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Unusual but consistent latitudinal patterns in macroalgal habitats and their invertebrate communities across two countries

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Abstract

Aim: The physical characteristics of biogenic habitats and environmental conditions are important determinants of biodiversity, yet their relative importance can change across spatial scales. We aimed to understand how relationships between the physical characteristics of macroalgal habitats and their invertebrate communities varied across spatial scales and whether general ecological patterns occurred across two countries.

Location: Eighteen sites across the temperate east coasts of Australia (over 1,300 km) and New Zealand (over 1,000 km), with the latitudinal gradient in the two countries overlapping by 6.73 decimal degrees.

Time period: January to early April 2012.

Major taxa studied: Three intertidal macroalgal habitats in each country and the invertebrate communities within them.

Methods: We measured variation in patch- and individual-level characteristics of macroalgal habitats and their invertebrate communities. Patterns in macroalgal characteristics and communities were compared across latitude, and at smaller spatial scales, and correlated with 26 abiotic environmental variables using multiple multivariate analyses.

Results: Separately, macroalgal habitat characteristics and communities showed unusual but consistent nonlinear latitudinal patterns, with greater similarity among sites at the edges of the sampled distribution (i.e., north and south) than at centrally located sites. Macroalgal characteristics did not correlate with a particular set of environmental variables; however, communities were structured by sea surface temperature at the country scale and by macroalgal habitat type and biomass within countries. Anthropogenic variables were also important and may have contributed to the unusual nonlinear patterns observed between macroalgal characteristics and communities across latitude.

Main conclusions: Our results support other studies showing that large-scale patterns can emerge from systems where there is high local-scale variability. The results show that communities within macroalgal habitats respond to both the physical characteristics of the habitat and external environmental conditions (e.g., temperature), suggesting that local-scale environmental factors, including anthropogenic stressors, may modulate environmental gradients over larger scales.

1 | INTRODUCTION

In an era of unprecedented biodiversity loss, there is an increasing need to understand how ecological processes operating at multiple spatial scales influence biodiversity to inform global conservation actions (Gaston, 2000; Loreau, 2001). Biogenic habitats such as trees, corals and seaweeds are foundation species (sensu Dayton, 1972) that have a range of important ecological roles (Angelini, Altieri, Silliman, & Bertness, 2011; Bellwood, 2001; Ellison et al., 2005; Harley et al., 2012), most obviously they create physical habitat for other species (hereafter "communities"). The physical structure provided by biogenic habitats supports diverse communities by providing surfaces for colonization, and/or a refuge from biological (e.g., predation) and environmental (e.g., temperature, water flow) stressors (Jones, Lawton, & Shachak, 1994; Kovalenko, Thomaz, & Warfe, 2012; Romero, Gonçalves-Souza, Vieira, & Koricheva, 2015; Tews et al., 2004; Wright & Gribben, 2017). Thus, biogenic habitats typically have strong positive effects on community diversity (see Bruno & Bertness, 2001; Bruno, Stachowicz, & Bertness, 2003; Ellwood & Foster, 2004; Gribben et al., 2019; Thomsen et al., 2018).

The physical characteristics of habitats can significantly change localized environments, which may, in turn, alter associated community structure (Heck & Orth, 1980; Jones, Lawton, & Shachak, 1997). For example, at local scales, species abundances and diversity may correlate with a range of physical characteristics of habitats including patch size and shape (Airoldi, 2003; Andrén, 1994; Bruno & Kennedy, 2000), vegetation size (Kelaher, 2003a), density (Gribben & Wright, 2014; Heck & Orth, 1980; Nilsson, 1979), structural complexity (Matias, Underwood, Hochuli, & Coleman, 2010; Stein, Gerstner, & Kreft, 2014; Taniguchi, Nakano, & Tokeshi, 2003), frond length and surface area (Stelling-Wood, Gribben, & Poore, 2020) and multivariate structural gradients (Tews et al., 2004). In some cases, communities may vary due to the composition or diversity of habitats (Tews et al., 2004), whereas in others they may vary due to changes in the characteristics of individual biogenic habitats (e.g., density or frond length; Lawton, 1987) or both (Stelling-Wood et al., 2020). Interspecific variation in the physical characteristics of morphologically distinct

biogenic habitats can have important consequences for associated communities (e.g., Angelini et al., 2011). Much less, however, is known about how variation in physical characteristics within individual habitat-forming species or complexes of morphologically similar biogenic habitats influence associated communities (but see Badano & Cavieres, 2006; Kelaher, 2002) even though variation in the physical characteristics of individual biogenic habitats may have similar strong consequences for associated communities. In support of this, at one site, Stelling-Wood et al. (2020) found that intraspecific variation in morphological traits was more important than species identity in predicting epifaunal abundances.

Improving our understanding of the spatial relationships between the physical characteristics of biogenic habitats and associated communities is critical to developing effective conservation management strategies (Byers et al., 2006) and for predicting how biodiversity may respond to global environmental change (Wernberg, Thomsen, Tuya, & Kendrick, 2011). Some studies have addressed these relationships at local scales (e.g., Airoldi, 2003; Kelaher, Underwood, & Chapman, 2003; Palomo, People, Chapman, & Underwood, 2007); however, as biogenic habitats and their associated communities often co-occur across broad geographic ranges, there is a need to examine how these relationships change over large spatial scales, considering changes in the physical characteristics within (Fowler-Walker, Connell, & Gillanders, 2005a; Ralph, Morrison, & Addison, 1998; Rice, Kenchington, & Chapman, 1985) and among habitats (e.g., Messier, McGill, & Lechowicz, 2010). At present, we do not have a strong understanding of how these relationships vary across biogeographic gradients (but see Heck & Orth, 1980; Stein et al., 2014).

There is a range of environmental conditions—operating across multiple spatial scales—known to influence community structure. Latitude, and its common covariate temperature, is often related to the composition of communities (Cruz-Motta et al., 2010; Hillebrand, 2004; Schemske, Mittelbach, Cornell, Sobel, & Roy, 2009), as are moisture (Meynard et al., 2013), tidal height (Underwood & Chapman, 1998) and site exposure (Blanchette, 1997; Blanchette, Thornber, & Gaines, 2000). Anthropogenic factors such as pollution (Terlizzi, Scuderi, Fraschetti, & Anderson, 2005) and human population (Bloch & Klingbeil, 2016) have also been associated with
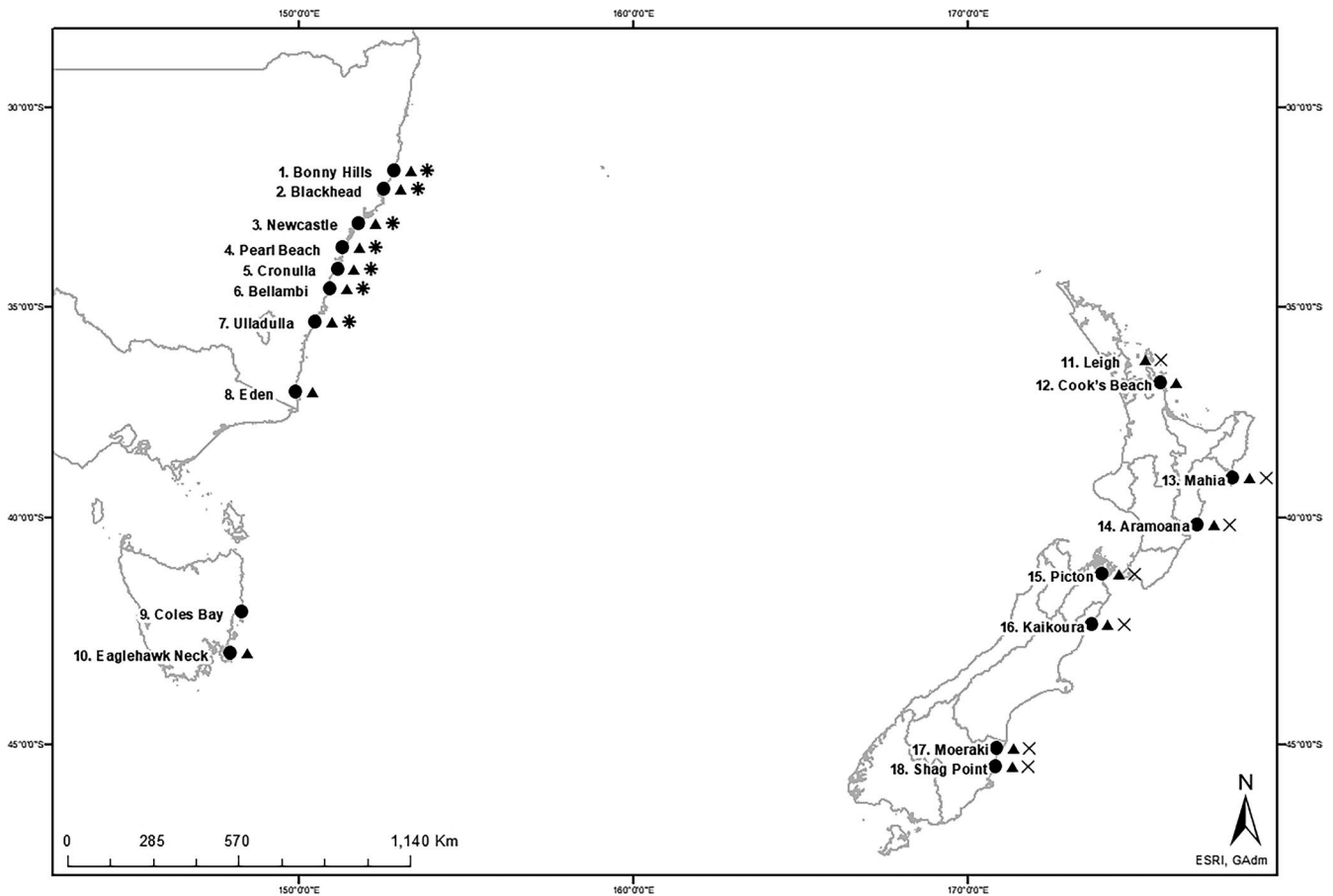
FIGURE 1 Study area including 18 sites along the east coast of Australia (10 sites) and New Zealand (8 sites). Symbols show the macroalgal habitats that were sampled at each site: *Hormosira banksii* (●), Coralline (▲), *Sargassum* (*) and *Cystophora* (×). Coordinate system: GCS_WGS_1984

changes in community structure. Given that biogenic habitats can facilitate associated communities by dampening particular environmental stressors at small spatial scales (Bruno & Kennedy, 2000; Dijkstra, Boudreau, & Dionne, 2012; Wright & Gribben, 2017), then it could be hypothesized that the physical characteristics of habitats may be particularly important predictors of their associated communities as they can weaken gradients in external abiotic conditions at biogeographic scales (McAfee, Cole, & Bishop, 2016; Silliman et al., 2011). However, some abiotic stressors (e.g., pollution) may not be moderated by habitats and as such may either affect habitats and communities to similar degrees or may only affect either the community or the habitat.

Macroalgae create some of the most conspicuous and ecologically important habitats on rocky reefs in temperate regions around the world (Bellgrove, McKenzie, Cameron, & Pocklington, 2017; Schiel & Foster, 1986). To investigate the relationships between the physical characteristics of macroalgae and the invertebrate communities within them, we conducted biogeographic surveys of intertidal macroalgae on the temperate east coasts of Australia and New Zealand. Surveys were conducted across multiple spatial scales including between countries, sites within countries, and macroalgae within sites. We related observed spatial patterns in

macroalgal physical characteristics and their invertebrate communities to 26 abiotic variables (natural and anthropogenic) sourced for each site. First, we tested the hypothesis that the physical characteristics (individual and patch level) of each macroalga were related to latitudinal gradients. Second, we hypothesized that invertebrate communities would vary in their structure and composition with latitudinal gradients. Third, we hypothesized that patterns in macroalgal physical characteristics and their invertebrate communities would relate to similar external environmental variables across the study area, but that the invertebrate communities would mostly correlate with changes in macroalgal physical characteristics. We did not sample across the total distribution of each macroalgal habitat but selected a study area where the habitats co-occurred across a similarly large latitudinal range in both countries. Biogeographic studies often use univariate measures of species richness or abundance to describe changes in community composition. In this study, we used multivariate analyses of invertebrate community structure and composition across a broad range of taxa, but with a lower taxonomic resolution as this approach can be effective at detecting large-scale diversity patterns even when there is high local-scale variability (Anderson, Connell, et al., 2005).

FIGURE 2 Survey design showing replicates at each scale of the study area. Each country (*n* = 2) included 8–10 sites sampled across the latitudinal gradient. Within each site, 2–3 macroalgal habitats were sampled with six replicate patches of each (see Figure 1 for the number of sites and habitats at each scale). Within each patch multiple habitat characteristics and invertebrate communities were measured. The spatial scales are shown at the base of the figure. Patterns were determined at large (latitude, country) and small (site, patch) spatial scales. All environmental covariates were sourced or collected at the site scale
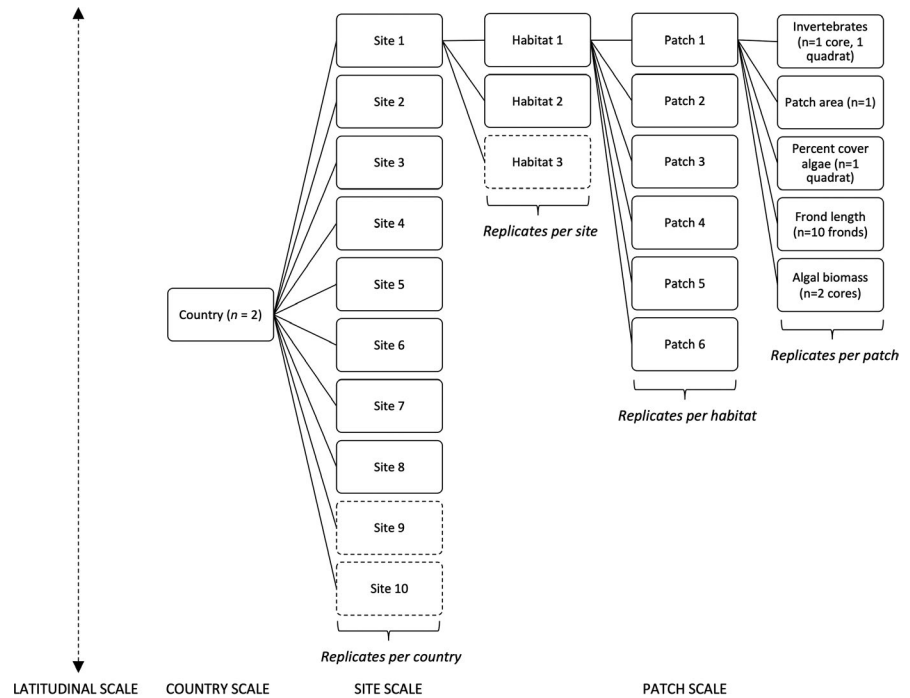
2 | METHODS

2.1 | Study sites

We sampled a single rock platform (25–75 m long) at each of 18 sites across the temperate east coasts of Australia and New Zealand (Figure 1). In Australia, we surveyed 10 sites from Bonny Hills in Northern NSW to Eaglehawk Neck in Tasmania, ranging across more than 1,300 km (linear distance; Figure 1). In New Zealand, we surveyed eight sites from Leigh (northern New Zealand) to Shag Point, Otago (southern New Zealand) ranging across more than 1,000 km (Figure 1). We selected Bonny Hills as the upper latitudinal limit of the study, as this coincides with the transition from temperate to sub-tropical climate, based on Köppen climate classes (Bureau of Meteorology, 2014). Within countries, sites were at least 10 km apart; however, sites were generally over 100 km linear distance from each other (Figure 1). The latitudinal gradients sampled in both countries overlapped by 6.73 decimal degrees (Figure 1). The east coasts of both countries were suitable for comparison as they have similar macroalgae and physiographic conditions—including large, flat rock platforms and moderate wave climates (National Institute of Water & Atmospheric Research, 2016; Shand & Carley, 2011).

2.2 | Study organisms

We sampled three macroalgal species/complexes with distinctive physical characteristics in each country; two of which were shared between countries: *Hormosira banksii* (Turner) and red turfing algae (hereafter Coralline; see Figure S1). *Hormosira banksii* is a prostrate brown alga with beaded vesicles that are connected in chains

10–30 cm long. It is distributed in Tasmania and NSW in Australia and is widely distributed on both islands in New Zealand (Edgar, 2008). Coralline included several morphologically similar species from the family Corallinaceae (e.g., *Corallina officinalis*, *Amphiroa* spp., *Jania* spp.). Species from the family Corallinaceae are widely distributed in temperate Australia and New Zealand (Atlas of living Australia website, 2018 at http://www.ala.org.au. Accessed 01 July 2018) and different species occurred interchangeably throughout the study area. Grouping of Coralline species at the family level as a morphologically similar complex has also been done in other similar studies on habitat–community associations (Kelaher, 2002, 2003a). The third macroalgal habitat sampled was *Sargassum* spp. (hereafter *Sargassum*) in Australia and *Cystophora* spp. (hereafter *Cystophora*) in New Zealand, which are closely related brown algae that occur in the lower intertidal zone (Edgar, 2008). These two habitats are both brown frondose, branching seaweeds, with receptacles either on branches in *Sargassum* or on vegetative fronds in *Cystophora* (Edgar, 2008). *Cystophora* was sampled at the genus level as multiple species occurred throughout the study area (e.g., *Cystophora retroflexa*, *Cystophora scalari*, and *Cystophora torulosa*) that would provide a broadly similar physical habitat structure compared to the other habitats, as fucoids with branching fronds. For *Sargassum*, numerous, morphologically similar, species co-occur in Australia and accurate identification is difficult, being based on the seasonal size and shape of receptacles (reproductive structures at the end of the algal branches; Edgar, 2008); therefore, this habitat was categorized to genus. *Sargassum* are broadly distributed in Australia (though absent at some specific study sites, see below), and *Cystophora* are widely distributed in New Zealand (Atlas of living Australia website, 2018 at http://www.ala.org.au. Accessed 01 July 2018; Edgar, 2008). At each site, we sampled three macroalgal habitats except in: (a) Leigh and Picton in New Zealand where *H. banksii*

was absent, (b) Cook's Beach in New Zealand where *Cystophora* was absent, (c) Coles Bay in Australia where Coralline was absent, and (d) Eden and the two Tasmanian sites in Australia where *Sargassum* was absent (Figure 1).

2.3 | Spatial patterns in macroalgal habitat characteristics

All macroalgal taxa were surveyed from January 2012 to early April 2012. Australian sites were sampled in a random order between January and April and New Zealand sites were sampled over a three-week period in February. As ocean temperatures lag seasonally, the sampling period represented summer water temperatures. At each site, we sampled six replicate patches of each macroalgal habitat during low tide across the length of the rock platform (Figure 2). The habitat patches selected occurred as discrete mono-specific patches with less than 10% of other habitat-forming organisms present.

Two patch-level characteristics were measured (patch area and percentage cover), plus two individual-level characteristics (frond length and biomass) of the macroalgae. Patch area was estimated by multiplying the longest and widest dimensions of each patch. Frond length was determined from the average of 10 randomly selected fronds measured at the patch centre. Percentage cover of algae was approximated using a grid of regularly spaced points in a 25 × 25 cm quadrat. Macroalgal biomass was determined from two replicate core samples per patch. PVC cores (10 cm diameter) were collected near the centre of each patch, with algae scraped off at the rock surface with a paint scraper and placed into labelled plastic bags (Kelaher, Castilla, & Seed, 2004; Thrush et al., 2011). Biomass samples were rinsed over a 1 mm sieve to remove trapped sediment. After excess water was drained, the algae were weighed in the field on digital scales (nearest 1 g). The two samples were then pooled to determine patch biomass. To ensure wet weight was an appropriate measure of biomass, samples of each macroalgal taxa were taken back to the laboratory and oven-dried at 60°C for 48 hr to determine dry weight (n = 12 cores/habitat). For each macroalga, wet and dry weights all were significantly correlated (Pearson's Correlation coefficient; $r > 0.90$).

2.4 | Spatial patterns in communities

Invertebrate communities in macroalgal patches were sampled using one of the PVC cores and collecting the invertebrates retained on the 1 mm sieve. To capture large or benthic invertebrates that may not be collected in the cores, a 25 × 25 cm quadrat with a 5 × 5 cm grid was used to survey larger, benthic invertebrates in each patch. The survey was conducted by searching the fronds and substrate in each of the quadrat grid cells for macroinvertebrates (>2 cm). All invertebrates from each patch (core + quadrat) were combined in a labelled plastic bag to capture one composite replicate patch (Figure 2). The sample was later fixed in 7% formalin for a minimum

of one week before being washed and transferred to 80% ethanol for preservation.

In the laboratory, all animals were identified and counted under a dissecting microscope. Molluscs were identified to family level and below (down to species), polychaetes to family level, crustaceans to order or suborder, echinoderms to class, Anthozoa to order, and foraminifera to phylum. The level of taxonomic identification related to the taxonomic group's dominance among samples and the condition of the samples required for fine-scale identification (e.g., although amphipods were a dominant group due to the high volume of collections and the time required to process the samples, some diagnostic features degraded after collection). It was also deemed more useful to include a large range of taxonomic groups identified to a coarse taxonomic level rather than a smaller range of taxa identified to species level in order to maximize chances of detecting habitat–community associations (Anderson, Connell, et al., 2005). Although our sampling methods may not capture all invertebrate taxa (e.g., barnacles, tube-dwelling polychaetes and colonial species such as sponges and bryozoans; Kelaher & Castilla, 2005), these did not appear common when sampling, most likely due to an absence of the bare rock they need for colonization (Edgar, 2008), and were excluded from the data set.

2.5 | Environmental variables

We sourced data on 40 environmental variables (13 of which were later excluded) related to coastal abiotic conditions (natural and anthropogenic) for each site from publicly available databases (Halpern et al., 2008), satellite images (e.g., NASA/NOAA; Meeus, 1991) and field observations (Table 1). All variables were sourced or determined at the site scale.

2.6 | Data analysis

All analyses were conducted using the PRIMER V7-PERMANOVA *add on* software (Anderson, Gorley, & Clarke, 2008; Clarke & Gorley, 2015). For all analyses on macroalgal habitat characteristics and environmental data, we used Euclidean distance matrices. Prior to the analyses, we normalized habitat characteristics and environmental variables as the data were measured in various units. For analyses on invertebrate communities, we used Bray–Curtis matrices. Community data were standardized by totals to reduce the influence of habitat patches with high biomass, and then square-root transformed to reduce the influence of a few highly abundant taxa on the results, while still preserving patterns of relative abundances among samples (Clarke, 1993; Clarke & Gorley, 2015). To visualize spatial patterns in habitat characteristics and communities at each site in each country, we produced principal coordinate analyses (PCO) plots. We did not evaluate patterns of spatial variation of environmental variables as they were used as predictor variables for the invertebrate and macroalgal habitat data.

TABLE 1 Description and source of environmental variables used in the analyses

Variable	Description
Latitude	Latitude in decimal degrees
Longitude	Longitude in decimal degrees
Sea surface temperature (SST; °C)	Average and standard deviations of monthly values of the MODIS Aqua mission from July 2002 to December 2015. Averages and standard deviations were estimated for the following: the full year during the day; the summer months (Dec–Feb) during the day[a]; the full year during the night[a]; and the summer months (Dec–Feb) during the night[a] (Meeus, 1991).
Chlorophyll-a (Chl-a; mg/m^3)	Average and standard deviations of monthly values of the MODIS Aqua mission from July 2002 to December 2015. Averages and standard deviations were estimated for both the full year and for the summer months only (Dec–Feb; Meeus, 1991).
Chlorophyll-a anomalies[a]	Number of events that surpassed 2 standard deviations of the average chlorophyll-a for a given year (Meeus, 1991).
Rainfall (mm)	Average and standard deviations of monthly accumulated rainfall from January 1979 through September 2015 obtained using TOVAS web-based application (Halpern et al., 2008).
Rainfall anomalies[a]	Number of events that surpassed 2 standard deviations of the average rainfall for a given year.
Photosynthetically active radiation[a] (E*m^2*day)	Average and standard deviations of monthly values of the MODIS Aqua mission from July 2002 to December 2015. Averages and standard deviations were estimated for both the full year and the summer months only (Dec–Feb; Meeus, 1991).
Dissolved organic matter (chromophoric) (index)	Average and standard deviations of monthly values of the MODIS Aqua mission from July 2002 to December 2015. Averages and standard deviations were estimated for both the full year and for the summer months only (Dec–Feb; Meeus, 1991).
Particulate organic carbon (mg/m^3)	Average and standard deviations of monthly values of the MODIS Aqua mission from July 2002 to December 2015. Averages and standard deviations were estimated for both the full year and for the summer months only (Dec–Feb; Meeus, 1991).
Ultraviolet light intensity (index)	Radiation reaching the surface of earth (1996–2004) measured with the GSFC TOMS EP/TOMS satellite program at NASA (Halpern et al., 2008).
Photoperiod[a] (index)	The difference between the sunrise and the sunset time, based on common astronomical formulae (Meeus, 1991).
Inorganic pollution (index)	Urban run-off estimated from land use categories, US Geological Survey (http://edcsns17.cr.usgs.gov/glcc/; Halpern et al., 2008).
Organic pollution (index)	Food and Agriculture Organization (FAO) national pesticide statistics (1992–2001; http://faostat.fao.org; Halpern et al., 2008).
Nutrient contamination (index)	FAO national pesticide statistics (1992–2001; http://faostat.fao.org; Halpern et al., 2008).
Ocean acidification (index)	Aragonite saturation state 1870–2000/2009, 1-degree latitude/longitude resolution (Halpern et al., 2008).
Human population pressure (index)	Estimated as the sum of total human population adjacent to the ocean within a 25 km radius. From LandScan 30 arc-second population data of 2005 (Halpern et al., 2008).
Ocean-based pollution (index)	Model based on combined commercial shipping traffic data and port data (Halpern et al., 2008).
Wave exposure	Categorical variable with four levels indicating wave exposure at the site level. Categories were based on commonly used fetch measurements, with exposure defined by the openness of the site including the presence of offshore islands and protection provided by headlands (see Wernberg & Thomsen, 2005), though submerged reefs were not considered.

[a]Variables that were excluded from the analysis: (i) the chlorophyll-a anomalies and (ii) rainfall anomalies indexes as they correlated with their respective standard deviation (>95%); (iii) photosynthetically active radiation (all variables—summer and annual averages and standard deviations) as they correlated with sea surface temperature annual day average (>95%); (iv) summer average and standard deviations for sea surface temperature during the day and night, as they correlated with the annual average of sea surface temperature day and night (>95%); (v) annual average and standard deviations of sea surface temperature during the night, which correlated with annual sea surface temperature during the day (95%); (vi) photoperiod as it correlated with annual average and standard deviations of sea surface temperature during the night.

We used RELATE analyses to test for linear latitudinal patterns in macroalgal habitats and communities, separately. RELATE is a nonparametric matrix correlation routine that measures how closely related two sets of multivariate data are by calculating a rank correlation coefficient (e.g., Spearman's) between paired samples in two similarity matrices (Clarke & Gorley, 2015). In this case, the biotic similarity matrices (habitats or communities) were compared to a "model matrix," which is an idealized distance matrix representing the structure of a hypothesized serial distribution representing a linear latitudinal gradient (Clarke & Gorley, 2015). This model determined

whether sites located next to each other were more similar (in terms of the structure and composition of communities or habitat characteristics) than sites located further apart. Seriation models implicitly test for spatial autocorrelation in patterns of spatial distribution of the communities and habitat characteristics. As the macroalgal habitats had different physical characteristics (see Figure S1) and the communities had different taxonomic structure, we analysed each macroalgal habitat and community separately; however, our aim was to determine if the matrices for each habitat in both countries would correlate with the spatial models and with each other (i.e., habitats and their associated community). RELATE analyses compared the ranks of the habitat characteristic data matrix and the ranks of the community data matrix separately against each model. If patterns of spatial variation of the matrix were similar to the model, we would expect high and significant correlation values. RELATE analyses used Spearman rank correlations that tested for significance using permutations (999) of the original data to construct a null distribution. Shade plots were used to visualize the relative abundances of taxa within each habitat across the latitudinal gradient in each country. In each plot, taxa are clustered in a dendrogram based on an index of association (determined using a SIMPROF routine) with the dendrogram discriminating taxa that have correlated spatial distributions along the latitudinal gradient from those that do not (Clarke & Gorley, 2015).

For each macroalgal habitat, BEST analyses based on Spearman rank correlations were used to determine which environmental variables were most correlated with spatial patterns of habitat characteristics, or which variables and characteristics were most correlated with community structure. BEST is a nonparametric routine that finds the best match between two data matrices and searches over all possible subsets/combinations of variables to find the optimal model (Clarke & Gorley, 2015; Clarke & Warwick, 2001). Prior to the analyses, Draftsman plots were used to detect collinearity among environmental data and to identify suitable transformations of individual variables. A total of 26 environmental variables were included in the models after removing variables that covaried (Table 1). The index of inorganic contamination, index of organic contamination and nutrients were Log + 1 transformed because some values were high in relation to other scales. All data were normalized because variables were estimated in different units.

To determine the scale at which these variables influenced communities (i.e., country, site or habitat patch), we conducted a linkage tree (LINKTREE) analysis using the entire community similarity matrix and the entire environmental and habitat characteristic distance matrix (i.e., all countries, sites and habitats). LINKTREE is a non-metric, nonlinear, non-additive technique that links patterns of spatial variation to a suite of environmental or biological data. It is a modification of classification trees, but involves nonparametric binary divisive clustering in which the various divisions (i.e., groupings) of the community data are constrained by "optimal" combinations of the environmental data (Clarke & Gorley, 2015). Since environmental variables were estimated at the scale of sites and habitat and community were sampled at the patch level (different spatial scales),

centroids per site were estimated for habitats and communities to run the BEST and LINKTREE correlation analyses.

3 | RESULTS

3.1 | Spatial patterns in macroalgal habitat characteristics

Multivariate macroalgal habitat characteristics did not follow linear latitudinal gradients (i.e., the seriation model) for any of the habitats (Figure 3; Table 2). However, the PCO plot suggested a nonlinear (C-shaped) gradient in the multivariate distribution in 5 of the 6 cases (except Coralline in Australia). To better describe the spatial pattern of macroalgal habitat characteristics (and test for the existence of a C-shaped pattern), RELATE was used with a cyclicity model, which tested whether sites at either end of the sampled distribution were generally more similar to each other than to adjacent sites, this showed a significant correlation for 5 or the 6 models (Table 2, Figure 3).

3.2 | Correlations between macroalgal habitat characteristics and environmental conditions

The macroalgal habitat characteristics of *H. banksii* correlated significantly with abiotic environmental variables in Australia and New Zealand. Otherwise, only Coralline habitat characteristics in New Zealand significantly correlated with environmental variables. Sea surface temperature was generally an important correlate along with different measures of human disturbance (Table 3a). Note that the BEST analyses took the factor "country" into consideration, but since results were consistent between countries (within each habitat), general interpretations were made for each habitat regardless of country.

3.3 | Spatial patterns in communities

High abundances and diversity within invertebrate communities were observed throughout the study, with 10 s to 100 s of individuals collected in each habitat patch, and 77 taxonomic groups found across the study area. Taxon richness was not highly variable among habitats, with values per site ranging from 5 to 21 (mean 13, $SD \pm 5$) in *Hormosira banksii*, 11–23 (mean 18, $SD \pm 4$) in Coralline, 10–23 (mean 16, $SD \pm 5$) in *Sargassum*, and from 6 to 18 (mean 11, $SD \pm 2$) in *Cystophora* (see Figure S2). Communities in each habitat were generally distinct, except for *H. banksii* communities which had similarities with most other communities—except Coralline in Australia (see Figure S3). Abundances of invertebrates in *H. banksii* were the lowest and ranged from 62 to 628 per site (mean 224, $SD \pm 168$), Coralline abundances were the highest and ranged from 86 to 8,048 per site (mean 1,486, $SD \pm 2,136$), *Sargassum* ranged from 151 to

FIGURE 3 Principal coordinate analysis (PCO) showing centroids of (a) habitat characteristics and (b) communities for each macroalgal habitat and site in Australia (AUS) and New Zealand (NZ). Vectors follow the latitudinal gradient to show the spatial relationships between sites. Symbols represent the three macroalgal habitats sampled in each country: *Hormosira banksii* (●), Coralline (▲), *Sargassum* (*) and *Cystophora* (×). Sites are numbered as shown in Figure 1
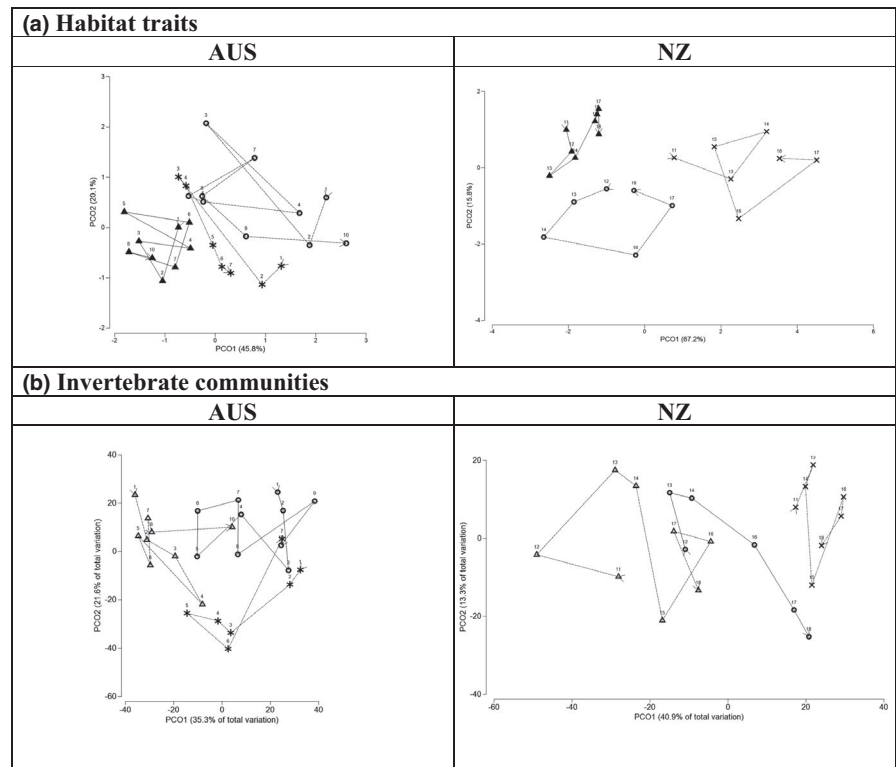

(a) Habitat traits

(b) Invertebrate communities

TABLE 2 RELATE analyses showing correlations of (a) habitat characteristics and (b) communities for macroalgal habitats sampled in Australia (AUS; n = 10 sites) and New Zealand (NZ; n = 8 sites)

| | AUS | | NZ | |
	Seriation	Cyclicity	Seriation	Cyclicity
(a) Habitat characteristics				
Coralline	−0.228 (0.98)	−0.014 (0.54)	0.202 (0.08)	**0.284 (0.01)**
Hormosira banksii	0.151 (0.14)	**0.181 (0.03)**	0.044 (0.41)	**0.546 (0.02)**
Sargassum	0.056 (0.32)	**0.274 (0.01)**	—	—
Cystophora	—	—	0.03 (0.45)	**0.164 (0.05)**
(b) Communities				
Coralline	0.236 (0.11)	0.081 (0.19)	0.175 (0.21)	−0.039 (0.58)
Hormosira banksii	0.007 (0.44)	**0.172 (0.05)**	**0.817 (<0.01)**	0.483 (0.05)
Sargassum	0.203 (0.14)	**0.501 (0.01)**	—	—
Cystophora	—	—	0.074 (0.40)	−0.138 (0.82)

Note: The seriation model tested the prediction about linear latitudinal gradients, while the cyclicity model tested the significance of the "C-shaped" patterns (i.e., greatest similarities between southern and northern sites) that were apparent from the PCO results. The results show the Spearman rank correlations with the significance of the correlations (*p* values) shown in brackets. Significant results are highlighted in bold. Where there were two significant models for *Hormosira banksii* in NZ the highest correlation was considered to be the dominating pattern, accounting for some of the redundancy in the explicative models.

955 (mean 372, *SD* ± 269), and *Cystophora* from 412 to 3,040 (mean 1,475, *SD* ± 968) per site (see Figure S4). Though we expected differences in community structure between habitats because of their very different morphology, we were most interested in whether these distinct macroalgal habitats and communities would share similar spatial patterns and relationships with environmental drivers.

Consistent with analyses on macroalgal habitat characteristics, communities did not follow linear latitudinal gradients (Table 2), except for communities associated with *H. banksii* in New Zealand

(seriation Rho = 0.81). Instead, invertebrate communities associated with *H. banksii* in Australia and *Sargassum* (which was only sampled in Australia) appeared to have "C-shaped" latitudinal gradients in the PCO plots, similar to those described for the macroalgal habitat characteristics (Figure 3). Again, RELATE analysis confirmed that these communities were significantly correlated with the cyclical model (Table 2), meaning that for these habitats' communities at the edges of the gradient were more similar to each other than to communities in the middle of the gradient. Although the remaining

TABLE 3 BEST analyses showing (a) the combination of environmental variables (*n* = 26) that best correlate with habitat characteristics, and (b) the combination of environmental variables and habitat characteristics that best correlate with communities

Coralline		*Hormosira banksii*		*Sargassum*	*Cystophora*
AUS	**NZ**	**AUS**	**NZ**	**AUS**	**NZ**
(a) Habitat characteristics					
0.362 (0.29)	**0.582 (0.05)**	**0.546 (<0.001)**	**0.643 (0.05)**	0.614 (0.08)	0.542 (0.32)
	• Sea surface temperature • Inorganic pollution • Human population pressure • Dissolved organic matter	• Inorganic pollution	• Sea surface temperature • Dissolved organic matter • Chlorophyll-*a*		
(b) Communities					
0.503 (<0.05)		**0.552 (<0.05)**		**0.916 (<0.01)**	**0.882 (<0.01)**
• Human population pressure • Sea surface temperature • Habitat biomass • Habitat patch area		• Human population pressure • Sea surface temperature • Habitat biomass • Habitat frond length • Latitude • Ocean acidification • Chlorophyll-*a* • Ultraviolet light		• Human population pressure • Habitat biomass • Ocean acidification	• Human population pressure • Sea surface temperature • Habitat percentage cover • Longitude • Ocean-based pollution index

Note: The results show the Spearman correlation coefficients for each of the three macroalgal habitats sampled in Australia (AUS; *n* = 10 sites) and New Zealand (NZ; *n* = 8 sites). For the community analysis, country was taken into consideration, but overall results were consistent across countries so the combined results are presented. The significance of the correlations (*p* values) is shown in brackets. Significant results are highlighted in bold.

habitats (Coralline in both countries and *Cystophora* in New Zealand) were not correlated significantly with either a linear or cyclical distribution, they also appeared to have communities that were similar at the edges of the sampled distributions in the PCO plots, with sites at the north and south for both habitats generally clustering together, away from those in central sites (Figure 3). We do not present results from the third RELATE correlation as there were no significant correlations. Shade plots comparing relative abundances of taxa among sites and habitats showed that the dominant taxa in communities differed between macroalgal habitats. They also showed that some individual taxa exhibited spatial patterns across latitude that were consistent with the community patterns described above (see Figure S5). *H. banksii* communities were primarily dominated by amphipods and the molluscs Trochidae in New Zealand and *Lasaea australis* in Australia. Trochids and amphipods were less abundant at lower latitudes in New Zealand, which may have contributed to the linear community pattern identified in this country. Among *H. banksii* in Australia, the two dominant taxa had opposing patterns, with fewer Amphipoda and more *L. australis* at centrally located sites, likely contributing to the cyclicity model result (Figure S5a,b). Coralline communities in Australia had high abundances of *L. australis*, which had similar spatial patterns to the chiton family Acanthochitonidae and the polychaetes Nereididae and Syllidae. In New Zealand, Coralline communities had some taxa that were highly abundant in specific sites (e.g., the bivalve *Kellia* spp., and the gastropod family Eatoniellidae), as well as taxa that were common across sites (e.g., Nereididae and Amphipoda). The latitudinal patterns were not strong for these taxa, although they had smaller

relative abundances at some central sites in Australia (Figure S5c,d). *Sargassum* communities also had some common taxa (e.g., Trochidae) across sites and some that were particularly abundant at specific sites (e.g., Amphipoda—which was also less abundant in the centre of the range; Figure S5e). *Cystophora* communities had large abundances of Eatoniellidae, Trochidae, Amphipoda and Isopoda. Again, the spatial patterns of individual taxa in *Cystophora* were not strong, but there were some large relative abundances of amphipods at the most southern and northern site (Figure S5f).

3.4 | Correlations between communities, macroalgal habitat characteristics and environmental conditions

The communities, in contrast to macroalgal habitat characteristics, correlated significantly with environmental variables for all habitats in Australia and New Zealand, though the relationships between communities, macroalgal habitat characteristics and environmental conditions differed for each habitat (Table 3). Overall, human population pressure was an important component of the models and correlated with all communities. Sea surface temperature was also important for three of four communities. At least one habitat characteristic was included in the models for all communities. Biomass was included in the models for three of four communities, but other habitat characteristics were also important including frond length, canopy percentage cover and patch area. Some additional environmental or spatial variables were included in the models that were unique to individual communities, such as latitude, longitude, chlorophyll-*a* and ultraviolet light (Table 3b). The

variables that were significant to multiple communities had contrasting spatial distribution patterns across latitude. Human population peaked towards the centre of the sampled range in Australia, though was relatively consistent in New Zealand (Figure S6). Sea surface temperature, as is well known, decreased with increasing latitude towards the south of both countries. The habitat characteristic biomass was important for three of four communities, so we examined the univariate patterns in biomass across latitude for the relevant habitats. Coralline biomass peaked in the most northern site, though this appeared to be an outlier more than a trend and if removed there did not appear to be a latitudinal trend. *Hormosira banksii* biomass was smallest at the centre of the latitudinal range sampled. *Sargassum* biomass was also smallest at the centre of the sampled range—though it was sampled over the smallest range (Figure 4).

The LINKTREE analyses enabled comparisons of invertebrate communities among macroalgal habitats in all sites in Australia and New Zealand and indicated the relative importance of macroalgal habitat characteristics and external abiotic variables at different spatial scales. These analyses highlighted the importance of sea surface temperature in explaining differences in communities between countries (split A in Figure 5). All sites in New Zealand (lower sea surface temperature) are grouped on the left of the dendrogram, together with the two southern-most Australian sites (Coles Bay and Eaglehawk Neck in Tasmania), while all other Australian sites (higher sea surface temperature) are in the right grouping (Figure 5 split A). The results showed that the communities within the macroalgal habitats that were common to each country (i.e., *H. banksii* and Coralline) were generally distinct between countries. Within each one of these two temperature groups, differences in macroalgal biomass were important in distinguishing communities. In Australia, communities associated with the larger *H. banksii* clearly separated from those associated with the lighter weight Coralline macroalgal habitat (Figure 5, split P), while *Sargassum* communities were divided between these two groups depending on the biomass of the *Sargassum*, which varied considerably among sites separated by 194–380 km (average biomass in Blackhead/Bonny Hills/Ulladulla group = 140.83 g (±14.72 g) vs. Cronulla/Newcastle/Pearl Beach/Bellambi group = 73.69 g (±22.87 g)). Similarly, in New Zealand, communities associated with the larger *Cystophora* were distinct from those in the physically lighter Coralline (split B, Figure 5), while *H. banksii* communities were divided between these two subgroups depending on macroalgal biomass (distinguishing sites on the north island from those on the south). Other macroalgal habitat characteristics were also important for further distinguishing communities in some sites for example per cent cover of algae related to Coralline and *Sargassum* communities in many Australian sites (split Q, Figure 5).

4 | DISCUSSION

In this study, we investigated the role of environmental factors in shaping the physical characteristics of macroalgae and the invertebrate communities inhabiting them at continental scales. We found little support for our hypotheses that the physical characteristics

of macroalgae and communities would follow latitudinal gradients. Instead, patterns in both macroalgal habitat characteristics and associated communities generally shared unusual nonlinear patterns, where habitat characteristics and communities were more similar at the edges of the sampled distribution (i.e., north and south) compared to those at centrally located sites. Our models suggest that these patterns resulted from the influences of both small- and large-scale environmental conditions and that communities within macroalgae were related to both macroalgal habitat characteristics and external environmental factors.

Individual macrophyte characteristics (e.g., growth habit, leaf size, seed mass and specific leaf area) often show linear latitudinal gradients (Gallagher & Leishman, 2012; Westoby & Wright, 2006). In our study, we wanted to test whether a suite of macrophyte characteristics would change across latitude, given that combinations of characteristics contribute to microhabitat environments (Airoldi, 2003; Heck & Orth, 1980; Kelaher, 2003a, 2003b; Matias et al., 2010; Nilsson, 1979; Taniguchi et al., 2003). We found unusual nonlinear gradients in suites of macroalgal habitat characteristics across latitude for five of the six macroalgae examined. The consistent pattern was observed across the macroalgal habitats, despite each of the taxa sampled having very different morphologies (e.g., turfing red algae versus. brown frondose algae; see Figure S1) and Australian macroalgae (Coralline and *H. banksii*) being slightly larger on average than the same taxa sampled in New Zealand.

Because the nonlinear "C-shaped" pattern in macroalgal habitat characteristics occurred in 5 of 6 tests, we expected there would be a clear large-scale factor driving the result; however, this was not the case. In fact, three of the models showed no significant variables and the others showed a combination of either localized environmental conditions (e.g., pollution and human population pressure) or large-scale conditions (e.g., sea surface temperature). As the habitat characteristics did not correlate consistently with environmental variables, the nonlinear pattern is hard to reconcile. One explanation is that at the centre of the temperate ranges sampled, abiotic conditions related to latitude (e.g., temperature) may be generally favourable and macrophytes more strongly respond to local conditions (e.g., Maggi, Milazzo, Graziano, Chemello, & Benedetti-Cecchi, 2015). However, at the edge of the distributions sampled, large-scale environmental conditions may be the dominant driver of macrophyte characteristics. The result of this may mean that localized abiotic drivers at the centre of the range may mask macroecological patterns (e.g., Kerswell, 2006), which may only exert influence over communities at their edges. In fact, the peak hypothesis of range edges predicts that intraspecific traits change from the centre to the periphery of a species distribution due to systematic changes in biogeographic factors from the species core habitat (Gaston, Chown, & Evans, 2008; Lloyd, Murray, & Gribben, 2012). However, we did not cover the total distributions of each macroalgae in this study so we cannot generalize about their global distribution pattern.

The latitudinal diversity gradient is one of the most widely studied ecological patterns (Hillebrand, 2004; Kraft et al., 2011). Similar to the habitat patterns, communities also generally displayed
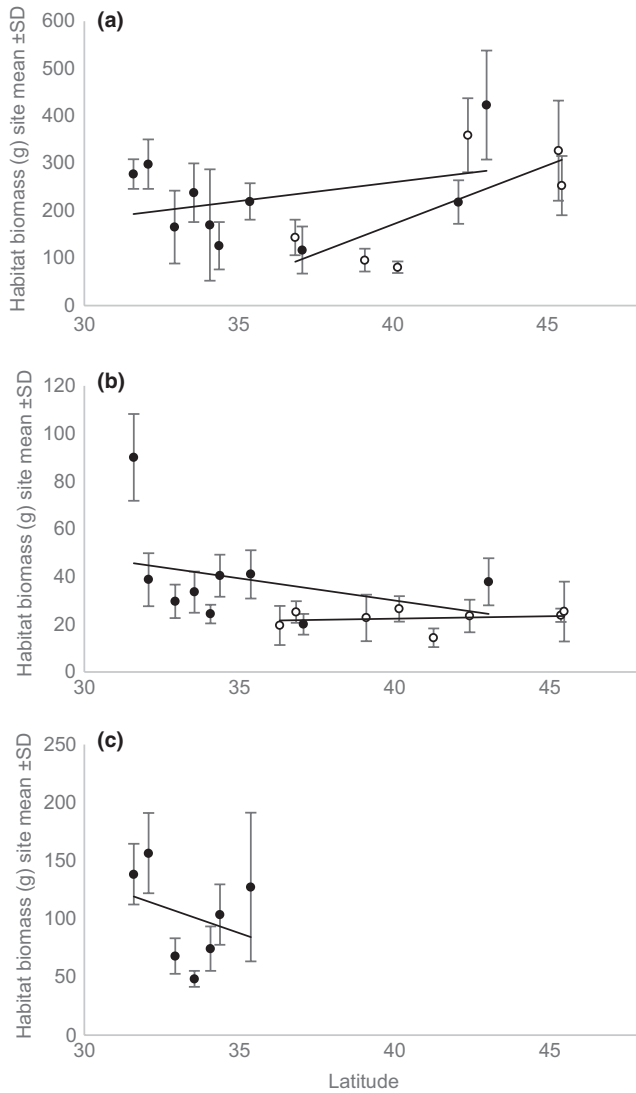
FIGURE 4 Macroalgal habitat biomass (g) per site (mean ± *SD*) across the latitudinal gradient for (a) *Hormosira banksii*, (b) Coralline, (c) *Sargassum* in Australia (black circles) and New Zealand (white circles). *Cystophora* biomass is not shown as it was not a significant characteristic for those communities. Latitude is negative as sites are in the Southern Hemisphere.

"C-shaped" biodiversity patterns. Interestingly, the nonlinear biodiversity pattern occurred despite each of the macroalgal habitats in each of the countries housing distinct communities (see Figure S3). Examination of abundance patterns for individual taxa across latitude (see Figure S5) revealed that few taxa showed strong C-shaped patterns across latitude, indicating that the result was due primarily to the changing abundance and composition of the entire community. The distinction between communities in different macroalgal habitats and countries was expected because of their very different physical structures (see habitat-specific examples in: Edgar & Klumpp, 2003; Gemelli, Johnson, & Wright, 2019; Kelaher, 2003b). For example, Coralline had large relative abundances of polychaetes, which was expected due to its dense turf-like structure (see Figure S5c,d). Although the communities differed between habitats, the

majority of the taxa sampled (75%) were shared between the two countries. Macroalgal characteristics can be an important driver of associated community structure and the similarities between macroalgal habitat and community patterns suggest that communities were responding to variation in the physical habitat characteristics. Only *H. banksii* in New Zealand showed a traditional latitudinal gradient in community variation. The reason for this difference is not clear, though these communities had stronger associations with climatic variables including ultraviolet light and chlorophyll-*a*. Communities may have responded more strongly to these large-scale external abiotic variables as *H. banksii* occurs slightly higher on the shore than *Cystophora* and has less dense protective canopy cover than both *Cystophora* and Coralline.

When we investigated the environmental conditions that may be driving these patterns, we could not identify a consistent factor that correlated with all macroalgal habitats and communities. Although we predicted that communities would mostly correlate with habitat characteristics, we found that both habitat characteristics and external environmental variables were important. Of the characteristics that were significant, habitat biomass was the most common characteristic explaining differences in communities between sites within countries (see also Stelling-Wood et al., 2020). For *H. banksii*, the univariate graph of biomass showed a nonlinear pattern in Australia and a linear pattern in New Zealand (consistent with the RELATE models), whereas Coralline biomass did not show a strong trend in either country (consistent with the RELATE models)—though the most northern site in Australia had the highest biomass and the lowest biomass was at the centre of the latitudinal range sampled. *Sargassum* also had a nonlinear pattern with biomass the smallest at the centre of the study area and largest at the north and south (Figure 4). Biomass was not a significant variable for *Cystophora* communities. Canopy percentage cover was also an important factor structuring communities and other characteristics (e.g., patch size and frond length) also appeared within the habitat-specific models, suggesting the unique physical multivariate environment may promote distinctive communities by providing specific microhabitat conditions for the species they house (Angelini et al., 2011). The dominant factors such as habitat biomass and canopy percentage cover were expected to be an important factor in community structure as they are a proxy for habitat availability such as structural complexity and surface area (Kovalenko et al., 2012). In the exposed and highly variable system of rocky shores, space is a limiting factor and so the provision of structure for colonization is important to diversity (Matias et al., 2010; McGuinness & Underwood, 1986) as is their role in mediating environmental stressors (Dayton, 1972; Jones et al., 1994; Jurgens & Gaylord, 2017).

In the external abiotic environment, human population pressure was the only variable that correlated with all communities. Large human populations are known to have negative effects on rocky intertidal communities (Bloch & Klingbeil, 2016; Terlizzi et al., 2005; Thompson, Crowe, & Hawkins, 2002) and can cause reductions in canopy forming algae cover (Benedetti-Cecchi et al., 2001). Abundance patterns of some of the dominant taxa showed that
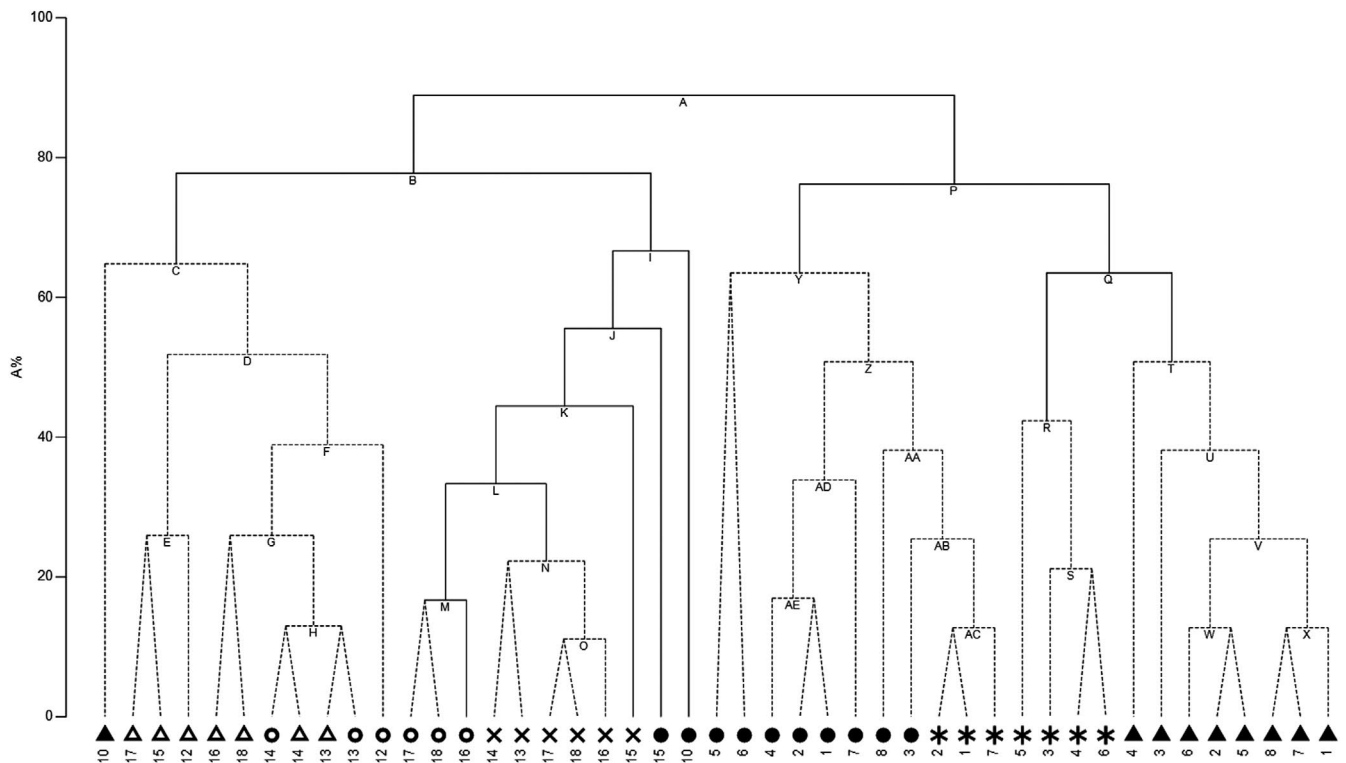
FIGURE 5 LINKTREE analysis showing the environmental and macroalgal habitat characteristics that correlated with spatial patterns in communities across countries, sites and habitats. *Hormosira banksii* = ●, Coralline = ▲, *Sargassum* = *, and *Cystophora* = ×; Australian sites are the filled symbols and New Zealand sites are open. Sites are numbered as shown in Figure 1. The *y*-axis (A%) is the equi-spaced representation of the average between groups ranked Bray–Curtis dissimilarities, representing the magnitude of differences between the subset of samples. Continuous lines represent statistically significant splits, dotted lines represent non-significant splits or groupings. Letters on each split represent subgroups of the environmental or habitat variables that correlated with each split. Split A shows sea surface temperature (SST) differences across the study area (R = .48, B = 83%) left split < right split. Split B = habitat biomass within the lower SST group (R = .54, B = 61%) left split < right split. Split P = habitat biomass within the higher SST group (R = 0.55, B = 70%) left split > right split. Split Q = % cover of macroalgal habitat (R = 0.80, B = 76%) left split < right split. The remaining splits were not significant or were related to differences between individual sites

amphipods, some polychaetes (e.g., Nereididae and Syllidae) and the abundant bivalve *Lasaea australis* tended to be less common at the sites with greater human populations, particularly in Australia where human populations are higher than New Zealand. Most individual taxa, however, did not show clear patterns with human population density. Human population may have contributed to the nonlinear distribution pattern of invertebrate communities given that urban areas did not occur linearly across the study area (e.g., the city of Sydney was near the centre of the Australian study area). Factors associated with high human populations (e.g., pollution from nutrients and contaminants) are often diffuse and may be unlikely to be moderated by habitat characteristics, meaning they could have direct effects on communities (Glasby, Gibson, & Cruz-Motta, 2017). Sea surface temperature was also important to three of the four communities in the BEST models. *Sargassum* was the only taxa that did not correlate with sea surface temperature, and this habitat was also sampled across the smallest spatial scale (over which temperature did not vary greatly). Although temperature decreased linearly with increasing latitude across both countries and was important to most communities, the community patterns rarely correlated with latitude specifically. Latitude is often used as a proxy for detecting

correlations with large-scale environmental drivers such as temperature. This result shows that large-scale variation in temperature was important, but that other environmental variables—which were also significant—may have altered the expected latitudinal pattern related to sea surface temperature.

Sea surface temperature was the most important correlate with communities in the LINKTREE analysis at the country scale, with temperature strongly related to differences between the countries and also between mainland Australia and the island of Tasmania suggesting there may be a spatial hierarchy in its influence. Both large- and small-scale temperature gradients are frequently recognized as having effects on rocky shore biota (e.g., Cruz-Motta et al., 2010; Harley et al., 2012; Mabin, Gribben, Fischer, & Wright, 2013). Temperature influences community structure in both marine and terrestrial environments (Brown, 2014; Gaston, 2000). The differences in the invertebrate taxa sampled in each of the countries may have also influenced this distinction—though the majority of invertebrates sampled were common to both countries. The taxonomic resolution of invertebrate communities in our study may have also influenced the spatial patterns we identified, as coarser taxonomic identification (i.e., above species level) can have a higher likelihood of detecting large-scale

diversity patterns (Anderson, Connell, et al., 2005). Nevertheless, we detected multi-scale variation in habitat characteristics and communities, indicating the resolution was not too coarse to detect a range of variation. Few studies have investigated the response of communities to large-scale differences in multivariate habitat characteristics both within and between biogenic habitats. In considering the importance of multivariate habitat characteristics to communities, the specific habitat characteristics that influenced communities differed between macroalgal habitats, but that across all habitats their characteristics generally played an important role in shaping communities. We also found that a combination of characteristics contributed to community structure patterns and so using a multivariate approach is important for observing associations at large scales. As the environmental conditions that related to community composition were idiosyncratic, our results highlight the importance of observing multiple scales of variation in biogeographic research (Fraschetti, Terlizzi, & Benedetti-Cecchi, 2005; Hewitt, Thrush, Dayton, & Bonsdorff, 2007). These results are important, as a lack of generality in biogeographic patterns is frequently cited as a reason for discounting the need for macroecological comparisons (Fowler-Walker, Connell, & Gillanders, 2005b; Hewitt et al., 2007). Our results support other studies that have shown that large-scale patterns can emerge from systems where there is high local-scale variability and that local-scale conditions can mask biogeographic gradients, including multiple examples of kelp characteristics responding to variation across both small and large spatial scales (Bearham, Vanderklift, & Gunson, 2013; Fowler-Walker et al., 2005a; Wernberg, Coleman, Fairhead, Miller, & Thomsen, 2003).

Although this research identified novel patterns in macroalgal habitat characteristics and associated communities, further research is needed to test the generality of these patterns, particularly in relation to the nonlinear (C-shaped) distribution patterns across latitude. Understanding the relative contributions of large- and small-scale factors to community structure and how they interact with habitat characteristics to determine biodiversity patterns also needs more targeted research (Bruno et al., 2003; Bulleri et al., 2012; Maggi et al., 2015). Although we surveyed broad temperature gradients over 1,000 km in each country, we did not cover the entire distributions of the macroalgal taxa (this would be challenging as some of the genera sampled have global distributions). As such, our results do not show their entire distribution pattern, and instead tested for consistencies between countries across the latitudinal gradients sampled. *Sargassum*, which was sampled across the smallest climatic temperature range, did not correlate with large-scale drivers and may have displayed more correlations if it was sampled across a larger range. Despite this, *Sargassum* still correlated with the cyclical model consistent with most other habitats. Furthermore, as both habitat characteristics (e.g., the reproductive fronds of *Sargassum* spp.) and environmental conditions vary temporally, further investigation into how temporal influences alter the observed spatial patterns would be an interesting next step to this research.

This study demonstrated that multi-scale factors are important in determining patterns in community structure, including those operating across latitudinal and local scales. We also showed that it

is important to consider variation in biogenic habitat characteristics when aiming to understand relationships between habitats and communities across large spatial scales (Gaston et al., 2008). In fact, our data suggest that habitat characteristics and the communities within biogenic habitats respond similarly to differing but potentially stressful environmental conditions. Though much research has focussed on identifying the most important spatial scale for driving biodiversity, this study and other research in this area (e.g., Anderson, Diebel, Blom, & Landers, 2005; Kerswell, 2006; Meynard et al., 2013) show that a more nuanced approach is needed that considers that biodiversity patterns at local scales can be nested within a hierarchy of regional and global-scale processes (Gaston, 2000; Ricklefs, 2004). Understanding these driving factors is important given the changes occurring in intertidal environments due to increasing anthropogenic stressors.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Dryad at: https://doi.org/10.5061/dryad.51c59zw53.

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REFERENCES

Airoldi, L. (2003). Effects of patch shape in intertidal algal mosaics: Roles of area, perimeter and distance from edge. *Marine Biology*, *143*(4), 639–650. https://doi.org/10.1007/s00227-003-1119-3

Anderson, M. J., Connell, S. D., Gillanders, B. M., Diebel, C. E., Blom, W. M., Saunders, J. E., & Landers, T. J. (2005). Relationships between taxonomic resolution and spatial scales of multivariate variation. *Journal of Animal Ecology*, *74*(4), 636–646. https://doi.org/10.1111/j.1365-2656.2005.00959.x

Anderson, M. J., Diebel, C. E., Blom, W. M., & Landers, T. J. (2005). Consistency and variation in kelp holdfast assemblages: Spatial patterns of biodiversity for the major phyla at different taxonomic resolutions. *Journal of Experimental Marine Biology and Ecology*, *320*(1), 35–56. https://doi.org/10.1016/j.jembe.2004.12.023

Anderson, M. J., Gorley, R. N., & Clarke, K. R. (2008). *PERMANOVA+ for PRIMER: Guide to software and statistical methods*. Plymouth, UK: PRIMER-E Ltd.

Andrén, H., & Andren, H. (1994). Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: A review. *Oikos*, 71(3), 355. https://doi.org/10.2307/3545823

Angelini, C., Altieri, A. H., Silliman, B. R., & Bertness, M. D. (2011). Interactions among foundation species and their consequences for community organization, biodiversity, and conservation. *BioScience*, 61(10), 782–789. https://doi.org/10.1525/bio.2011.61.10.8

Atlas of living Australia website (2018). *Atlas of Living Australia website*. Retrieved 1 July 2018 from http://www.ala.org.au

Badano, E. I., & Cavieres, L. A. (2006). Ecosystem engineering across ecosystems: Do engineer species sharing common features have generalized or idiosyncratic effects on species diversity? *Journal of Biogeography*, 33(2), 304–313. https://doi.org/10.1111/j.1365-2699.2005.01384.x

Bearham, D., Vanderklift, M. A., & Gunson, J. R. (2013). Temperature and light explain spatial variation in growth and productivity of the kelp *Ecklonia radiata*. *Marine Ecology Progress Series*, 476, 59–70. https://doi.org/10.3354/meps10148

Bellgrove, A., McKenzie, P. F., Cameron, H., & Pocklington, J. B. (2017). Restoring rocky intertidal communities: Lessons from a benthic macroalgal ecosystem engineer. *Marine Pollution Bulletin*, 117, 17–21. https://doi.org/10.1016/j.marpolbul.2017.02.012

Bellwood, D. R. (2001). Regional-scale assembly rules and biodiversity of coral reefs. *Science*, 292(5521), 1532–1535. https://doi.org/10.1126/science.1058635

Benedetti-Cecchi, L., Pannacciulli, F., Bulleri, F., Moschella, P. S., Airoldi, L., Relini, G., & Cinelli, F. (2001). Predicting the consequences of anthropogenic disturbance: Large-scale effects of loss of canopy algae on rocky shores. *Marine Ecology Progress Series*, 214, 137–150. https://doi.org/10.3354/meps214137

Blanchette, C. A. (1997). Size and survival of intertidal plants in response to wave action: A case study with *Fucus gardneri*. *Ecology*, 78(5), 1563–1578. https://doi.org/10.1890/0012-9658(1997)078[1563:SASOIP]2.0.CO;2

Blanchette, C. A., Thornber, C., & Gaines, S. D. (2000). Effects of wave exposure on intertidal fucoid algae. In *Proceedings of the California Islands Symposium* (vol.5. 347–355).

Bloch, C. P., & Klingbeil, B. T. (2016). Anthropogenic factors and habitat complexity influence biodiversity but wave exposure drives species turnover of a subtropical rocky inter-tidal metacommunity. *Marine Ecology*, 37(1), 64–76. https://doi.org/10.1111/maec.12250

Brown, J. H. (2014). Why are there so many species in the tropics? *Journal of Biogeography*, 41(1), 8–22. https://doi.org/10.1111/jbi.12228

Bruno, J. F., & Bertness, M. D. (2001). Habitat modification and facilitation in benthic marine communities. In Bertness M. D., Gaines S. D. & Hay M. E.(Eds,).*Marine community ecology*. Sunderland, MA: Sinauer Associates Inc.

Bruno, J. F., & Kennedy, C. W. (2000). Patch-size dependent habitat modification and facilitation on New England cobble beaches by *Spartina alterniflora*. *Oecologia*, 122(1), 98–108. https://doi.org/10.1007/PL00008841

Bruno, J. F., Stachowicz, J. J., & Bertness, J. D. (2003). Inclusion of facilitation into ecological theory. *Trends in Ecology and Evolution*, 18(3), 119–125. https://doi.org/10.1016/S0169-5347(02)00045-9

Bulleri, F., Benedetti-Cecchi, L., Cusson, M., Maggi, E., Arenas, F., Aspden, R., ... Paterson, D. M. (2012). Temporal stability of European rocky shore assemblages: Variation across a latitudinal gradient and the role of habitat-formers. *Oikos*, 121(11), 1801–1809. https://doi.org/10.1111/j.1600-0706.2011.19967.x

Bureau of Meteorology (2014). *The key climate groups Australia*. Retrieved from http://www.bom.gov.au/iwk/climate_zones/map_1.shtml

Byers, J. E., Cuddington, K., Jones, C. G., Talley, T. S., Hastings, A., Lambrinos, J. G., ... Wilson, W. G. (2006). Using ecosystem engineers to restore ecological systems. *Trends in Ecology and Evolution*, 21(9), 493–500. https://doi.org/10.1016/j.tree.2006.06.002

Clarke, K. R. (1993). Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, 18, 117–143. https://doi.org/10.1111/j.1442-9993.1993.tb00438.x

Clarke, K. R., & Gorley, R. N. (2015). *PRIMER v7 user manual/tutorial*. Plymouth, UK: PRIMER-E Ltd.

Clarke, K. R., & Warwick, R. M. (2001). *Change in marine communities. An approach to statistical analysis and interpretation*. Plymouth, UK: Primer-E Ltd.

Cruz-Motta, J. J., Miloslavich, P., Palomo, G., Iken, K., Konar, B., Pohle, G., ... Shirayama, Y. (2010). Patterns of spatial variation of assemblages associated with intertidal rocky shores: A global perspective. *PLoS ONE*, 5(12), e14354. https://doi.org/10.1371/journal.pone.0014354

Dayton, P. K. (1972). Toward an understanding of community resilience and the potential effects of enrichments to the benthos at McMurdo Sound, Antarctica. In B. C. Parker (Ed.), *Proceedings of the Colloqium on conservation problems in Antarctica* (pp. 81–96). Lawrence, KS: Allen Press.

Dijkstra, J. A., Boudreau, J., & Dionne, M. (2012). Species-specific mediation of temperature and community interactions by multiple foundation species. *Oikos*, 121(5), 646–654. https://doi.org/10.1111/j.1600-0706.2011.19712.x

Edgar, G. J. (2008). *Australian marine life: The plants and animals of temperate waters* (2nd ed.). Sydney, NSW: New Holland Publishers.

Edgar, G. J., & Klumpp, D. W. (2003). Consistencies over regional scales in assemblages of mobile epifauna associated with natural and artificial plants of different shape. *Aquatic Botany*, 75(4), 275–291. https://doi.org/10.1016/S0304-3770(02)00194-8

Ellison, A. M., Bank, M. S., Clinton, B. D., Colburn, E. A., Elliott, K., Ford, C. R., ... Webster, J. R. (2005). Loss of foundation species: Consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment*, 3(9), 479–486. https://doi.org/10.1890/1540-9295(2005)003[0479:LOFSCF]2.0.CO;2

Ellwood, M. D. F., & Foster, W. A. (2004). Doubling the estimate of invertebrate biomass in a rainforest canopy. *Nature*, 429(6991), 549–551. https://doi.org/10.1038/nature02560

Fowler-Walker, M. J., Connell, S. D., & Gillanders, B. M. (2005a). To what extent do geographic and associated environmental variables correlate with kelp morphology across temperate Australia? *Marine and Freshwater Research*, 56(6), 877–887. https://doi.org/10.1071/MF05042

Fowler-Walker, M. J., Connell, S. D., & Gillanders, B. M. (2005b). Variation at local scales need not impede tests for broader scale patterns. *Marine Biology*, 147(3), 823–831. https://doi.org/10.1007/s00227-005-1605-x

Fraschetti, S., Terlizzi, A., & Benedetti-Cecchi, L. (2005). Patterns of distribution of marine assemblages from rocky shores: Evidence of relevant scales of variation. *Marine Ecology Progress Series*, 296, 13–29. https://doi.org/10.3354/meps296013

Gallagher, R. V., & Leishman, M. R. (2012). A global analysis of trait variation and evolution in climbing plants. *Journal of Biogeography*, 39(10), 1757–1771. https://doi.org/10.1111/j.1365-2699.2012.02773.x

Gaston, K. J. (2000). Global patterns in biodiversity. *Nature*, 405, 220–227. https://doi.org/10.1038/35012228

Gaston, K. J., Chown, S. L., & Evans, K. L. (2008). Ecogeographical rules: Elements of a synthesis. *Journal of Biogeography*, 35(3), 483–500. https://doi.org/10.1111/j.1365-2699.2007.01772.x

Gemelli, F., Johnson, C. R., & Wright, J. T. (2019). Gastropod communities associated with different morphologies of the intertidal seaweed *Hormosira banksii*. *Marine and Freshwater Research*, 70(2), 280–291. https://doi.org/10.1071/MF18159

Glasby, T. M., Gibson, P. T., & Cruz-Motta, J. J. (2017). Differences in rocky reef habitats related to human disturbances across a latitudinal gradient. *Marine Environmental Research*, *129*, 291–303. https://doi.org/10.1016/j.marenvres.2017.06.014

Gribben, P. E., Angelini, C., Altieri, A. H., Bishop, M. J., Thomsen, M. S., & Bulleri, F. (2019). Facilitation cascades in marine ecosystems: A synthesis and future directions. *Oceanography and Marine Biology: An Annual Review*, *57*, 127–168.

Gribben, P. E., & Wright, J. T. (2014). Habitat-former effects on prey behaviour increase predation and non-predation mortality. *Journal of Animal Ecology*, *83*(2), 388–396. https://doi.org/10.1111/1365-2656.12139

Halpern, B. S., Walbridge, S., Selkoe, K. A., Kappel, C. V., Micheli, F., D'Agrosa, C., … Fujita, R. (2008). A global map of human impact on marine ecosystems. *Science*, *319*(5865), 948–952.

Harley, C. D. G., Anderson, K. M., Demes, K. W., Jorve, J. P., Kordas, R. L., Coyle, T. A., & Graham, M. H. (2012). Effects of climate change on global seaweed communities. *Journal of Phycology*, *48*(5), 1064–1078. https://doi.org/10.1111/j.1529-8817.2012.01224.x

Heck, K. L., & Orth, R. J. (1980). Seagrass habitats: the roles of habitat complexity, competition and predation in structuring associated fish and motile macroinvertebrate assemblages. In Kennedy V. S. (Ed,). *Estuarine perspectives* (pp. 449–464). New York, NY: Academic Press.

Hewitt, J. E., Thrush, S. F., Dayton, P. K., & Bonsdorff, E. (2007). The effect of spatial and temporal heterogeneity on the design and analysis of empirical studies of scale-dependent systems. *The American Naturalist*, *169*(3), 398–408. https://doi.org/10.1086/510925

Hillebrand, H. (2004). On the generality of the latitudinal diversity gradient. *The American Naturalist*, *163*(2), 192–211. https://doi.org/10.1086/381004

Jones, C. G., Lawton, J. H., & Shachak, M. (1994). Organisms as ecosystem engineers. *Oikos*, *69*, 373–386. https://doi.org/10.2307/3545850

Jones, C. G., Lawton, J. H., & Shachak, M. (1997). Positive and negative effects of organisms as physical ecosystem engineers. *Ecology*, *78*(7), 1946–1957. https://doi.org/10.1890/0012-9658(1997)078[1946:PANEOO]2.0.CO;2

Jurgens, L. J., & Gaylord, B. (2017). Physical effects of habitat-forming species override latitudinal trends in temperature. *Ecology Letters*, *21*(2), 190–196. https://doi.org/10.1111/ele.12881

Kelaher, B. P. (2002). Influence of physical characteristics of coralline turf on associated macrofaunal assemblages. *Marine Ecology Progress Series*, *232*, 141–148. https://doi.org/10.3354/meps232141

Kelaher, B. P. (2003a). Changes in habitat complexity negatively affect diverse gastropod assemblages in coralline algal turf. *Oecologia*, *135*(3), 431–441. https://doi.org/10.1007/s00442-003-1196-5

Kelaher, B. P. (2003b). Effects of frond length on diverse gastropod assemblages in coralline turf. *Journal of the Marine Biological Association of the United Kingdom*, *83*(1), 159–163. https://doi.org/10.1017/S0025315403006921h

Kelaher, B. P., & Castilla, J. C. (2005). Habitat characteristics influence macrofaunal communities in coralline turf more than mesoscale coastal upwelling on the coast of Northern Chile. *Estuarine, Coastal and Shelf Science*, *63*(1–2), 155–165. https://doi.org/10.1016/j.ecss.2004.10.017

Kelaher, B. P., Castilla, J. C., & Seed, R. (2004). Intercontinental test of generality for spatial patterns among diverse molluscan assemblages in coralline algal turf. *Marine Ecology Progress Series*, *271*, 221–231. https://doi.org/10.3354/meps271221

Kelaher, B. P., Underwood, A. J., & Chapman, M. G. (2003). Experimental transplantations of coralline algal turf to demonstrate causes of differences in macrofauna at different tidal heights. *Journal of Experimental Marine Biology and Ecology*, *282*(1–2), 23–41. https://doi.org/10.1016/S0022-0981(02)00443-4

Kerswell, A. P. (2006). Global biodiversity patterns of benthic marine algae. *Ecology*, *87*(10), 2479–2488. https://doi.org/10.1890/0012-9658(2006)87[2479:GBPOBM]2.0.CO;2

Kovalenko, K. E., Thomaz, S. M., & Warfe, D. M. (2012). Habitat complexity: Approaches and future directions. *Hydrobiologia*, *685*(1), 1–17. https://doi.org/10.1007/s10750-011-0974-z

Kraft, N. J. B., Comita, L. S., Chase, J. M., Sanders, N. J., Swenson, N. G., Crist, T. O., … Myers, J. A. (2011). Disentangling the drivers of β diversity along latitudinal and elevational gradients. *Science*, *333*(2011), 1755–1758. https://doi.org/10.1126/science.1208584

Lawton, J. H. (1987). Are there assembly rules for successional communities? In Cray A. J., Crawley M. J. & Edwards P. J.(Eds,). *Colonisation, succession and stability*. Oxford: Blackwell Scientific Publications.

Lloyd, H. B., Murray, B. R., & Gribben, P. E. (2012). Trait and abundance patterns in two marine molluscs: The influence of abiotic conditions operating across multiple spatial scales. *Marine Ecology Progress Series*, *463*, 205–214. https://doi.org/10.3354/meps09847

Loreau, M. (2001). Biodiversity and ecosystem functioning: Current knowledge and future challenges. *Science*, *294*(5543), 804–808. https://doi.org/10.1126/science.1064088

Mabin, C. J. T., Gribben, P. E., Fischer, A., & Wright, J. T. (2013). Variation in the morphology, reproduction and development of the habitat-forming kelp *Ecklonia radiata* with changing temperature and nutrients. *Marine Ecology Progress Series*, *483*, 117–131. https://doi.org/10.3354/meps10261

Maggi, E., Milazzo, M., Graziano, M., Chemello, R., & Benedetti-Cecchi, L. (2015). Latitudinal- and local-scale variations in a rocky intertidal interaction web. *Marine Ecology Progress Series*, *534*, 39–48. https://doi.org/10.3354/meps11415

Matias, M. G., Underwood, A. J., Hochuli, D. F., & Coleman, R. A. (2010). Independent effects of patch size and structural complexity on diversity of benthic macroinvertebrates. *Ecology*, *91*(7), 1908–1915. https://doi.org/10.1890/09-1083.1

McAfee, D., Cole, V. J., & Bishop, M. J. (2016). Latitudinal gradients in ecosystem engineering by oysters vary across habitats. *Ecology*, *97*(4), 929–939. https://doi.org/10.1890/15-0651.1

McGuinness, K. A., & Underwood, A. J. (1986). Habitat structure and the nature of communities on intertidal boulders. *Journal of Experimental Marine Biology and Ecology*, *104*, 97–123. https://doi.org/10.1016/0022-0981(86)90099-7

Meeus, J. (1991). *Astronomical algorithms*. Richmond, VA: Willmann-Bell, Incorporated.

Messier, J., McGill, B. J., & Lechowicz, M. J. (2010). How do traits vary across ecological scales? A case for trait-based ecology. *Ecology Letters*, *13*(7), 838–848. https://doi.org/10.1111/j.1461-0248.2010.01476.x

Meynard, C. N., Lavergne, S., Boulangeat, I., Garraud, L., Van Es, J., Mouquet, N., & Thuiller, W. (2013). Disentangling the drivers of metacommunity structure across spatial scales. *Journal of Biogeography*, *40*(8), 1560–1571. https://doi.org/10.1111/jbi.12116

National Institute of Water and Atmospheric Research (2016). *Wave climate around New Zealand*. Retrieved 8 August 2013 from https://www.niwa.co.nz/our-science/coasts/research-projects/all/physical-hazards-affecting-coastal-margins-and-the-continental-shelf/news/waves

Nilsson, S. G. (1979). Density and species richness of some forest bird communities in South Sweden. *Oikos*, 392–401. https://doi.org/10.2307/3544327

Palomo, M. G., People, J., Chapman, M. G., & Underwood, A. J. (2007). Separating the effects of physical and biological aspects of mussel beds on their associated assemblages. *Marine Ecology Progress Series*, *344*, 131–142. https://doi.org/10.3354/meps07002

Ralph, P. J., Morrison, D. A., & Addison, A. (1998). A quantitative study of the patterns of morphological variation within *Hormosira banksii* (Turner) Decaisne (Fucales: Phaeophyta) in South-Eastern Australia.

Journal of Experimental Marine Biology and Ecology, *225*(2), 285–300. https://doi.org/10.1016/S0022-0981(97)00232-3

Rice, E. L., Kenchington, T. J., & Chapman, A. R. O. (1985). Intraspecific geographic-morphological variation patterns in *Fucus distichus* and *F. evanescens*. *Marine Biology*, *88*(2), 207–215. https://doi.org/10.1007/BF00397168

Ricklefs, R. E. (2004). A comprehensive framework for global patterns in biodiversity. *Ecology Letters*, *7*(1), 1–15. https://doi.org/10.1046/j.1461-0248.2003.00554.x

Romero, G. Q., Gonçalves-Souza, T., Vieira, C., & Koricheva, J. (2015). Ecosystem engineering effects on species diversity across ecosystems: A meta-analysis. *Biological Reviews*, *90*(3), 877–890. https://doi.org/10.1111/brv.12138

Schemske, D. W., Mittelbach, G. G., Cornell, H. V., Sobel, J. M., & Roy, K. (2009). Is there a latitudinal gradient in the importance of biotic interactions? *Annual Review of Ecology Evolution and Systematics*, *40*(2009), 245–269. https://doi.org/10.1146/annurev.ecolsys.39.110707.173430

Schiel, D. R., & Foster, M. S. (1986). The structure of subtidal algal stands in temperate waters. In Barnes H. & Barnes M.(Eds.), *Oceanography and marine biology* (vol. *24*, pp. 265–307).

Shand, T. D., & Carley, J. T. (2011). Long-term trends in NSW coastal wave climate and derivation of extreme design storms. In *NSW Coastal Conference* (vol. *2*, pp. 8–11).

Silliman, B. R., Bertness, M. D., Altieri, A. H., Griffin, J. N., Bazterrica, M. C., Hidalgo, F. J., … Reyna, M. V. (2011). Whole-community facilitation regulates biodiversity on Patagonian rocky shores. *PLoS ONE*, *6*(10), e24502. https://doi.org/10.1371/journal.pone.0024502

Stein, A., Gerstner, K., & Kreft, H. (2014). Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecology Letters*, *17*(7), 866–880. https://doi.org/10.1111/ele.12277

Stelling-Wood, T. P., Gribben, P. E., & Poore, A. G. B. (2020). Habitat variability in an underwater forest: Using a trait-based approach to predict associated communities. *Functional Ecology*, *34*(4), 888–898.

Taniguchi, H., Nakano, S., & Tokeshi, M. (2003). Influences of habitat complexity on the diversity and abundance of epiphytic invertebrates on plants. *Freshwater Biology*, *48*(4), 718–728. https://doi.org/10.1046/j.1365-2427.2003.01047.x

Terlizzi, A., Scuderi, D., Fraschetti, S., & Anderson, M. J. (2005). Quantifying effects of pollution on biodiversity: A case study of highly diverse molluscan assemblages in the Mediterranean. *Marine Biology*, *148*(2), 293–305. https://doi.org/10.1007/s00227-005-0080-8

Tews, J., Brose, U., Grimm, V., Tielborger, K., Wichmann, M. C., Schwager, M., & Jeltsch, F. (2004). Animal species diversity driven by habitat heterogeneity/diversity: The importance of keystone structures. *Journal of Biogeography*, *31*, 79–92. https://doi.org/10.1046/j.0305-0270.2003.00994.x

Thompson, R. C., Crowe, T. P., & Hawkins, S. J. (2002). Rocky intertidal communities: Past environmental changes, present status and predictions for the next 25 years. *Environmental Conservation*, *29*(2), 168–191. https://doi.org/10.1017/S0376892902000115

Thomsen, M. S., Altieri, A. H., Angelini, C., Bishop, M. J., Gribben, P. E., Lear, G., … Zotz, G. (2018). Secondary foundation species enhance biodiversity. *Nature Ecology and Evolution*, *2*(4), 634–639. https://doi.org/10.1038/s41559-018-0487-5

Thrush, S. F., Chiantore, M., Asnaghi, V., Hewitt, J., Fiorentino, D., & Cattaneo-Vietti, R. (2011). Habitat-diversity relationships in rocky shore algal turf infaunal communities. *Marine Ecology Progress Series*, *424*, 119–132. https://doi.org/10.3354/meps08960

Underwood, A. J., & Chapman, M. G. (1998). Spatial analyses of intertidal assemblages on sheltered rocky shores. *Australian Journal of Ecology*, *23*(2), 138–157. https://doi.org/10.1111/j.1442-9993.1998.tb00712.x

Wernberg, T., Coleman, M., Fairhead, A., Miller, S., & Thomsen, M. (2003). Morphology of *Ecklonia radiata* (Phaeophyta: Laminarales) along its geographic distribution in south-western Australia and Australasia. *Marine Biology*, *143*(1), 47–55. https://doi.org/10.1007/s00227-003-1069-9

Wernberg, T., & Thomsen, M. S. (2005). The effect of wave exposure on the morphology of *Ecklonia radiata*. *Aquatic Botany*, *83*(1), 61–70. https://doi.org/10.1016/j.aquabot.2005.05.007

Wernberg, T., Thomsen, M. S., Tuya, F., & Kendrick, G. A. (2011). Biogenic habitat structure of seaweeds change along a latitudinal gradient in ocean temperature. *Journal of Experimental Marine Biology and Ecology*, *400*(1–2), 264–271. https://doi.org/10.1016/j.jembe.2011.02.017

Westoby, M., & Wright, I. J. (2006). Land-plant ecology on the basis of functional traits. *Trends in Ecology and Evolution*, *21*(5), 261–268. https://doi.org/10.1016/j.tree.2006.02.004

Wright, J. T., & Gribben, P. E. (2017). Disturbance-mediated facilitation by an intertidal ecosystem engineer. *Ecology*, *98*(9), 2425–2436. https://doi.org/10.1002/ecy.1932

BIOSKETCH

The research team is interested in the ecological processes structuring biodiversity and how communities respond to biotic and abiotic variation from local to biogeographic scales. The team has multidisciplinary experience in spatial ecology, taxonomy, biostatistics and conservation management. The authors are focussed on applied research that brings together spatial ecology and biogeographic theory to better inform conservation management.

Author contribution: H.B.L. led the research and writing, J.J.C.M led the analyses, P.E.G., T.M.G. and P.A.H. oversaw the research and study design. All authors contributed to the writing of this manuscript.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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