GROUPS TO TOTAL BIOMASS (AFDW) OF BENTHIC COMMUNITIES AND THE PERCENTAGE OF ALL SITES AT WHICH EACH GROUP OCCURRED (% OCC.)

PHYLA	STRUCTURAL GROUP	MEAN (g/m^2)	% TOTAL	% OCC. (SITES)
Algae	Leathery macrophytes	286.45	66.91	95.55
Algae	Corticated terete algae	27.86	6.51	93.52
Algae	Corticated foliose algae	19.75	4.61	98.79
Porifera	Massive sponge	18.04	4.21	74.90
Porifera	Encrusting sponge	16.52	3.86	94.33
Algae	Crustose algae	14.64	3.42	100.00
Mollusca	Large mussels	12.33	2.88	23.89
Algae	Articulated algae	12.10	2.83	90.69
Ascidian	Solitary ascidian	5.67	1.32	88.66
Bryozoan	Branched bryozoan	2.30	0.54	54.66
Ascidian	Compound ascidian	1.94	0.45	83.81
Algae	Filamentous	1.68	0.39	88.66
Porifera	Finger sponge	1.59	0.37	22.67
Mollusca	Small mussels	1.17	0.27	2.02
Annellida	Serpulid tubeworms	1.12	0.26	21.86
Ascidian	Sea tulip	1.08	0.25	21.86
Algae	Foliose algae	0.92	0.21	38.06
Coelenterate	Colonial anemone	0.85	0.20	53.44
Hydrozoa	Hydroid turf	0.51	0.12	46.56
Crustacea	Barnacles	0.40	0.09	17.81
Ascidian	Stalked ascidian	0.35	0.08	40.08
Coelenterate	Cup coral	0.27	0.06	19.84
Mollusca	Oyster	0.20	0.05	16.60
Coelenterate	Large solitary anemone	0.18	0.04	32.79
Bryozoan	Encrusting bryozoan	0.17	0.04	41.30
Coelenterate	Black coral	0.01	0.00	2.02
Coelenterate	Soft coral	0.01	0.00	3.24
Hydrozoa	Hydroid tree	0.01	0.00	3.24
Brachiopod	Brachiopod	0.01	0.00	4.05

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