Quantitative description of mainland New Zealand's shallow subtidal reef communities

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Cover: New Zealand's common sea urchin *Evechinus chloroticus* feeding on blades of the dominant kelp *Ecklonia radiata* at Leigh, northeastern New Zealand.
Photo: N.T. Shears.

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ABSTRACT

Conservation and management of the marine environment requires a general understanding of how biological communities differ from place to place and the major factors that control them. Current knowledge of the ecology of New Zealand's subtidal reefs is limited, being based on studies from a small number of locations. In this study, surveys of shallow subtidal reef communities were carried out at 43 locations (247 sites) throughout mainland New Zealand. National and regional patterns in community structure are described, and their relationships with environmental variables are investigated. The shallow reefs (< 12 m depth) surveyed were generally typical of temperate systems, being dominated by large leathery seaweeds. However, other algal groups, sponges, mussels, ascidians and bryozoans were also abundant at some places where large seaweeds were rare, e.g. locations subjected to extreme wave action and poor water clarity (Raglan, Karamea, Cape Foulwind, Jackson Head), or where sea urchins (*Evechinus chloroticus*) were abundant (Gannet Rock, Abel Tasman, Nelson, Paterson Inlet). Strong associations were found between the biological patterns and environmental conditions such as water clarity and wave exposure, but these associations differed among regions. This unprecedented New Zealand-wide survey of subtidal reefs provides a framework for marine conservation planning and further ecological study, and a valuable baseline for assessing change associated with environmental variation, human-related impacts and management actions (e.g. marine reserves).

Keywords: bioregions, community structure, kelp forests, macroalgae, macroinvertebrates, marine reserves, sea urchins, temperate reefs

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1. Introduction

The systematic collection of biological data and description of patterns across large spatial scales is necessary for understanding important structuring processes and trophic relationships in communities (Underwood et al. 2000). Furthermore, large-scale studies aid in interpreting variability seen across smaller spatial scales (e.g. Broitman et al. 2001). From a conservation management perspective, the collection of quantitative data on species composition and community structure over a variety of spatial scales is valuable not only for developing a large-scale biogeographic framework for systematic planning (Lourie & Vincent 2004), but also for understanding local- and regional-scale variation in biodiversity. This is essential to ensure that conservation efforts achieve their goals of establishing networks of marine protected areas that are representative and comprehensive (Day et al. 2002). Systematically collected biological data also provide a valuable baseline for assessing changes associated with management actions (e.g. establishment of marine reserves), anthropogenic disturbance, introduced species and environmental change.

Shallow subtidal reef communities represent one of the most productive habitats in temperate marine ecosystems (Schiel & Foster 1986) and are of enormous commercial, recreational and cultural value to society. These habitats are typically dominated by large brown algae of the orders Laminariales and Fucales (Schiel & Foster 1986), although in many systems throughout the world grazing by sea urchins may remove large areas of kelp forest and form an 'urchin barrens' habitat (Lawrence 1975; Harrold & Pearse 1987). In addition to grazing by sea urchins and to a lesser extent fishes (Jones & Andrew 1990), the organisation of an algal community is strongly influenced by the life history characteristics of its key species (Reed 1990), as well as a variety of physical factors such as storms (Cowen et al. 1982), temperature (Leliaert et al. 2000), climatic variations (Dayton 1985), eutrophication (Eriksson et al. 2002), salinity (Schils et al. 2001), turbidity (Lumb 1989) and sedimentation (Airoldi & Virgillio 1998). Algal assemblage structure and species composition vary across environmental gradients (e.g. Harrold et al. 1988; Gorostiaga et al. 1998; Leliaert et al. 2000), and the physical factors responsible for those gradients are often strongly inter-related and covary, making it difficult to separate the effects of differing factors (Irving & Connell 2002; Schiel et al. 2006). In order to understand fundamental ecological processes, there is a need for biotic patterns to be described (Fowler-Walker & Connell 2002), and for environmental gradients to be quantified.

For mainland New Zealand, much of our understanding of subtidal reef community structure is based on descriptive studies carried out along the northeastern coast (Choat & Schiel 1982; Grace 1983; Cole 1993; Walker 1999; Shears & Babcock 2004b) and a few locations further south, e.g. Abel Tasman (Davidson & Chadderton 1994), Wellington, Kaikoura, Banks Peninsula and Fiordland (Schiel 1990; Schiel & Hickford 2001). From these studies, subtidal reef communities in New Zealand appear to be typical of most temperate areas in that they are dominated by large brown algae (Schiel 1990), and sea urchins are a conspicuous component of many reefs. The common sea urchin *Evechinus chloroticus* has been shown to have an important top-down influence on algal assemblages (Andrew

& Choat 1982; Shears & Babcock 2002) and it forms urchin barrens habitat in northern New Zealand. However, in central and southern parts of the country, urchin-dominated areas are thought to be rare (Schiel 1990; Schiel & Hickford 2001), with the exception of Abel Tasman (Davidson & Chadderton 1994) and Fiordland (Villouta et al. 2001). Descriptive studies of the northeastern part of New Zealand have shown that algal community structure and the abundance of sea urchins changes in a predictable manner over a wave-exposure gradient (Grace 1983; Cole 1993; Walker 1999; Shears & Babcock 2004b) with sea urchins being rare on sheltered reefs but becoming more prevalent, and overgrazing to greater depths, with increasing exposure. However, at the most exposed of these northeastern sites, sea urchins are rare and mixed stands of large brown algae predominate (Choat & Schiel 1982; Shears & Babcock 2004b). These findings suggest that the association between macroalgae and sea urchins varies across environmental gradients, but the applicability of findings from these studies to other regions of New Zealand is not known. In general much of the New Zealand coastline remains undescribed and our understanding of the important factors structuring algal assemblages both within and across regions in New Zealand is poor (Schiel 1990; Hurd et al. 2004).

A nationwide study of mainland New Zealand's subtidal benthic reef communities was carried out between 1999 and 2005. One component of this study has resulted in the division of the mainland New Zealand coast, based on macroalgae species composition, into two biogeographic provinces ('Northern' and 'Southern') and 11 biogeographic regions (hereafter 'bioregions') (Fig. 1; Shears et al. in press). This provides a hierarchical spatial framework for conservation planning but also for investigating ecological processes responsible for maintaining the observed patterns and their association with environmental variables. This report aims to provide a resource for ecologists and conservation workers by providing a national overview of New Zealand's subtidal reef communities, as well as descriptions of reef assemblages within bioregions and how these vary across environmental gradients.

2. Methods

2.1 STUDY LOCATIONS

Shallow subtidal reef communities were quantified at 247 sites within 43 locations throughout New Zealand (Fig. 1; see Appendices 1 and 2 for site positions). Locations were selected to provide a representative coverage of mainland New Zealand's subtidal reefs, but were somewhat determined by ease of access, availability of sufficient subtidal reef systems and sea conditions. Where conditions allowed, sites were stratified within locations across wave-exposure gradients (e.g. Fiordland and Stewart Island locations). An attempt was made to space sites every 0.5–1 km within locations; however, at exposed locations the position and number of sites were restricted by sea conditions during the sampling period. In most cases, sites with moderately sloping reefs were selected so that reefs could be sampled to a depth of 12 m. However, at some coastal locations the depth of available reef was insufficient to sample all

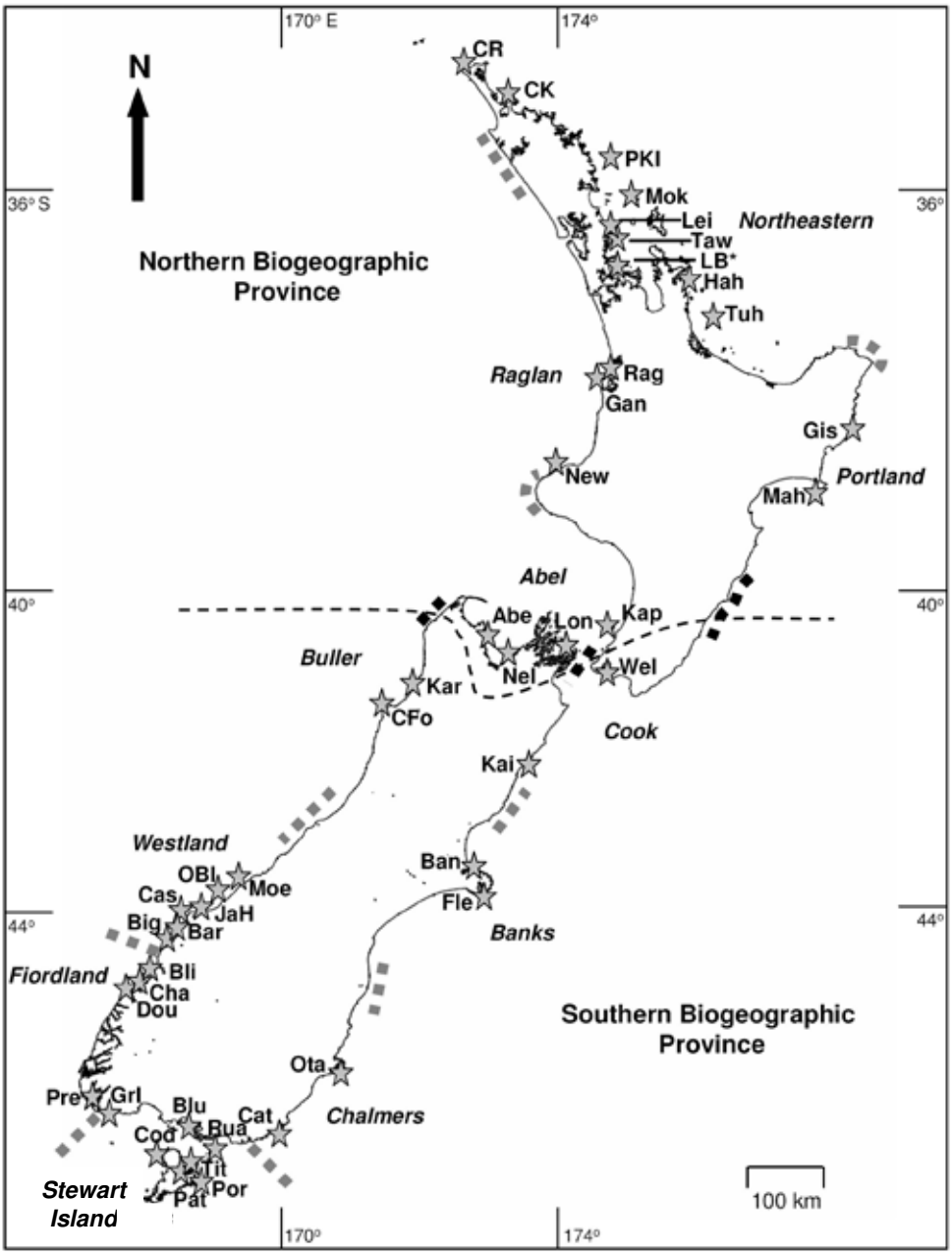

Figure 1. Sampling locations around New Zealand and the two biogeographic provinces and 11 bioregions (*italicised*) for mainland New Zealand based on macroalgal species composition (Shears et al. in press). Dashed line indicates the proposed biogeographic division between the Northern and Southern Provinces, and dashed grey bars indicate proposed transition zones between bioregions. See Appendices 1 and 2 for site positions within each location. Locations: Cape Reinga (CR), Cape Karikari (CK), Poor Knights Islands (PKI), Mokohinau Islands (Mok), Leigh (Lei), Tawharanui (Taw), Long Bay (LB) (not included in the biogeographic analyses of Shears et al. in press), Hahei (Hah), Tuhua (Tuh), Gisborne (Gis), Mahia (Mah), Raglan (Rag), Gannet Rock (Gan), New Plymouth (New), Kapiti Island (Kap), Wellington (Wel), Long Island (Lon), Nelson (Nel), Abel Tasman (Abe), Karamea (Kar), Cape Foulwind (CFo), Kaikoura (Kai), Banks Peninsula North (Ban), Flea Bay (Fle), Moeraki (Moe), Open Bay Islands (OBI), Jackson Head (JaH), Cascades (Cas), Barn (Bar), Big Bay (Big), Bligh Sound (Bli), Charles Sound (Cha), Doubtful Sound (Dou), Preservation Inlet (Pre), Green Islets (GrI), Bluff (Blu), Codfish-Ruggedy (Cod), Ruapuke Island (Rua), Titi Islands (Tit), Paterson Inlet (Pat), Port Adventure (Por), Otago Peninsula (Ota) and Catlins (Cat).

depth ranges (e.g. Raglan). For this reason, sites from Long Bay (located in the inner Hauraki Gulf) were not included in the biogeographic analyses of Shears et al. (in press) as only one or two depth strata could be sampled due to the limited extent of subtidal reef. The majority of the sampling was carried out over the summer of 1999/2000 and 2000/2001, although additional sampling was carried out at Gisborne and Mahia in January 2002, Moeraki, Big Bay and Barn in December 2003, and Preservation Inlet, Green Islets, Bluff, Ruapuke Island, Codfish-Ruggedy and Port Adventure in February 2005. To assess any effects of temporal variation on comparisons between sites sampled in 2000 and 2005 in the Stewart Island region two sites in Paterson Inlet (Ulva East and Tamihou Island; originally sampled 1 February 2000) were re-sampled on 19 March 2005. No differences were found in macroalgal community structure or macroinvertebrate assemblages between these two sampling dates suggesting the communities remained stable over this period.

2.2 SAMPLING PROCEDURE

At each site a lead-weighted transect line was run perpendicular to the reef from the mean low water mark out to a maximum depth of 12 m or the reef edge (whichever came first sand). Mean low water was approximated by the lower limit of intertidal species and upper limit of the subtidal macroalgal assemblage. Five 1-m^2 quadrats, placed as randomly as possible in each of four depth ranges (< 2 m, 4–6 m, 7–9 m and 10–12 m), were sampled to provide information on the abundance and size structure of macroalgae and macroinvertebrates. Depths were corrected to the mean low water mark to ensure accurate positioning of quadrats within the desired depth range. When the maximum depth of the reef was less than 10 m, the deepest strata were omitted. Within each quadrat all large brown macroalgae and conspicuous mobile macroinvertebrates (> 1 cm maximum length) were counted and measured, using a 1-m-long measuring tape marked at 5-cm intervals for macroalgae and a 200-mm ruler marked at 5-mm intervals for macroinvertebrates. Individual thalli were counted for macroalgae, as it is often difficult to determine individual plants for many species. The total lengths of macroalgae were measured, with an additional measure of stipe length made for *Ecklonia radiata* and *Durvillaea* spp. The stipe diameter for *Durvillaea* spp. was also recorded. For *Lessonia variegata* the stipe length and total length of the whole plant was measured and the number of thalli counted. For *Carpophyllum* spp. it was not always possible to measure all thalli, so those greater than 25 cm total length were grouped into 25-cm length categories (25–50 cm, 50–75 cm, etc.) and counted. The primary (substratum) percentage cover of foliose algae (c. 5–25 cm height), turfing algae (< 5 cm height), encrusting algal species, encrusting invertebrates, bare rock and sediment were visually assessed for each quadrat and recorded. Quadrats were divided into quarters to assist in estimating percentage cover of dominant forms, whereas the cover of minor forms was estimated on the basis that a 10 × 10-cm area equates to 1% cover. This technique was considered to be the most suitable as it is efficient and ensures that percentage covers are recorded for all forms, unlike point-intercept methods (Benedetti-Cecchi et al. 1996). Furthermore, the same two experienced divers carried out 73% of the quadrat sampling, reducing the potential influence of inter-observer variability. Macroalgal species were identified using Adams

(1994) and with the assistance of Dr Wendy Nelson (Museum of New Zealand Te Papa Tongarewa). The test diameter (TD) of all sea urchins greater than 5 mm was measured, and their behaviour recorded (cryptic or exposed). The largest shell dimension (width or length) was measured for gastropods, the actual measurement depending on species shell morphology (i.e. shell height for *Cantharidus purpureus*; shell width for *Turbo smaragdus*, *Trochus viridis* and *Cookia sulcata*). All macroalgae thalli were carefully searched for gastropods. The total length of *Haliotis* spp., limpets (*Cellana stellifera*) and chitons was also measured.

2.3 BIOLOGICAL DATASETS

2.3.1 Macroalgal community structure

Patterns in macroalgal community structure were investigated among sites and locations using a structural group-type approach to reduce the influence of species composition and emphasise structural patterns among algal communities. Genera of large habitat-forming brown algae (orders Laminariales, Durvillaeales and Fucales) formed their own groups, whereas less conspicuous brown, red and green algal species were grouped (Table 1). In total, all macroalgae species were divided into 23 species groups. Algal measurements were converted to biomass in order to allow comparisons between all algal groups irrespective of sampling units (e.g. percentage cover as compared to counts), and also to adjust counts for different sizes of algae. The dry weight of large algal species was calculated using length–weight relationships whereas percentage cover–weight relationships were used for turfing and encrusting algal species groups. Biomass equations were calculated for all of the dominant species and where possible at several locations (Appendix 3). To establish length–weight relationships, plants covering a range of sizes were collected, length was measured to the nearest centimetre, and they were dried at 80°C for a minimum of 3 days and weighed to the nearest 0.1 g. The weights of the stipe and lamina were calculated for *Ecklonia radiata* using two separate equations (Shears & Babcock 2003). To convert percentage cover estimates of foliose, turfing and encrusting algae to dry weight, several 10 × 10-cm samples were collected (equivalent to 1% of a 1-m^2 quadrat), dried and weighed. It was not possible to calculate biomass equations for all species, so for some of the rarer species, which were typically only small contributors to total biomass, an equation from a species with similar morphology was used. Dry-weight estimates were converted to ash-free dry weight (AFWD) for all macroalgae, excluding corallines, by multiplying the dry weight by 0.91. This constant was based on the assumption that the proportion of $CaCO_3$ and other inorganic material is relatively constant among a variety of New Zealand seaweeds (9% of the dry weight; R.B. Taylor, unpubl. data). For coralline algae, however, $CaCO_3$ made up c. 45% of the dry weight (N.T. Shears, unpubl. data).

2.3.2 Mobile macroinvertebrate assemblages

This dataset included count data, averaged for each site across all quadrats, for 47 of the mobile macroinvertebrate species recorded.

TABLE 1. MACROALGAL SPECIES GROUPS USED IN ANALYSES OF MACROALGAL COMMUNITY STRUCTURE. CODE INDICATES THE ABBREVIATION USED FOR EACH SPECIES GROUP IN FIG. 2.

GROUP/SPECIES	CODE	NO. OF TAXA	DESCRIPTION/SPECIES
Phaeophyta			
Ecklonia radiata	Eckl	1	
*Carpophyllum flexuosum**	Flex	1	
Other *Carpophyllum*	Carp	3	*Carpophyllum angustifolium*, *C. maschalocarpum*, *C. plumosum*
Lessonia variegata	Less	1	
Landsburgia quercifolia	Land	1	
Sargassum spp.	Sarg	2	*Sargassum sinclairii*, *S. verruculosum*
Xiphophora spp.	Xiph	2	*Xiphophora chondrophylla*, *X. gladiata*
Macrocystis pyrifera	Macr	1	
Marginariella spp.	Marg	2	*Marginariella urvilliana*, *M. boryana*
Durvillaea willana	Durv	1	
Cystophora spp.	Cysto	4	e.g. *Cystophora retroflexa*, *C. platylobium*
Small browns	SmBr	9	Small terete brown algal species; e.g. *Carpomitra costata*, *Halopteris* spp., *Zonaria* spp.
Ephemeral browns	EpBr	8	Small foliose brown algal species; e.g. *Dictyota* spp., *Desmarestia ligulata*, *Glossophora kunthii*, *Spatoglossum chapmanii*
Brown encrusting	BrEn	2	Encrusting fleshy brown algae, e.g.*Ralfisa* sp.
Rhodophyta			
Red foliose	ReFo	89	5–30 cm in height; e.g. *Osmundaria colensoi*, *Euptilota formosissima*
Red encrusting	ReEn	2	Encrusting fleshy red algae, e.g. *Hildenbrandia* spp.
Red turf	ReTu	8	Fleshy red algae less than 5 cm in height
Coralline turf	CoTu	1	Geniculate coralline algae
Crustose corallines	CCA	1	Non-geniculate coralline algae
Chlorophyta			
Caulerpa spp.	Caul	5	e.g. *Caulerpa flexilis*, *C. brownii*
Codium spp. (encrusting)	Codi	2	*Codium convolutum*, *C. cranwelliae*
Ulva spp.	Ulva	1	
Other greens	Gree	9	e.g. *Codium fragile*, *Chaetomorpha* spp., *Cladophora* spp.

* *Carpophyllum flexuosum* was treated as a separate group because of its differing morphology and habitat (generally deeper water) compared with other *Carpophyllum* species.

2.3.3 Benthic community structure

All sessile organisms were divided into 29 structural groups (Table 2), using a functional group-type approach (cf. Steneck & Dethier 1994). Macroalgae were divided into functional groups based on Steneck & Dethier (1994), whereas sessile

invertebrates were divided subjectively into broad structural classes for each phylum (Table 2). This approach was used to allow comparisons of the relative contributions of phylogenetically distinct taxonomic groups, e.g. macroalgae v. sessile invertebrates, in the same analysis of overall benthic community structure. The biomass (AFDW) of macroalgal groups was calculated using the same procedure as above, whereas for sessile invertebrate groups biomass was calculated using percentage cover–biomass relationships (Appendix 4). To convert percentage cover estimates to AFDW, conversion values were calculated for several species within each structural group. Three 10 × 10-cm samples were collected for each species, shell-free dry weight was measured by drying samples to a constant weight at 80°C, and AFDW was then determined by incineration at 500°C in a muffle furnace. Most invertebrate structural group samples were collected from Leigh and the Mokohinau Islands. It was therefore assumed that

TABLE 2. BENTHIC STRUCTURAL GROUPS USED IN ANALYSES OF BENTHIC COMMUNITY STRUCTURE. NR = NOT RECORDED TO THE SPECIES LEVEL. CODE INDICATES THE ABBREVIATION USED FOR EACH GROUP IN FIG. 9.

PHYLA	GROUP	CODE	NO. OF TAXA	EXAMPLE
Algae*	Crustose	Al_crust	3	*Ralfsia* spp., crustose corallines
	Articulated	Al_artic	1	*Corallina officinalis*
	Filamentous	Al-fil	16	*Cladophora feredayi*, *Chaetomorpha coliformis*
	Foliose	Al_fol	1	*Ulva* sp.
	Corticated foliose	Al_CFA	61	*Dictyota* spp., *Kallymenia* spp.
	Corticated terete	Al_CTA	53	*Pterocladia lucida*, *Caulerpa* spp., *Halopteris* spp.
	Leathery macrophytes	Al_leath	21	*Carpophyllum* spp., *Marginariella* spp.
Annellida	Serpulid tubeworms	Tube	NR	*Galeolaria* sp.
Chordata	Compound ascidian	As_comp	NR	*Didemnum* spp.
	Sea tulip	As_tulip	1	*Pyura pachydermatina*
	Solitary ascidian	As_sol	NR	*Asterocarpa* spp.
	Stalked ascidian	As_stalk	NR	*Pseudodistoma* spp.
Crustacea	Barnacles	Barn	NR	*Balanus* spp.
Mollusca	Oyster	Oyster	NR	*Anomia walteri*
	Large mussels	Mus_lge	NR	*Perna canaliculus*, *Mytilus* spp.
	Small mussels	Mus_sm	NR	*Xenostrobus pulex*
Brachiopoda	Brachiopod	Brachi	NR	
Bryozoa	Branched bryozoan	Br_br	NR	*Bugula dentata*
	Encrusting bryozoan	Br_enc	NR	*Membranipora* sp.
Cnidaria	Colonial anemone	An_col	NR	*Anthothoe albocincta*, *Corynactis australis*
	Large solitary anemone	An_sol	NR	*Oulactis* sp., *Phlyctenactis* sp.
	Black coral	Co_black	1	*Antipathes fiordensis*
	Cup coral	Co_cup	2	*Culicia rubeola*, *Monomyces rubrum*
	Soft coral	Co_soft	NR	*Alcyonium* sp.
Hydrozoa	Hydroid turf	Hy_turf	NR	*Amphisbetia bispinosa*
	Hydroid tree	Hy_tree	NR	*Solanderia ericopsis*
Porifera	Encrusting sponge	Sp_enc	NR	*Cliona celata*
	Finger sponge	Sp_fing	NR	*Raspailia topsenti*
	Massive sponge	Sp_mas	NR	*Ancorina alata*

* Algal groups include Chlorophyta, Phaeophyta and Rhodophyta and are based on the definitions of Steneck & Dethier (1994).

the biomass of structural groups would be broadly consistent among regions. Because percentage cover estimates did not take into account differences in the vertical height or size of encrusting forms (e.g. sponges, mussels), an attempt was made to collect specimens covering a range of sizes for biomass estimates. These potential artefacts were considered to have little effect on interpretation of overall patterns as analyses were based on fourth-root transformed data.

2.4 ENVIRONMENTAL VARIABLES

The environmental variables that were assessed for each site included wind fetch (as an estimate of wave exposure), turbidity, sedimentation, reef slope and maximum depth. Wind fetch (km) was calculated for each site by summing the potential fetch for each 10-degree sector of the compass rose. For open sectors of water the radial distance was arbitrarily set to be 300 km. Turbidity was measured using a standard 25-cm-diameter black and white Secchi disc (Larson & Buktenica 1998). The reading taken was the average depth (m) of descending disappearance and ascending reappearance. The percentage cover of sediment on the reef (measured during quadrat sampling) was used as an estimator of sedimentation. Reef slope at each site was expressed as a percentage calculated by dividing the maximum depth sampled by the length of the transect line run from the low water mark to a depth of 12 m or the edge of the reef. The density of exposed *Evechinus chloroticus* (averaged across all depths at each site) was also used as an explanatory variable in multivariate analyses given its strong controlling influence on macroalgal community structure (Andrew 1988). The management status of each site (i.e. Reserve or Non-reserve) was also treated as an explanatory variable as increased predator abundance in marine reserves can have indirect effects on urchins and macroalgal assemblages (Shears & Babcock 2002, 2004a).

2.5 STATISTICAL ANALYSES

All analyses were carried out at the level of individual sites, based on biological data averaged for all quadrats across all depths. However, given that the vertical structure of reef communities is highly variable and likely to be related to environmental conditions, it was necessary to assess the extent to which depth-averaged biomass was representative of a species' biomass at individual depth strata. Calculation of Spearman's rank correlations between biomass at each depth stratum and the depth-averaged biomass, for a subset of species, revealed that there was generally high correspondence across individual depths (65–72%). This can be interpreted as the depth-averaged biomass being able to explain approximately 70% of the variation at any individual depth stratum. Variation in benthic communities with depth is described separately for each bioregion in section 3.4.

2.5.1 Principal coordinates analysis

To visualise the variation in community patterns among locations and sites, and how the patterns relate to explanatory variables, principal coordinates analysis

was carried out based on Bray-Curtis similarities using the PCOORD program (Anderson 2000). All datasets were fourth-root transformed. The environmental and species group variables were correlated with principal coordinates (PC) axes 1 and 2 and the correlation coefficients plotted as bi-plots, in which the position of the symbol indicates the correlation between the explanatory variable and the PC axes.

2.5.2 Multiple regression

The relationships between the multivariate datasets and explanatory variables were investigated using non-parametric multivariate multiple regression (McArdle & Anderson 2001). This technique investigates the relationships between community data and sets of explanatory variables (e.g. Anderson et al. 2004), using the computer program DISTLM (Anderson 2002). The spatial variables Northing and Easting (New Zealand Map Grid) for each site were included as a set of explanatory variables, along with the set of environmental variables measured at each site. For each set of explanatory variables, individual variables were analysed for their relationship with the biological dataset, then subjected to a forward selection procedure whereby each variable was added to the model in the order of greatest contribution to total variation. All analyses were based on Bray-Curtis similarities, calculated on fourth-root transformed site-level data for each biological dataset. Marginal tests (examining a single variable or set of variables) were carried out with 4999 permutations of the raw data, whereas conditional tests (used for the forward selection procedure) were based on 4999 permutations of residuals under the reduced model. Analyses were carried out on each biological dataset at all spatial scales. However, bioregional analysis was carried out only for Northeastern, Abel, and Stewart Island sites, as the number of sites sampled in other bioregions was too low for analysis.

To investigate potential associations between the abundance of *Evechinus chloroticus* and both the environmental and spatial variables a forward-backward stepwise multiple regression was run in the statistical program S+. Analyses were carried out at two spatial scales (national and bioregional) to generate hypotheses about the important environmental factors controlling urchin abundance at different spatial scales.

2.5.3 Bioregional patterns in reef communities

To investigate variation in algal community structure among sites within each bioregion, principal coordinates analysis was carried out on site-level data (based on the macroalgal community structure dataset that had been fourth-root transformed), using the same procedure as for the national level analysis (see above). There were too many sites within each location to present data for each site and pooling data across all sites potentially masks important variation among sites within each location. Therefore, sites within each bioregion were grouped using hierarchical cluster analysis (PRIMER, Clarke & Warwick 1994), based on the macroalgal group data that had been fourth-root transformed. Depth-related patterns in algal communities, urchin abundance, mobile invertebrates and dominant substratum cover were then described for the groupings of sites identified for each location. In each case, data for the ten most abundant taxa or species groups for a particular bioregion are presented.

3. Results

Sections 3.1–3.3 describe national and bioregional patterns in macroalgal community structure (3.1), mobile macroinvertebrate species assemblages (3.2) and benthic community structure (3.3) among locations, and their association with key environmental variables.

Section 3.4 describes variation in reef communities among sites within each bioregion and the association between biological patterns and environmental gradients. Depth-related patterns in abundance, biomass or cover are also described for dominant species or groups.

3.1 MACROALGAL ASSEMBLAGES

3.1.1 National variation in macroalgal community structure

Over 150 macroalgal taxa were recorded at the shallow reef sites sampled in this study (Appendix 5). Large brown algal species made up 79% of the total biomass, with *Ecklonia radiata* and *Carpophyllum maschalocarpum*, the two most common large brown macroalgal species, accounting for 48% of the total macroalgal biomass (25% and 23%, respectively, Table 3). There was large variation in macroalgal community structure, based on the biomass of the 23 macroalgal species groups, among sites both within and among locations (Fig. 2A). Locations with the greatest variation among sites were where sites were sampled across a large environmental gradient, e.g. Paterson Inlet, Flea Bay and Long Island, or where only a small number of sites were sampled, e.g. Gannet Rock and Charles Sound. The spread of locations along the axis of greatest variation PC1 reflected a weak latitudinal gradient from north to south (Fig. 2B), with sites of the Northern Province generally being located on the left of the ordination and Southern sites on the right, and PC1 strongly correlated with the spatial variables (Northing and Easting) (Fig. 2B). Notable exceptions were the Banks locations, which were grouped with Northern locations. There was some division between east and west coast locations along PC2 with the majority of west coast locations grouped on the lower poriton of the ordination. All of the environmental variables were significantly related to macroalgal community structure and explained 31% of the variation (Table 4). Individually, these variables explained only a low proportion of the variation at the national scale and were not strongly correlated with PC1 or PC2. Several species groups were strongly correlated with PC1: *Carpophyllum* spp. were negatively correlated, whereas coralline turf, red turfing and foliose algae, and some large brown algal species (*Lessonia variegata*, *Landsburgia quercifolia*, *Xiphophora* spp. and *Marginariella* spp.) were positively correlated (Fig. 2C). *Ecklonia radiata* and *Carpophyllum flexuosum* were strongly correlated with PC2 and were absent at most locations clustered in the lower portion of the ordination, e.g. Raglan, Karamea, Cape Foulwind, Jackson Head and Cascades on the west coast, and Otago Peninsula and Catlins on the east coast (Appendix 5).

At the provincial level the importance of the variables varied between the two provinces (Table 4). For the Northern Province, Secchi explained the greatest

TABLE 3. DOMINANT MACROALGAL SPECIES OR SPECIES COMPLEXES ACCORDING TO THEIR CONTRIBUTION TO TOTAL BIOMASS (AFDW) AND THE PERCENTAGE OF ALL SITES AT WHICH EACH SPECIES OCCURRED (% OCC.).

NO.	SPECIES	GROUP	% OCC.	MEAN AFWD (g/m^2)	% AFWD	GENERAL DISTRIBUTION
1	*Ecklonia radiata*	Phaeophyta	63.2	102.14	25.47	New Zealand
2	*Carpophyllum maschalocarpum*	Phaeophyta	60.3	92.30	23.01	Northern
3	*Lessonia variegata*	Phaeophyta	29.6	30.61	7.63	New Zealand
4	*C. flexuosum*	Phaeophyta	56.7	19.56	4.88	New Zealand
5	Crustose corallines*	Rhodophyta	100.0	15.46	3.86	New Zealand
6	*C. angustifolium*	Phaeophyta	16.6	14.39	3.59	Northeastern
7	Articulated coralline turf*	Rhodophyta	90.7	13.29	3.31	New Zealand
8	*Landsburgia quercifolia*	Phaeophyta	37.2	11.69	2.92	New Zealand
9	*Durvillaea willana*	Phaeophyta	9.7	10.93	2.73	Southern
10	*Xiphophora gladiata*	Phaeophyta	21.9	8.11	2.02	Southern
11	Red turfing algae*	Rhodophyta	79.8	7.79	1.94	New Zealand
12	*Marginariella boryana*	Phaeophyta	12.6	7.20	1.80	Southern
13	*M. urvilliana*	Phaeophyta	12.6	5.84	1.46	Southern
14	*Macrocystis pyrifera*	Phaeophyta	12.1	5.43	1.36	Southern
15	*Caulerpa brownii*	Chlorophyta	21.1	4.93	1.23	Southern
16	*Cystophora platylobium*	Phaeophyta	9.3	3.84	0.96	Southern
17	*Halopteris* spp.	Phaeophyta	55.5	3.82	0.95	New Zealand
18	*Pterocladia lucida*	Rhodophyta	42.9	3.59	0.90	Northern
19	*Osmundaria colensoi*	Rhodophyta	21.9	2.96	0.74	Northern
20	*Plocamium* spp.*	Rhodophyta	57.1	2.72	0.68	New Zealand
21	*Asparagopsis armata*	Rhodophyta	29.1	2.66	0.66	New Zealand
22	*Ballia callitrichia*	Rhodophyta	20.6	2.15	0.54	Southern
23	*Codium convolutum*	Chlorophyta	50.6	1.89	0.47	New Zealand
24	*C. plumosum*	Phaeophyta	21.1	1.89	0.47	Northeastern
25	*Zonaria* spp.	Phaeophyta	56.7	1.72	0.43	New Zealand
26	*Hymenena durvillaei*	Rhodophyta	17.8	1.59	0.40	Southern
27	*Hymenena palmata*	Rhodophyta	20.6	1.58	0.39	Southern
28	*Lophurella hookeriana*	Rhodophyta	24.3	1.19	0.30	Southern
29	*Cystophora retroflexa*	Phaeophyta	18.2	1.17	0.29	New Zealand
30	*Sargassum sinclairii*	Phaeophyta	55.1	1.13	0.28	New Zealand
31	*Ulva* spp.*	Chlorophyta	37.2	1.01	0.25	New Zealand
32	*Euptilota formosissima*	Rhodophyta	36.0	1.00	0.25	New Zealand
33	*Rhodymenia* spp.*	Rhodophyta	10.5	0.93	0.23	New Zealand
34	*Xiphophora chondrophylla*	Phaeophyta	21.1	0.91	0.23	Northern
35	*Microzonia velutina*	Phaeophyta	29.6	0.91	0.23	Southern
36	*Anotrichium crinitum*	Rhodophyta	29.1	0.90	0.22	Southern
37	*Craspedocarpus erosus*	Rhodophyta	18.6	0.70	0.17	Southern
38	*Rhodophyllis gunnii*	Rhodophyta	28.7	0.69	0.17	Southern
39	*Caulerpa flexilis*	Chlorophyta	7.7	0.67	0.17	Northern
40	*Glossophora kunthii*	Phaeophyta	54.7	0.58	0.14	New Zealand

* Groups of species that were not identified to the species level. The distribution patterns in biomass of some of these species groups are given in Fig. 4.

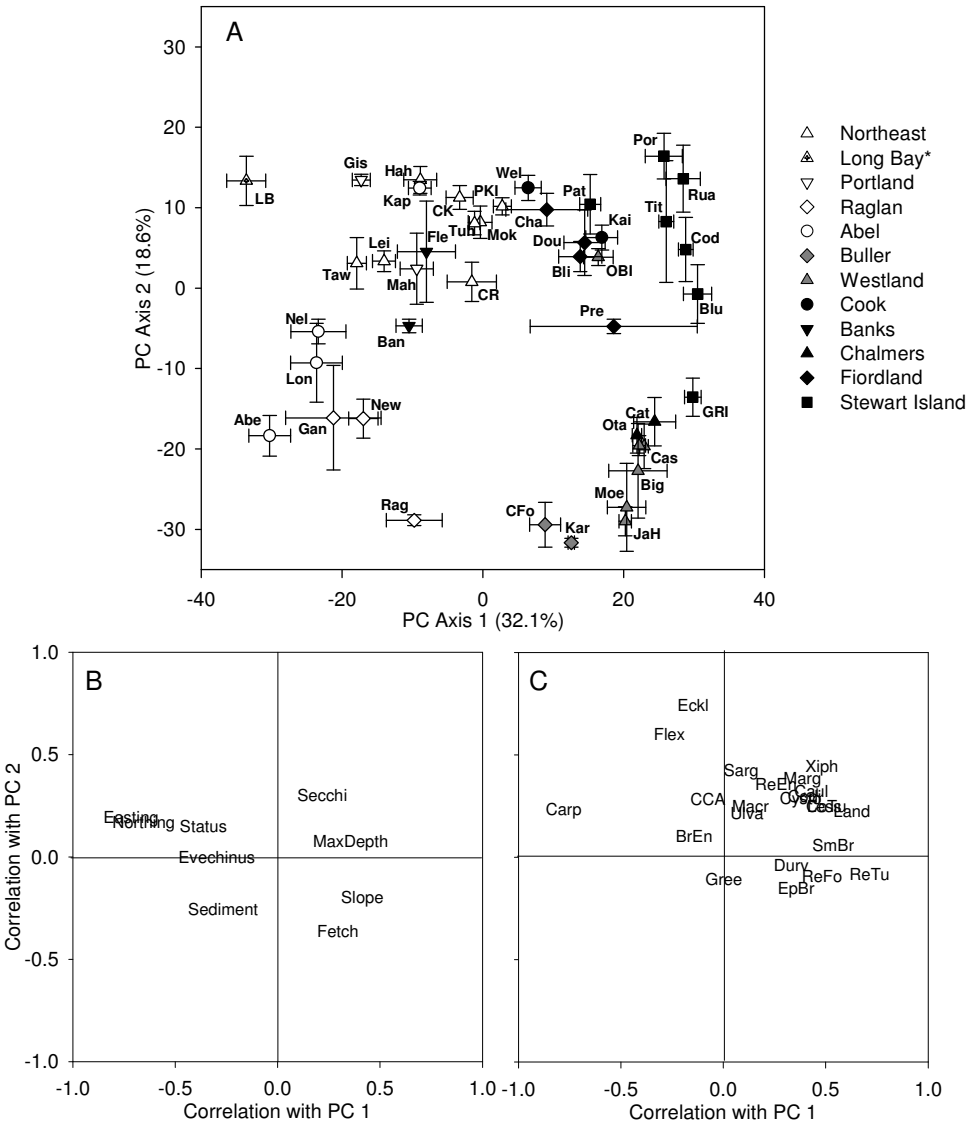

Figure 2. Macroalgal community structure (fourth-root transformed biomass of 23 groups) from principal coordinates analysis on all 247 sites (A) (see Fig. 1 for location codes and Table 1 for species group codes). Centroids are plotted for each location; standard error bars indicate the variation among 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 original macroalgal species groups (C). * Long Bay is distinguished from other Northeastern locations as it was not included in biogeographic analyses (Shears et al. in press).

variation (13%), whereas for the Southern Province, Fetch explained 14% of the variation. Evechinus accounted for only a small proportion of the variation in algal community structure at the national (4%) and provincial scale (< 5%), but between 9% (Northeastern) and 17% (Stewart Island) at the bioregional level. Overall, the amount of variation explained by site-level environmental variables tended to increase with decreasing spatial scale: national < biogeographic province < bioregion. These patterns in algal community structure and their relationship with environmental variables are described in detail for each bioregion in section 3.4.

3.1.2 National patterns in dominant macroalgal species

Clear differences were apparent in total algal biomass among bioregions, despite considerable variability among sites and locations within each (Fig. 3). Macroalgal biomass was lowest at west coast bioregions, particularly in the Southern Province. *Ecklonia radiata* and *Carpophyllum* spp., predominantly *C. maschalocarpum*, dominated in Northern bioregions, whereas the Southern bioregions were dominated by a mixture of large brown algae including *E. radiata*, *Lessonia variegata*, *Landsburgia quercifolia*, *Durvillaea willana*, *Macrocystis pyrifera*,

TABLE 4. RESULTS OF NON-PARAMETRIC MULTIVARIATE REGRESSION OF MACROALGAL COMMUNITY STRUCTURE DATA (FOURTH-ROOT TRANSFORMED BIOMASS OF 23 ALGAL GROUPS), AND ENVIRONMENTAL AND SPATIAL VARIABLES AT DIFFERING BIOGEOGRAPHIC SCALES. THE PERCENTAGE VARIANCE EXPLAINED BY 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		
				NORTHEASTERN	ABEL	STEWARTI
	NZ	NORTHERN	SOUTHERN			
n	247	135	112	81	37	42
Local variables						
Fetch	7.3	3.9	13.6	8.3	6.5	19.9
Status	5.1	ns	4.0	ns	ns	ns
Slope	6.7	4.2	ns	15.4	ns	ns
MaxDepth	5.1	8.1	3.6	25.2	ns	ns
Secchi	5.5	13.1	7.4	23.5	21.0	18.1
Evechinus	4.1	2.1	4.7	8.7	11.2	16.7
Sediment	4.5	8.0	5.4	6.0	18.8	19.9
Cumulative %	**30.9**	**29.5**	**36.6**	**37.5**	**41.1**	**32.3**
Significant factors	All	All, excl. Status	All	MaxDepth, Secchi, Fetch	Secchi, Sediment, Evechinus, Fetch	Fetch. Evechinus, Sediment
Spatial—Northing and Easting						
	22.4	24.3	26.4	30.7	23.1	22.5

Marginariella spp. and several other large brown algal species such as *Xiphophora gladiata* (Fig. 3A). *Ecklonia radiata* occurred throughout the country (Fig. 4A), although it was not recorded in some bioregions (Buller, Westland (excluding Open Bay Islands) and Chalmers) and some locations (Nelson, Abel Tasman, Raglan, Preservation Inlet, Bluff and Green Islets), and was rare at others, e.g. Banks Peninsula North, Flea Bay and New Plymouth (Appendix 5). *Ecklonia radiata* was typically most abundant at Northeastern locations, although dense forests were also present at Gisborne, Mahia and Kapiti Island.

The four *Carpophyllum* species made up 32% of the total macroalgal biomass recorded (Table 3). *Carpophyllum maschalocarpum* was the most abundant and had a northern distribution, but was also abundant in the Cook and Banks bioregions (Fig. 4A). Both *C. angustifolium* and *C. plumosum* were recorded only at locations in the Northeastern bioregion (Appendix 5). *Carpophyllum flexuosum* was an important contributor to total algal biomass at bioregions throughout the country (Figs 3A and 4A), but was not recorded at several bioregions including Raglan, Buller, Westland (excluding Open Bay Islands) and Chalmers, as well as some specific locations (Cape Reinga, Kaikoura and Green Islets; Appendix 5). *Lessonia variegata* was the third largest contributor to total algal biomass (8%) and was most abundant in Southern bioregions (e.g. Cook, Chalmers and Stewart Island) but also occurred at exposed locations in the Northeastern bioregion (Fig. 4A). *Lessonia variegata* was not recorded at Portland, Raglan, Abel, Buller

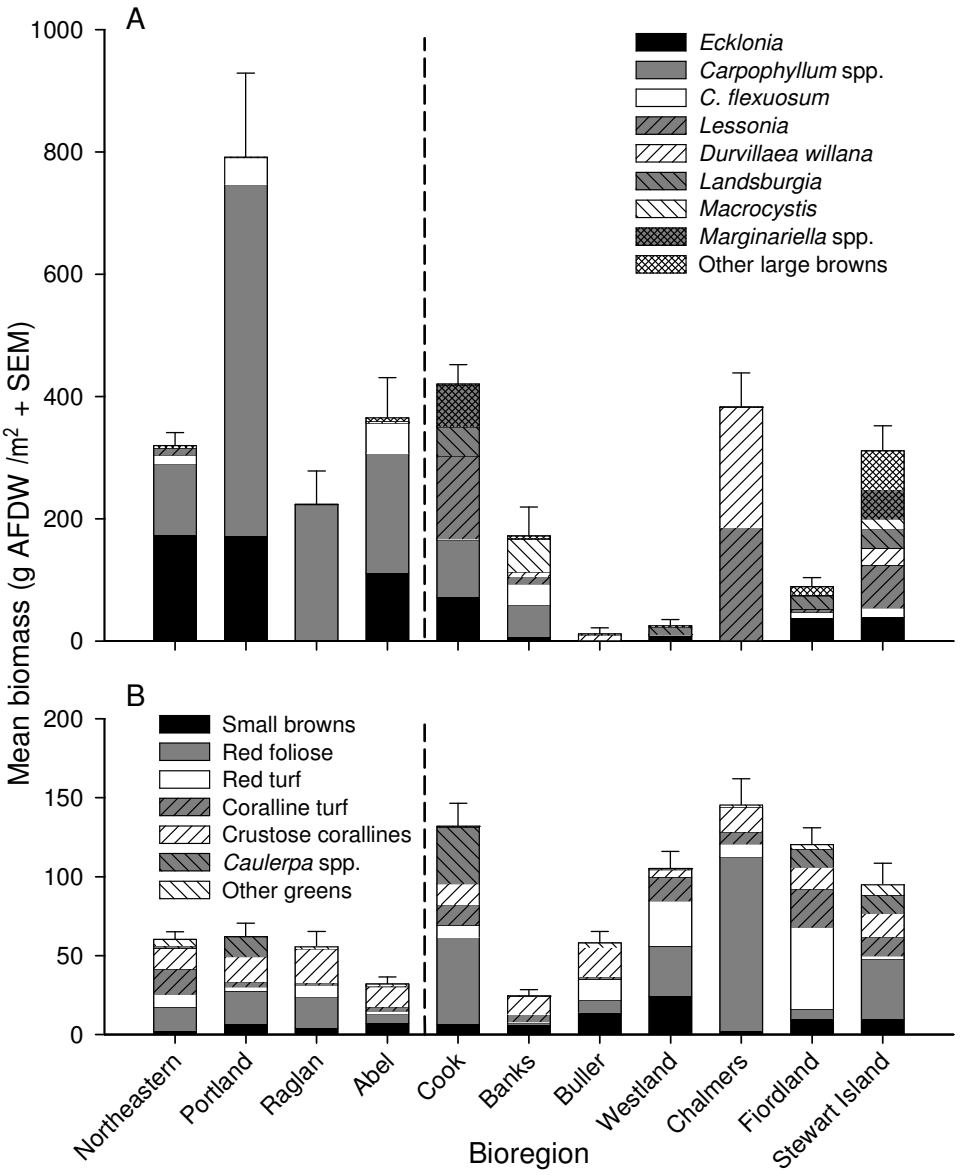

Figure 3. Mean biomass of dominant large brown algae (A) and other macroalgal groups (B) for all bioregions. Dashed line indicates division between the Northern and Southern Provinces.

or Westland (excluding Open Bay Islands). *Landsburgia quercifolia* exhibited a similar southern distribution but was also abundant in the Westland and Fiordland bioregions. Several other large brown algal species were regionally abundant, but made up only a small proportion of total algal biomass. For example, *Durvillaea willana* was the dominant large brown algae at Chalmers locations, and some Stewart Island sites, but rare in other regions (Figs 3A and 4B). *Macrocystis pyrifera* also had a southern distribution and was most abundant at Stewart Island and Banks Peninsula (Fig. 3A), but also occurred at some Wellington, Long Island and Fiordland sites. A number of other species were typically most abundant at locations in the Stewart Island bioregion, e.g. *Xiphophora gladiata*, *Marginariella* species and *Cystophora platylobium* (Fig. 4B).

The crustose coralline and articulated coralline turf species complexes were dominant contributors to total algal biomass on a national scale (3.9% and 3.3%, respectively), and were recorded at most sites (Table 3) and all bioregions (Fig. 3B). The red turf species complex made up c. 2% of the total algal biomass and on average was most abundant in Buller, Westland and Fiordland (Fig. 3B).

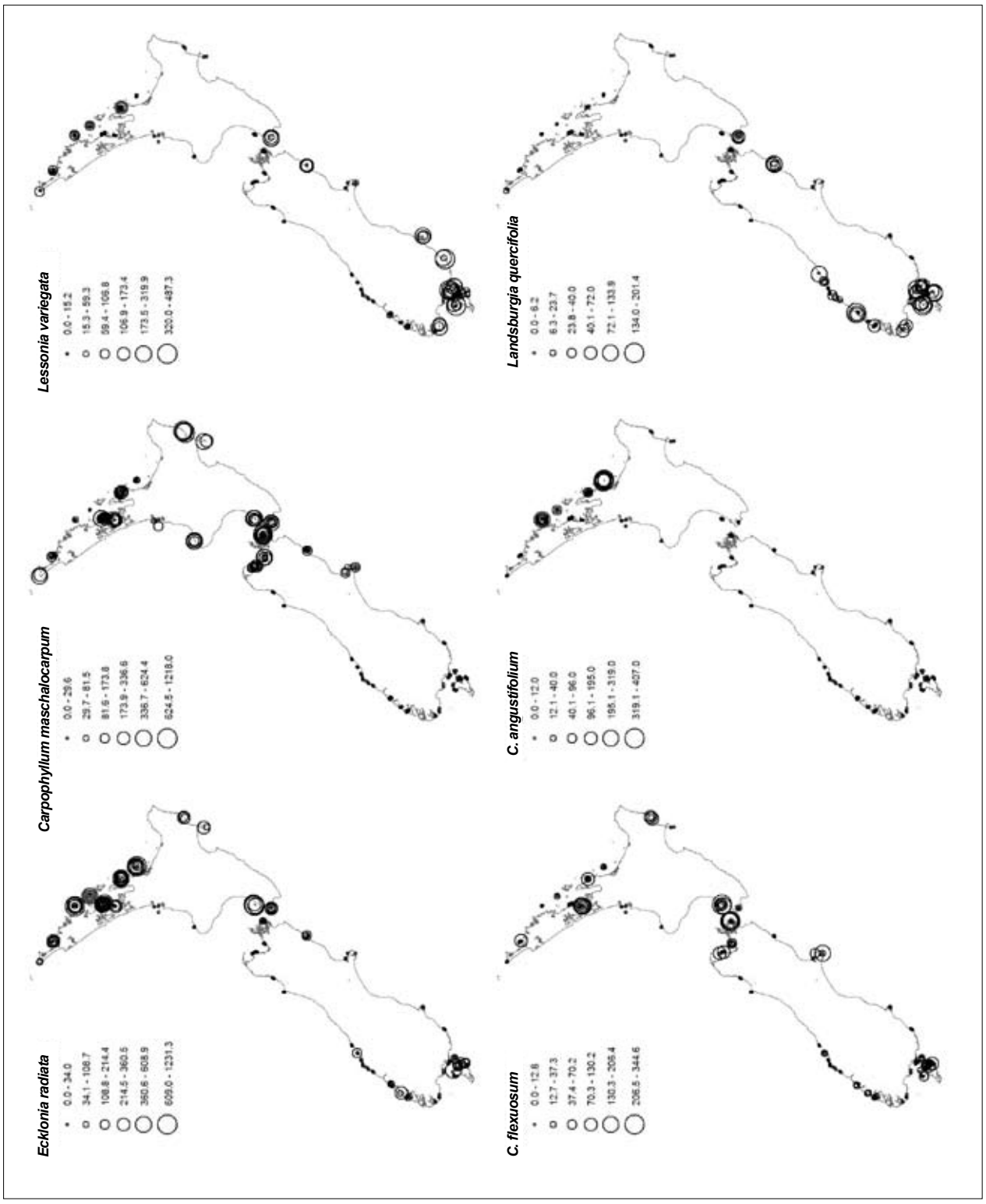

Figure 4A. Mean biomass (g AFDW/m^2) of dominant large brown macroalgal species at all sites, averaged across all depths sampled.

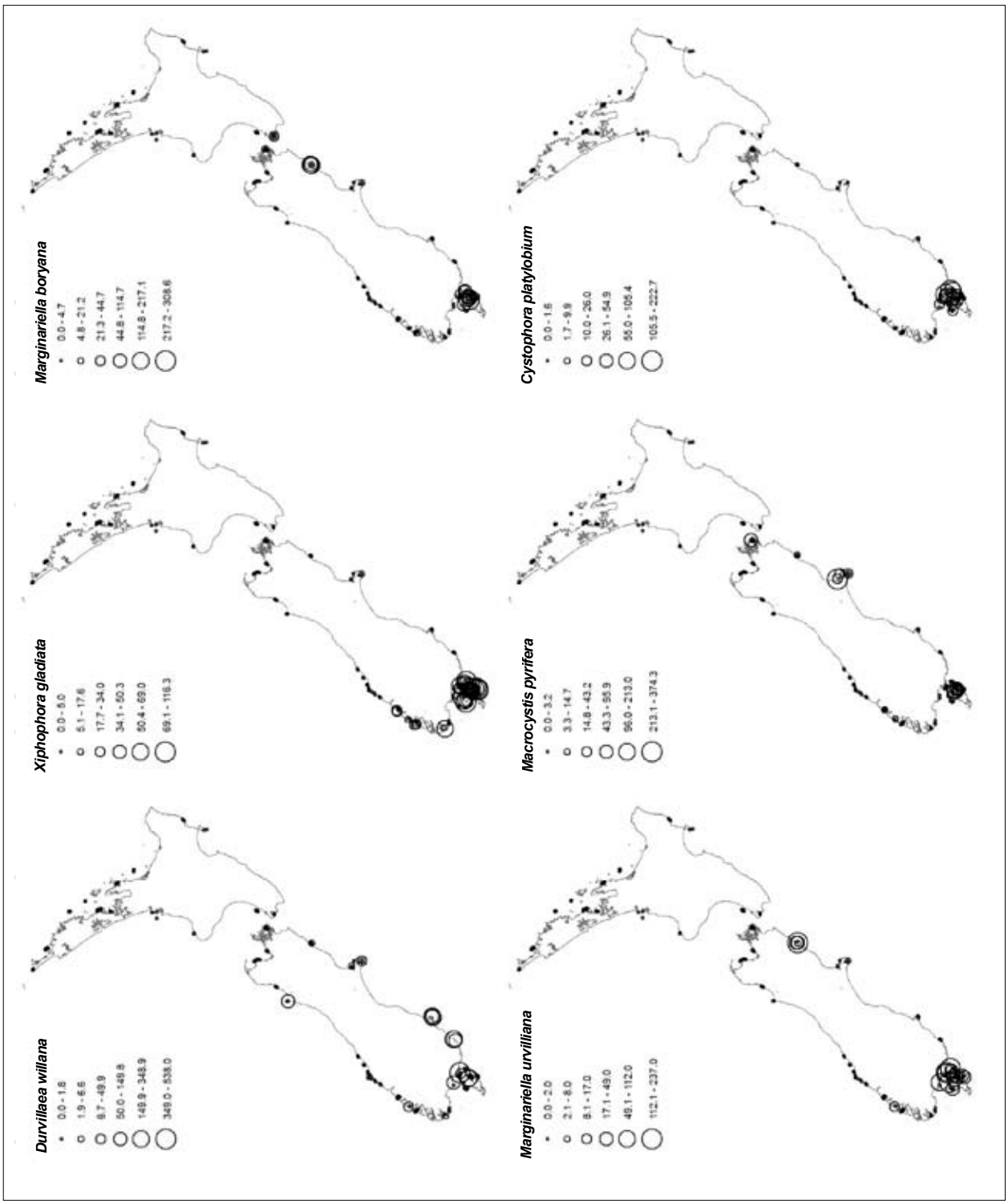

Figure 4B. Mean biomass (g AFDW/m^2) of other large brown macroalgal species at all sites, averaged across all depths sampled.

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