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Intercontinental patterns in intertidal biodiversity

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CERTIFICATE OF ORIGINAL AUTHORSHIP

I certify that the work in this thesis has not previously been submitted for a degree nor has it been submitted as part of requirements for a degree except as fully acknowledged within the text.

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“Climate is what we expect, weather is what we get”

- Mark Twain

ABSTRACT

Biogenic habitats are important conservation management tools across all ecosystems. The role of the traits of biogenic habitats (e.g. biomass) in facilitating biodiversity is well documented, particularly at local scales. However, patterns in habitat morphology can vary across broad spatial scales, which may have consequences for associated biodiversity. Moreover, biodiversity itself can vary with a range of spatially distributed environmental conditions (e.g. latitude) independent of habitat. However, little is known about how habitat-heterogeneity and spatial scale interact to determine biodiversity. To quantify the value of specific habitat-forming species we must consider: (1) how the morphology of habitats vary throughout their distribution, and (2) how spatially distributed abiotic conditions contribute to diversity patterns – whether indirectly via altering habitat traits, or by directly altering diversity patterns. The first aim of this study was to quantify variation in the morphology of a suite of temperate rocky-intertidal habitats (macro-algae) at multiple spatial scales (e.g. country, latitude, site). The second aim was to identify how changes in algal morphology and abiotic conditions influence the diversity of their associated invertebrate communities across the same spatial scales. To achieve this, I investigated patterns of algal traits and associated biodiversity in four intertidal macrophytes; *Hormosira banksii* and Coralline (Australia and New Zealand), *Sargassum* spp. (Australia only), and *Cystophora* spp. (New Zealand only). In total, I sampled 18 sites spanning over 2,000 km, along two coastlines, sharing similar latitudes in Australia (n=10) and New Zealand (n=8). I used PERMANOVA and DISTLM (distance based linear models) to investigate the influence of spatial proxies (latitude, exposure, vertical shore height) and abiotic conditions (e.g. sea surface temperature, air temperature) on multivariate algal traits. The same analyses were used to investigate the influence of habitat identity, habitat traits (length, biomass, patch size, percentage cover) and spatial proxies (country, latitude, longitude, site exposure, vertical shore height) on multivariate community assembly. The macro-algae occurring in both countries (*H. banksii* and Coralline) varied most strongly at large scales (e.g. latitude). Both large and small spatial scales

(latitude vs. exposure, shore height) were important to *Cystophora* spp. in New Zealand, whereas in Australia, *Sargassum* spp. varied mostly at small-scales (exposure, shore height). Habitat identity was the strongest predictor of biodiversity with each habitat housing its own unique community. However, habitat-diversity relationships varied across multiple spatial scales, and the relative importance of each scale was particular to individual habitats. Thus, in order to conserve biodiversity and possibly ecosystem function, conservation strategies should aim to maintain high habitat diversity and consider both idiosyncratic spatial variation in habitat traits and the additive effects of environmental conditions on habitats and their associated biodiversity.

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General Introduction

Introduction

Biodiversity and spatial scale

The complexity of life on earth and evolution of highly diverse flora and fauna not only represent the intrinsic beauty of nature, but also determine how ecosystems function and the provision of essential ecosystem goods and services. Approximately 1.8 million species have been identified globally, however, estimates as high as 200 million have been made (Campbell et al. 2006). Although we do not have a complete picture of diversity, human impacts including climate change are causing extinctions at an accelerating rate; currently estimated at 100 times greater than those typical of fossil records (Millennium Ecosystem Assessment 2005). Research focussed on understanding the processes that facilitate biodiversity is essential to mitigate the accelerating decline in biodiversity and for judicious management of natural ecosystems (Cruz-Motta et al. 2010).

The term 'biodiversity' describes variation in organisms from the genetic to ecosystem level (Terlizzi et al. 2009). Current research concerning biodiversity from a species richness level aims to understand how species relate to their biological, physical and chemical environment in an attempt to develop a predictive understanding of the conditions that promote high biodiversity (Kelaher et al. 2007, Tam and Scrosati 2011, Virgós et al. 2011). One powerful approach for detecting biodiversity trends is to observe changes in diversity in a spatial context (Whittaker et al. 2001, Anderson et al. 2005a, Anderson et al. 2005b). Determining how biodiversity responds to spatial and temporal variability is fundamental for understanding how biotic and abiotic factors drive diversity patterns. For example, in marine systems biodiversity patterns (e.g. fish) strongly correlate with depth gradients and associated gradients in light, temperature, and pressure (Anderson et al. 2013).

Large scale biogeographic studies have been criticised for not providing a quantitative explanation for species richness, trait and abundance patterns (Paine

2010). However, a long history of spatial ecology has uncovered several important diversity patterns, some of which are observed across global scales. They include, the latitudinal diversity gradient, where the diversity of several taxa is higher near the equator, the negative relationship between altitude and diversity on mountain slopes (Kraft et al. 2011), the zonation of communities along the tidal gradient on the rocky shore (Bertness et al. 2001), as well as the occurrence of biodiversity 'hot-spots' e.g. high diversity of macroalgae at mid latitudes (Kerswell 2006). Additionally, there are many biogeographic theories, related to several aspects of ecology, for which evidence is equivocal e.g. Rappaport's Rule (Stevens 1989), the Abundant-Centre Hypothesis (ACH) (Sagarin and Gaines 2002), Bergmann's Rule (Blackburn and Hawkins 2004b), and Niche (Kylafis and Loreau 2011), and Neutral theory (Hubbell 2005). One of the explanations for inconsistency in some biogeographic theories is that processes occurring at multiple spatial scales moderate predicted patterns (Ricklefs 2004). Physical, chemical and biological processes that operate across multiple spatial scales contribute to ecological patterns (Lloyd et al. 2012), yet observations are typically made at either large or small scales (Kerr et al. 2007). In response to this disparity, there has been a strong push in recent years to move away from 'spatially segregated' ecology to a comprehensive approach that examines patterns and processes at multiple spatial scales (Whittaker et al. 2001, Kelaher et al. 2004, Ricklefs 2004, Hewitt et al. 2007). Given that species respond to both locally and regionally distributed environmental variables, the most effective way for determining general ecological patterns is to conduct simultaneous measures of diversity and environmental conditions in a hierarchical framework (Ricklefs 2004, Connell and Irving 2008). This approach is vital if we wish to advance our understanding of the conditions that promote biodiversity and how multiple processes contribute to biodiversity patterns.

The incorporation of spatially explicit designs into ecological studies has led to a better understanding of how ecological interactions can alter the strength of predicted biodiversity and trait patterns. For example, Cole & McQuaid (2011) found that, although small scale habitat structure is recognised as an important

driver of biodiversity; the importance of the habitat structure of mussel beds was superseded by strong positive effects of regional upwelling and subsequent high productivity on the south coast of South Africa. Additionally, Pollock et al. (2012) found that the traits of Eucalypt species responded strongly to localised gradients in rocky substrate and large scale variation in rainfall and solar radiation. But that the influence of those variables was different in tall and short species, with rainfall and solar radiation having a stronger positive effect on the morphology of taller trees. These studies demonstrated that the influence of diversity drivers were spatially variable due to broad-scale interactions between key predictor variables. This novel approach is aided by the continued development of statistical techniques that allow for the analysis of complex ecological datasets that do not meet the assumptions of traditional statistics (e.g. PERMANOVA, geographically weighted and spatial regression models) (Anderson et al. 2005c, Rangel et al. 2010). The multi-scale approach has led to a clearer identification of ecological patterns, despite the inherent complexity of ecological interactions (Gilman 2005, Connell and Irving 2008, Schemske et al. 2009, Freestone et al. 2011, Kraft et al. 2011, Tam and Scrosati 2011). Therefore, spatially explicit studies are much more informative for addressing questions surrounding the responses of species' to large-scale environmental change.

Habitat-forming species as drivers of biodiversity

Globally, species that form habitats (e.g. trees, corals, seaweeds, mussel beds) are essential to maintaining biodiversity as they house large numbers of species (Hastings et al. 2007). Habitat-forming species, also termed biogenic habitats (Palomo et al. 2007) or ecosystem engineers (sensu Jones et al. 1994), typically alter biotic and abiotic conditions by forming complex structures. The habitat structure facilitates biodiversity by providing a refuge from predation (Gribben and Wright 2006), surfaces for colonisation (Gwyther and Fairweather 2002), and reducing environmental stress. Algal habitats are known to control abiotic factors by forming a canopy or structure that alters conditions such as wind and wave exposure, flow,

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sedimentation, and space availability (Bishop et al. 2012, Bishop et al. 2013). The changed conditions can then vary abiotic factors including the local chemistry (e.g. oxygen, pH, salinity), as well as light, nutrients, and temperature (Jones et al. 1994, 1997, Wright and Jones 2004). We know that the presence of algae changes localised environmental conditions and biodiversity. However, much less is understood about how specific morphological traits lead to changes in associated communities. Understanding the role of habitat traits in facilitating biodiversity is a critical step towards understanding the conditions that promote high biodiversity.

Although habitats have a positive influence on biodiversity, species richness is not homogenous within and among habitats. Habitat identity is important, and biodiversity patterns vary between co-occurring habitats in various ecosystems e.g. between algal turf and mussel beds in Sydney Harbour (Chapman et al. 2005). Interspecific differences in diversity facilitation are often attributed to structural differences between habitats. Thus, structural complexity (i.e. habitat morphology) is an important determinant of biodiversity. Intraspecific variation in the traits of important habitat-formers can also have consequences for associated biodiversity (e.g. with respect to the volume of kelp holdfasts across multiple spatial scales in New Zealand; Anderson et al. 2005b). Therefore, quantifying the importance of habitats must consider how their morphology varies throughout their distribution (Crain and Bertness 2006). The influence of both interspecific and intraspecific variation in habitat structure on biodiversity is seldom observed in single studies. Yet, this information can aid in the identification of the habitat characteristics that facilitate high biodiversity.

Not only does habitat structure alter diversity patterns, but independent effects of environmental conditions over and above that of habitat have an additional influence on biodiversity (Jones et al. 1994, Hastings et al. 2007, Berke 2012, Gribben et al. 2013). Recent studies have demonstrated that the strength of habitat provision varies in response to changes in abiotic conditions across multiple spatial scales. For example, facilitation by analogous habitats can be idiosyncratic with respect to site

conditions (e.g. in the diversity of cushion plants in the Chilean Andes; Badano and Cavieres 2006), regional conditions (e.g. in the diversity of plants in tussock grass habitat from upland and lowland sites in Argentina; Perelman et al. 2003), climate (e.g. the strength of invertebrate (Lepidoptera) habitat specialisation between tropical and temperate regions; Dyer et al. 2007) and latitude (e.g. in the abundance and engineering behaviour of an engineering polychaete across latitude with respect to abiotic conditions e.g. chl a, pH, temperature, salinity; Berke 2012).

Spatially explicit studies on habitat-diversity relationships enable researchers to address questions such as: do the traits of habitat-forming species change across multiple spatial scales? Is biodiversity dependent on habitat traits, and if so will diversity patterns reflect changes in habitat morphology? How do habitat provision and environmental conditions interact to determine biodiversity patterns? Although there have been some encouraging developments in this area, most studies to date have only considered variation in one habitat (but see Dijkstra et al. 2012). In turn, little is known about whether co-occurring macrophytes share the same trait distribution patterns, and how those patterns influence biodiversity. This study proposes to fill this knowledge gap for rocky intertidal habitat-forming species on the temperate east coasts of Australia and New Zealand.

Present study

Study system

Intertidal organisms are exposed to harsh conditions and often live at the edge of their biological limitations (Bertness et al. 2001). Exposure to waves and wind, fluctuating temperatures, desiccation, and submersion in saline and freshwater mean that intertidal organisms either need to be specially adapted to survive environmental extremes, or must utilise microhabitats as refuges (Dayton 1971, Bertness et al. 2001). Biotic microhabitats are those formed by benthic organisms such as sessile invertebrates (e.g. mussel beds) and macro-algae. These habitat-forming species are essential to the function of rocky shore ecosystems, and house

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large numbers of species (Chapman et al. 2005). The positive effect on biodiversity extends to the broader marine environment through the supply of resources including, primary productivity (e.g. from macro-algae), plankton (e.g. from intertidal invertebrates), and recruitment areas and nurseries for juvenile fish (Hobday et al. 2006b). Developing strategies for conserving coastal biodiversity requires an understanding of how intertidal habitats facilitate biodiversity. As populations of habitat-forming species differ in structure and composition it is also important to observe how habitat-diversity associations change at multiple spatial scales (Anderson et al. 2005b).

Previous research on biogenic habitats on rocky shores has found that habitat identity and structure (morphological traits) can be important determinants of biodiversity patterns (Airoldi 2003a, Kelaher 2003, Anderson et al. 2005b, Palomo et al. 2007). However most of this research was conducted at local scales (e.g. Airoldi 2003a, Palomo et al. 2007) and on only one or two habitats (e.g. Kelaher 2003, Kelaher et al. 2004, Anderson et al. 2005b, Kelaher et al. 2007). Intertidal rocky shores are ideal for latitudinal studies, as species are restricted to a narrow vertical distribution on the shore, but have large coastal distributions often across whole continents. This makes it easier to determine the extent of species' distributions and make conclusions about ecological patterns (Dayton 1971, Sagarin and Gaines 2002, Gilman 2005). Furthermore, a suite of discrete habitats commonly occur on rock platforms (e.g. macrophytes, mussel beds, ascidians, oysters) housing a diverse range of phyla that can be easily sampled to quantify diversity patterns (Dayton 1971, Connell and Irving 2008). This study expands on this research by investigating spatial patterns in habitat-diversity relationships in a suite of macro-algal habitats at an intercontinental scale. By observing biodiversity patterns across multiple habitats and along latitudinal gradients in two countries (Australia and New Zealand) this study provides one of the most robust assessments of spatial patterns in the biodiversity of rocky shore habitats conducted globally.

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Study area

The temperate east coasts of Australia and New Zealand are highly diverse and have some of the highest rates of endemism in the world. For example, in southern Australia >85% of fish, echinoderm and mollusc species are endemic (Poloczanska et al. 2007). Yet the species that occur there are threatened by intensive anthropogenic disturbances from development, recreational and commercial fishing activities, invasive species and both household and industrial pollution (Hobday et al. 2006a). The abiotic marine environment is also atypical with extremely variable precipitation patterns and oligotrophic water in Australia, and warm coastal currents i.e. the East Australian Current and the Subtropical Gyre in both countries (Waters and Roy 2003, Hobday et al. 2006a). The unique composition of these environments highlights the need for biogeographic research specific to the region. Currently the majority of research in biogeography has been conducted in the northern hemisphere and in terrestrial systems. Subsequently many of our assumptions for the causes of diversity patterns are founded in very different environments (Hobday et al. 2006a).

Aims and objectives

The aim of this project is to determine how biogenic habitats facilitate the biodiversity of intertidal invertebrates across multiple spatial scales. More specifically, I will determine how habitat morphology and abiotic conditions influence diversity and how those relationships vary spatially.

The objectives are to:

1. Determine how the morphology of four algal habitats varies across large and small spatial scales.
2. Determine whether different habitat-forming species house specific associated communities, how those associations vary spatially, and the gradients most strongly associated with that variation (e.g. habitat structure, vertical shore height, site exposure, latitude).

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3. Determine if habitat-diversity relationships can be generalised to different countries sharing similar latitudes and habitat types.

Chapter overview

This thesis includes two data chapters written as journal articles as intended for submission to relevant ecology journals.

Chapter 2: '*Morphological patterns of intertidal macro-algae from local to intercontinental scales*', describes spatial patterns in the morphology of four algal habitats to determine how the traits of important biogenic habitats respond to spatially distributed environmental conditions. This chapter investigates the hypotheses that: (1) Macro-algal traits will vary with temporal (season) and spatial (country, site) scales and will have similar size patterns across the latitudinal gradient in Australia and New Zealand. (2) Spatial proxies (latitude, wave exposure and vertical shore height) will correlate with variation in macro-algal traits across multiple spatial scales. (3) Macro-algal traits will correlate with changes in specific abiotic variables (e.g. sea surface temperature, air temperature, rainfall, and solar exposure).

Chapter 3: '*Intercontinental patterns in the biodiversity in intertidal biogenic habitats*', explores relationships between four specific algal habitats and their associated biodiversity. Including an investigation into how those associations vary with respect to variation in the morphology of the habitats and changing environmental conditions. This chapter tests the hypotheses that: (1) Individual habitats will house specific associated communities, but biodiversity patterns will respond to variation in the morphology of habitat-forming organisms across multiple spatial scales. (2) Biodiversity patterns within algal habitats will vary across small-scale (site exposure, vertical shore height) and large-scale (country, latitude) abiotic gradients.

This chapter has been formatted for submission for *Ecography* and subsequently there is some repetition in this paper from the previous two chapters including

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some background literature in the introduction and discussion and information about the study area and study species.

Chapter 4: provides a general discussion of the results of the study, its applications for conservation management, and areas for further research.

CHAPTER TWO

*Morphological patterns of intertidal macro-algae from
local to intercontinental scales*

Introduction

Foundation species (*sensu* Dayton 1972) are critical to the structure and function of ecosystems globally. In both marine and terrestrial systems primary producers such as macrophytes form the basis of the food web (Ellison et al. 2005, Gestoso et al. 2013). Macrophytes also enhance biodiversity by increasing structural complexity (Badano and Cavieres 2006), providing shelter and reducing abiotic (e.g. temperature) and biotic stress (e.g. predation) (Dijkstra et al. 2012). The structure or morphology of foundation species is an important determinant of community composition as their physical structure influences the prevailing biotic and abiotic environment. The altered environment creates ecological niches by increasing habitat heterogeneity, subsequently promoting overall biodiversity (Jones et al. 1994, 1997). For example, pneumatophore height has a positive effect on biodiversity in mangroves (Bishop et al. 2013). The importance of habitat morphology is well recognised, however, the consequences of intraspecific variation in the traits of important foundation species to biodiversity are not well known (but see; Anderson et al. 2005b, Kelaher et al. 2007). This information is important as it can help us to predict how changes in habitat traits may affect associated biodiversity (Anderson et al. 2005b, Crain and Bertness 2006).

Morphological traits can vary at multiple spatial scales. At small scales morphological responses tend to be species and context dependent, often resulting from limitations in important resources (e.g. nutrient availability in plants; López-Bucio et al. 2003, dissolved oxygen in estuarine molluscs; Lloyd et al. 2012). At the large scale, more generalised patterns have been observed with respect to changes in biotic and abiotic conditions along climatic gradients. For example, biogeographic theory suggests that there should be a positive relationship between the body size and biomass of species and increasing latitude (Brown and Lee 1968, Blackburn et al. 1999, Smith and Betancourt 2006). Species that follow this pattern include birds (Blackburn and Gaston 1996), mammals (Blackburn and Hawkins 2004a, Smith and Betancourt 2006), fish (Schemske et al. 2009) and trees (where lower latitude species

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grow faster to compete with higher densities, whilst higher latitude conspecifics have a slower growth rate, but greater biomass at maturity) (Murphy et al. 2006), among others. Spatially explicit research is important as it can help to reconcile why some species patterns do not conform to biogeographic theory by identifying competing drivers of diversity patterns (i.e. localised conditions), and whether there is a hierarchical structure in the influence of those drivers acting at different spatial scales (Lloyd et al. 2012).

Species on rocky shores are ideal organisms to study trait patterns as they are exposed to harsh and highly variable environmental conditions and often have broad distributions, resulting in plasticity in population traits across a range of taxa (Menge 1976, Paine 1976, Blanchette 1997). Macro-algae on temperate rocky shores are often the dominant foundation species in this ecosystem (Gestoso et al. 2013). Previous research on the traits of macroalgae has focussed primarily on small scale patterns, and has identified several factors that can influence morphology, most notably; wave exposure (Blanchette 1997, Wernberg and Thomsen 2005), temperature (Serisawa et al. 2002, Bearham et al. 2013) and depth (i.e. light) (Kirkman 1989, Bearham et al. 2013), but also oceanography and associated nutrient concentrations (Mabin et al. 2013), salinity (Kalvas and Kautsky 1993), as well as biotic interactions including density of conspecifics (Fowler-Walker et al. 2005a, b) and herbivory (Williams et al. 2013). While spatially explicit studies on macro-algal morphology are uncommon, some studies have shown that multiple scales of variation often contribute to morphological patterns of macrophytes. Fowler-Walker (2005b) showed that trait variation in the sub-tidal kelp *Ecklonia radiata* could be attributed to small-scale factors including exposure and algal density but that the primary source of variation was at the longitudinal scale (potentially related to limited gene flow or large-scale environmental variation e.g. salinity). Bearham et al. (2013) revealed that the relative importance of temperature, light, nutrients and water velocity on *E. radiata* traits vary spatially and temporally. Wernberg et al (2003) found that individual traits of *E. radiata* responded independently to different scales of variation suggesting morphological characters have their own structural

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adaptations to specific environmental conditions. These studies have provided important information about spatial patterns in macro-algae, however, not all species respond in the same way to environmental conditions. Therefore, more work is needed on trait distribution patterns of co-occurring species to tease out ecological generality from species specific responses i.e. do interspecific macro-algae traits vary consistently with changes in abiotic conditions?

In this study, I investigated spatial patterns in the morphology of macro-algal habitats across a latitudinal gradient in Australia and New Zealand to identify ecologically important scales of variation. I used a spatially explicit design to sample variation in the morphological traits of four intertidal macro-algal habitats on rock shore platforms in two seasons (summer and winter) at four spatial scales (1) across countries, (2) latitudinal gradients within countries, (3) wave exposure, and (4) within site shore height. I then correlated traits with abiotic environmental data for the Australian sites from the summer sampling period to link geographic variation to specific environmental conditions known to affect traits (e.g. sea surface temperature, air temperature and solar exposure). The east coast of Australia and New Zealand provide a unique opportunity in the search for ecological generality as both countries have overlapping latitudes, with physically comparable rocky shores, as well as matching biogenic habitats within them.

My specific hypotheses were:

1. Macro-algal traits will vary with temporal (season) and spatial (country, site) scales and will have similar size patterns across the latitudinal gradient in Australia and New Zealand.
2. Spatial proxies (latitude, wave exposure and vertical shore height) will correlate with variation in macro-algal traits across multiple spatial scales.
3. Macro-algal traits will correlate with changes in specific abiotic variables (e.g. sea surface temperature, air temperature, rainfall, and solar exposure).

Methods

Study area

The study was conducted on 18 rock platforms across the temperate east coasts of Australia and New Zealand. In Australia, 10 sites were surveyed from Bonny Hills, Northern NSW to Eaglehawk Neck, Tasmania, ranging across >1,300 km (linear distance) (Table 1, Fig 1). In New Zealand eight sites were surveyed from Leigh (northern NZ) to Shag Point, Otago (southern NZ) ranging across >1,000 km (Table 1, Fig 1). Bonny Hills was selected 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 (Australian Government Bureau of Meteorology 2013). Within countries, sites were separated by a minimum of 10 km to minimise spatial bias, however sites were generally >100 km apart (Table 1). The east coasts of both countries share similar biotic and abiotic conditions including large flat rock platforms with similar algal habitats making them suitable for ecological comparison. The study area included 6.73 decimal degrees of shared latitude between the two coastlines (Table 1) allowing for direct comparison of latitudinal patterns.

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Table 1. Coordinates (decimal degrees) of study sites, along the east coasts of Australia (n = 10 sites) and New Zealand (n = 8 sites), including the linear distance (km) between sites to the site directly above.

Site	Latitude	Longitude	Linear distance between sites (km)
<i>Australia</i>			
Bonny Hills	-31.59	152.84	-
Blackhead	-32.07	152.55	60
Newcastle	-32.93	151.79	118
Pearl Beach	-33.55	151.31	82
Cronulla	-34.07	151.16	58
Bellambi	-34.37	150.93	38
Ulladulla	-35.37	150.49	117
Eden	-37.06	149.91	194
Coles Bay	-42.12	148.28	578
Eaglehawk Neck	-43.03	147.95	103
<i>New Zealand</i>			
Leigh	-36.30	174.80	-
Cook's Beach	-36.83	175.72	100
Mahia	-39.09	177.93	315
Aramoana	-40.15	176.85	150
Picton	-41.26	174.04	267
Kaikoura	-42.40	173.68	130
Moeraki	-45.36	170.84	400
Shag Point	-45.47	170.83	12

Study organisms

The macrophytes studied included two seaweeds that occur in Australia and New Zealand; *Hormosira banksii* a brown alga, and Coralline algae a red turfing algae from the family Corallinaceae. Several species of morphologically similar Coralline were sampled in the study area (e.g. *Corallina officinalis*, *Metagoniolithon stelliferum*, *Jania microarthrodia*, *Amphiroa anceps*, *Spongites hyperellus*) (Kelaher et al. 2001, Edgar 2008). Two additional algae genera, *Sargassum* spp. and *Cystophora* spp., were sampled in Australia and New Zealand, respectively. Both are brown frondose seaweeds occurring at a similar level on the shoreline (Edgar 2008). These genera were included to determine whether different taxa with shared characteristics (e.g. brown frondose thallus, low shore distribution) would have similar size patterns across multiple spatial scales in their respective environments. Due to the large area sampled not all habitats were present at all sites. *H. banksii* was absent at Leigh and

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Picton in New Zealand (Fig 1). Coralline was absent at Coles Bay in Australia. *Sargassum* spp. was absent south of Ulladulla in Australia, and *Cystophora* spp. was absent at Cook's Beach in New Zealand (Fig 1).

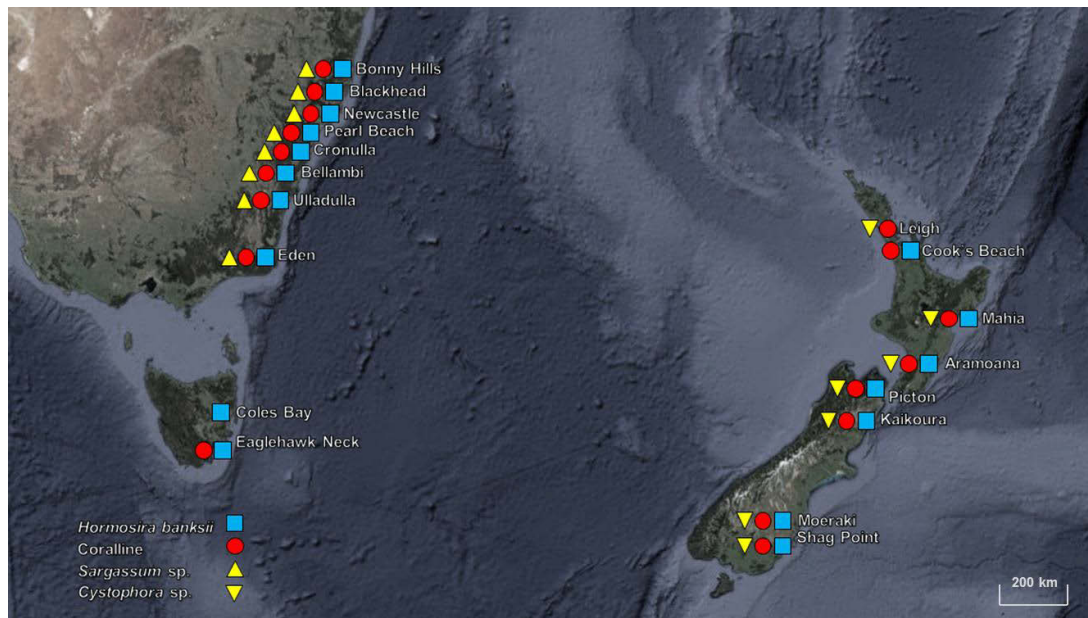


Figure 1. Study area including 18 sites along the east coasts of Australia (10 sites) and New Zealand (8 sites). Symbols show which of the four macro-algal habitats (*Hormosira banksii*, Coralline, *Sargassum* spp. and *Cystophora* spp.) were sampled at each site.

Field survey

Surveys were conducted from August to early October 2011 and January to early April 2012. As ocean temperatures lag seasonally, these periods were representative of low winter and high summer water temperatures. Australian sites were sampled in a random order (i.e. not north to south) and New Zealand sites in a three week time frame to minimize potentially confounding temporal effects. At each site, replicate patches of each habitat ($n=6/\text{habitat}/\text{site}$) were sampled during low tide (Kelaher et al. 2001). Patches selected occurred as discrete mono-specific patches with <10% of other habitat-forming organisms present. Each patch was measured for patch area (Airoldi 2003a), percentage cover (Ingolfsson 2005), frond length (Kelaher 2003) and biomass (Fowler-Walker et al. 2005a). The length and width of patches were measured (from the longest and widest part of the patch) and multiplied by each other to approximate patch area. Patches that were large and

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irregularly shaped and linked by small strips of habitat (<15 cm wide) and/or had noticeable elevation differences were divided into separate patches. Frond length was determined from the mean of 10 randomly selected fronds measured at the patch centre. Percentage algae cover was approximated using a grid of regularly spaced points in a 25 x 25 cm quadrat. Biomass was determined from replicate core samples (n=2 cores/patch). PVC cores (10 cm diameter) were driven into the centre of each patch, with algae scraped off at the rock surface with a paint scraper and placed into labelled plastic bags (Kelaheer et al. 2004, Thrush et al. 2011). Biomass samples were rinsed in 1 mm sieves to remove trapped sediment, as well as to trap fauna for diversity analysis (see Chapter 3). After excess water was drained the algae was weighed in the field on digital scales (nearest 1 g). Field scales were calibrated against laboratory scales to ensure measurements were accurate. To ensure wet weight was an appropriate measure of biomass, samples of each habitat type were taken back to the lab and oven dried at 60°C for 48 hours to determine dry weight (n=12 cores/habitat). The wet weight of those samples was compared to dry weights using Pearson's Correlation and all were significantly correlated ($R^2 > 0.90$; Appendix 1).

Environmental conditions

I used both spatial proxies and abiotic data to identify ecologically important scales of variation and potential drivers of that variation. Specifically I recorded vertical shore height (patch level), wave exposure (site level), and geographic position (site level) to act as proxies for spatially distributed environmental conditions. Vertical shore height (low, mid, high) was recorded as a proxy for within site conditions e.g. submersion, desiccation, grazing (Dayton 1971). As all habitats occurred in the low-mid shore range, height was relative to the distribution of the habitats and did not extend to the true high tide mark. Respectively, the three levels were proportional and varied slightly with respect to the size and slope of each rock platform (Kelaheer et al. 2001). Site exposure was recorded to account for the exposure of algae to wave action at each site (Blanchette 1997). Wave exposure was determined from Google

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Earth and each site categorised as either: exposed, semi-exposed, semi-sheltered or sheltered. Wave exposure 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. This method was adapted from Wernberg and Thompsen (2005); however submerged barriers (e.g. reefs) were not considered. Latitudinal coordinates for each site were used as a proxy for large-scale gradients in abiotic conditions (e.g. temperature).

For sites in Australia, to investigate potential drivers of morphological variation, external data were accessed for the summer sampling period (January-April). A subset of the data was modelled, as data was not freely available for New Zealand or the winter sampling period. Sea surface temperature buffered to 5 km was provided by Geosciences Australia for the 10 study sites with the average of monthly observations calculated for the survey period. Maximum Temperature (°C), Minimum Temperature (°C), Rainfall (mm), and Daily Global Solar Exposure (MJ/m²m) was accessed from the Australian Bureau of Meteorology's Climate Data Online service from weather stations < 20 km from the study sites (except for Eaglehawk Neck which was 39.5 km distance away from the nearest weather station) and the average calculated from daily observations during the sampling period. A combination of ocean and ambient temperatures has been used to determine distribution patterns for shallow macro-algal species (Martínez et al. 2012). Though weather stations were not located at the study site, these models were used to provide inferences about the potential drivers of spatial patterns in the dataset.

Data analysis

Spatial-temporal patterns

The trait distributions each algal habitat were analysed separately to identify variation in individual habitats across spatial and temporal scales (Wernberg and Vanderklift 2010). Each algal habitat was analysed individually as large differences

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in overall size between them could obscure differences at habitat level. Trait data were analysed using the mean of each trait per replicate patch (n=6 patches/site/habitat) to standardise the sample size between the different measurements (e.g. biomass n=2/patch, length n=10/patch). Trait data for *Cystophora* spp. at Aramoana in winter could not be included in the analyses as frond length was missing from this sampling period. For *H. banksii* and Coralline, univariate and multivariate trait patterns were analysed using 3 factor PERMANOVA's investigating the factors Season (fixed), Country (fixed), Site(nested within country; random) on algal traits. For *Sargassum* spp. and *Cystophora* spp. 2 factor PERMANOVA's were conducted for the factors Season (fixed) and Sites (random). Because of significant interactions (see results) I ran reduced models within each season investigating the influence of Country and Site(Country) for *H. banksii* and Coralline, and Sites for *Sargassum* spp. and *Cystophora* spp. For the multivariate analyses, the contribution of random factors to morphological variation was determined from the estimates of components of variation (Quinn and Keough 2002).

PERMANOVA's were conducted using Type III Sums of Squares, with 999 permutations and fixed effects were summed to zero for mixed terms. For the nested analysis, residuals were permuted under a reduced model, and for the orthogonal analysis, I used unrestricted permutation of raw data (Anderson and Ter Braak 2003). Prior to analyses draftsman plots were conducted in PRIMERv6 to ensure no correlation between traits and to detect skewed variables. Multivariate traits of all habitats were standardised to give equal weight in the analyses. Univariate traits were log transformed to reduce skewness. All analyses were conducted on Euclidian distance matrices.

Univariate analyses were conducted on the individual trait biomass for *H. banksii*, Coralline and *Sargassum* spp. This trait was selected as the best representative of overall trait variation for these habitats as they are a good approximation of overall size (Wernberg et al. 2003), and graphical exploration showed that they were

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variable throughout the study area (Fig 2). In contrast to the other habitats *Cystophora* spp. biomass was not the strongest predictor of trait variation due to the bulkier size of this alga. Length was selected as a better representative of trait variation for *Cystophora* spp. as it was more variable throughout the study area (Fig 2d). Multivariate analyses were conducted on all traits combined (biomass, frond length, patch area, percentage cover).

Spatial drivers

To identify relationships between spatial gradients and habitat traits, multivariate multiple regression models were conducted using DISTLM (distance based linear models) for individual habitats. Models were conducted using Akaike Information Criterion for model selection and the step-wise selection procedure with the traits biomass, frond length, patch area and percentage cover and the spatial proxies latitude, wave exposure and shore height. Graphical exploration revealed that *H. banksii* and Coralline, which occurred across both countries, had parabolic size distribution patterns (see results), with biomass smallest at the centre of the total distribution and larger at the edges (Fig 2a-b). The parabolic distribution pattern was particularly strong for *H. banksii* (Fig 2a). A squared term was added to the model for latitude for *H. banksii* and Coralline (Quinn and Keough 2002). Adding a squared term to a linear model (e.g. latitude + latitude²) modifies a linear regression into a polynomial regression so that it can detect a curve linear distribution pattern (Quinn and Keough 2002).

Abiotic drivers

Abiotic variables (Sea Surface Temperature, Maximum Temperature (°C), Minimum Temperature (°C), Rainfall (mm), and Daily Global Solar Exposure (MJ/m²*m)) were correlated with habitat traits (biomass, frond length, patch area) to identify associations with morphological trait patterns. To balance the algal data with the site data for abiotic variables the mean for each trait at each site was calculated for the Australian habitats (*H. banksii*, Coralline and *Sargassum* spp.) from the summer

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sampling period. Percentage cover was excluded from multivariate traits as site means were high and there was not enough variation between sites and habitats to detect any patterns. The traits of all habitats were standardised to give equal weight in the analyses. Draftsman plots were run with Pearson's Correlation to ensure there was no collinearity between abiotic variables and to detect skewed variables. Due to high correlations with rainfall and temperature variables, rain was removed from the model to reduce collinearity (Quinn and Keough 2002). Relationships were investigated using DISTLM with the Akaike Information Criterion corrected (AICc) for model selection and the BEST selection procedure (both appropriate for small sample sizes).

Results

Spatial-temporal patterns

Univariate trait patterns

Trait distribution patterns across latitude (biomass for *H. banksii*, Coralline and *Sargassum* spp. and length for *Cystophora* spp.) revealed an interspecific pattern where the smallest sizes occurred at approximately -36 to -40 degrees latitude (Fig 2). This was the centre of the range for *H. banksii* and Coralline, the southern end of the distribution of *Sargassum* spp. in Australia, and the northern end of the distribution for *Cystophora* spp. in New Zealand. For all habitats there was a significant interaction between Season and Sites (Appendix 2), thus Seasons were analysed separately. For *H. banksii*, biomass differed significantly among Sites within Countries for both summer and winter but not between Countries (Table 2), and was greatest at the range edges (Fig 2a). For Coralline, there were significant differences in biomass in Sites within Countries in both seasons, but biomass was only significant at the Country level during summer (Table 2). Coralline biomass was greatest at the boundaries of the study area especially at lower latitudes in Australia (Fig 2b). The biomass of *Sargassum* spp. varied significantly across Sites (Table 2) and showed a pattern of decreasing biomass with increasing latitude (Fig 2c). *Cystophora* spp. length was significantly different across Sites in winter and summer (Table 2) and was greater at lower latitudes (Fig 2d).

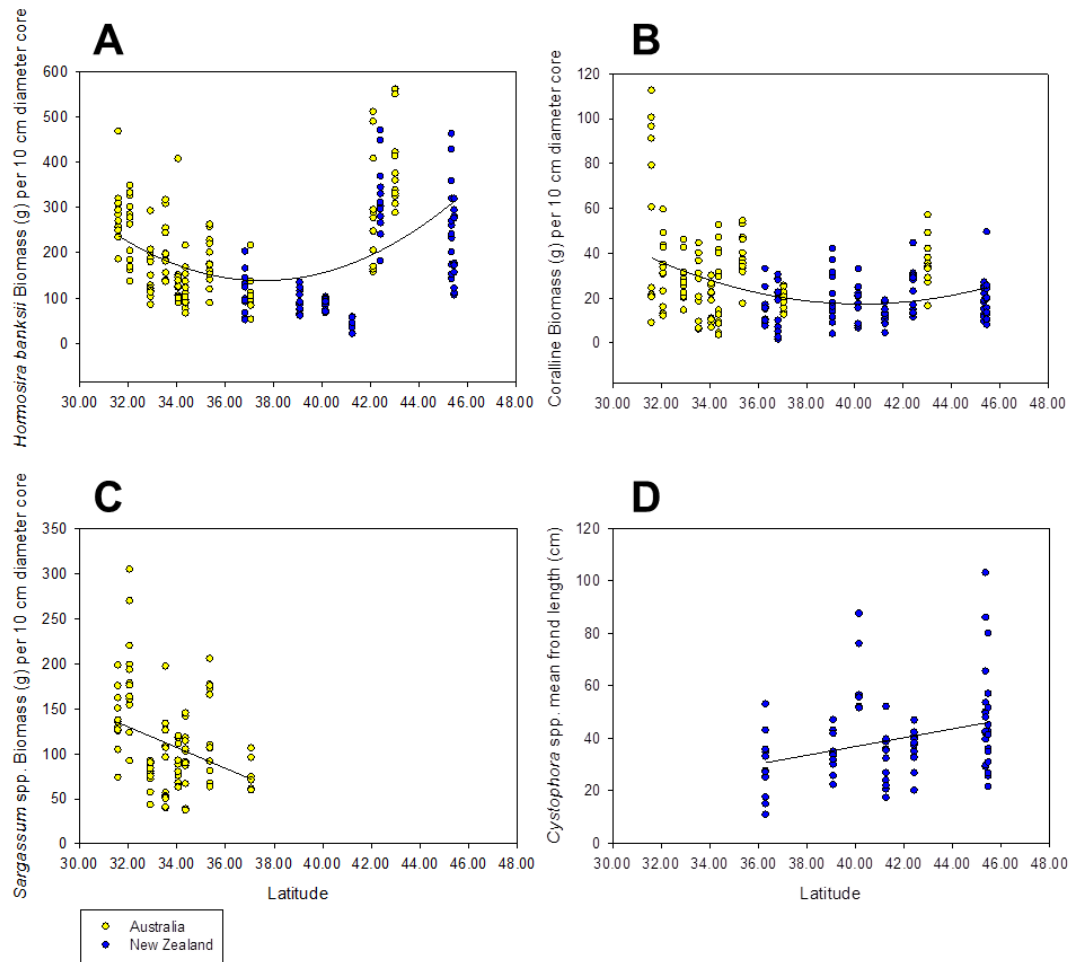


Figure 2. Univariate trait patterns of (A) *H. banksii* (B) Coralline and (C) *Sargassum* spp. biomass (g) (n=2 cores in 6 patches/site/season), and (D) *Cystophora* spp. frond length (cm) (n=10 fronds in 6 patches/site/season). *Hormosira banksii* and Coralline were sampled in Australia and New Zealand. *Sargassum* spp. was sampled in Australia, and *Cystophora* spp. was sampled in New Zealand. A polynomial curve was fitted to the data for *H. banksii* and Coralline ($R^2=0.20$, $P<0.0001$, $R^2=0.13$, $P<0.0001$, respectively) and a linear regression line for *Sargassum* spp. and *Cystophora* spp. ($R^2=0.11$ $P=0.0014$, $R^2=0.10$, $P=0.0040$, respectively).

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Table 2. Results of PERMANOVA for individual habitats in summer and winter; investigating the influence of Country (fixed factor, 2 levels; Australia and New Zealand), and Site (Country) (random factor) on the biomass of *Hormosira banksii* and Coralline, and Site (random factor) on biomass for *Sargassum* spp. and frond length for *Cystophora* spp. Significant factors are highlighted in bold.

Source	df	SS	MS	F	P(perm)
<i>H. banksii</i> biomass - winter					
Country	1	5.87	5.87	3.36	0.095
Site(Country)	15	26.16	1.74	21.43	0.001
Residual	85	6.92	0.08		
Total	101	38.95			
<i>H. banksii</i> biomass - summer					
Country	1	0.43	0.43	0.28	0.589
Site(Country)	14	21.35	1.53	17.50	0.001
Residual	80	6.97	0.09		
Total	95	28.76			
<i>Coralline</i> biomass - winter					
Country	1	3.99	3.99	3.19	0.099
Site(Country)	15	18.79	1.25	6.81	0.001
Residual	85	15.63	0.18		
Total	101	38.41			
<i>Coralline</i> biomass - summer					
Country	1	6.10	6.10	9.43	0.003
Site(Country)	15	9.70	0.65	9.11	0.001
Residual	85	6.04	0.07		
Total	101	21.84			
<i>Sargassum</i> biomass - winter					
Site	7	4.81	0.69	7.28	0.001
Residual	40	3.78	0.09		
Total	47	8.59			
<i>Sargassum</i> biomass - summer					
Site	6	6.13	1.02	12.22	0.001
Residual	35	2.93	0.08		
Total	41	9.06			
<i>Cystophora</i> length - winter					
Site	5	0.77	0.15	3.71	0.011
Residual	30	1.25	0.04		
Total	35	2.02			
<i>Cystophora</i> length - summer					
Site	6	5.25	0.87	9.13	0.001
Residual	35	3.35	0.10		
Total	41	8.60			

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Multivariate trait patterns

There was a significant interaction between Season and Sites in the PERMANOVA models for *H. banksii*, Coralline and *Cystophora* spp. and a borderline non-significant interaction term for *Sargassum* spp. so Seasons were analysed separately (Appendix 3). The morphology of all habitat patches varied across a range of spatial scales, with the importance of each scale varying among habitats. In both seasons, *H. banksii* traits varied with Sites within Countries but not among Countries. In winter, Sites accounted for 38% of the variation in traits, and in summer Sites accounted for 53% of the variation in traits (variance components estimates for random factor; Site) (Table 3). For Coralline, Sites within Country were significant in both seasons and Country was significant in winter. In winter, Sites within Country accounted for 19% of the variation in traits, in summer Sites within Country accounted for 29% of the variation in traits (Table 3). *Sargassum* spp. traits were significantly different among Sites in both seasons and accounted for 62% of variation in winter and 6% of variation in summer (Table 3). *Cystophora* spp. traits were significantly different among Sites in both seasons and accounted for 43% of variation in winter and 30% of variation in summer (Table 3). These results indicate varied relationships with the study habitats and seasons, with *Sargassum* spp. and *Cystophora* spp. variation stronger in winter, *H. banksii* variation stronger during summer, and Coralline showing stronger variation at the Site level during summer, but a significant difference between Countries in winter.

Table 3. Results of PERMANOVA for individual habitats in summer and winter; investigating the influence of Country (fixed factor, 2 levels; Australia and New Zealand), and Site (Country) (random factor) on multivariate habitat traits (biomass, frond length, patch area, percentage cover) for *Hormosira banksii* and Coralline, and Site (random factor) on multivariate habitat traits for *Sargassum* spp. and *Cystophora* spp. Significant factors are highlighted in bold.

Source	df	SS	MS	Pseudo-F	P(perm)	% Variation	Estimate of variance components
<i>H. banksii winter</i>							
Country	1	1.64	1.64	1.30	0.284	n/a*	0.01
Site(Country)	15	18.94	1.26	4.79	0.001	38	0.17
Residual	85	22.42	0.26			60	0.26
Total	101	43.00					
<i>H. banksii summer</i>							
Country	1	0.32	0.32	0.16	0.855	n/a	-0.04
Site(Country)	14	27.80	1.99	6.98	0.001	53	0.28
Residual	80	22.77	0.28			54	0.28
Total	95	50.88					
<i>Coralline winter</i>							
Country	1	8.30	8.30	7.14	0.010	n/a	0.14
Site(Country)	15	17.44	1.16	2.83	0.001	19	0.13
Residual	85	34.87	0.41			61	0.41
Total	101	60.61					
<i>Coralline summer</i>							
Country	1	2.96	2.96	1.73	0.162	n/a	0.02
Site(Country)	15	25.62	1.71	3.63	0.001	29	0.21
Residual	85	40.02	0.47			67	0.47
Total	101	68.60					
<i>Sargassum winter</i>							
Site	7	4.81	0.69	7.28	0.001	62	0.89
Residual	40	3.78	0.09			38	0.54
Total	47	8.59					

<i>Sargassum summer</i>							
Site	6	6.13	1.02	12.22	0.001	6	0.35
Residual	35	2.93	0.08			94	5.28
Total	41	9.06					
<i>Cystophora winter</i>							
Site	5	58.80	11.76	5.52	0.001	43	1.60
Residual	30	63.89	2.13			57	2.13
Total	35	122.69					
<i>Cystophora summer</i>							
Site	6	22.23	3.70	3.56	0.001	30	0.44
Residual	35	36.43	1.04			70	1.04
Total	41	58.66					

* Variance components should not be calculated for fixed factors so percentage variation was not calculated for Country (Quinn and Keough 2002).

Spatial drivers

The DISTLM model for *H. banksii* accounted for 20% (Adj R²) of variation in traits and showed a strong non-linear relationship with latitude. The final model included latitude² (10% of variation), wave exposure (9% of variation) and latitude (2% of variation) as significant predictors (Table 4). For Coralline the final model only accounted for 7% (Adj R²) of variation in traits, and included latitude (3% of variation), and height on shore (3% of variation) as significant predictors. Latitude² was not significant and only accounted for 1% of variation (Table 4). For *Sargassum* spp. small-scale factors had a more important role than large-scale factors. The final model accounted for 14% (Adj R²) of variation in traits and included height on shore (9% of variation) and wave exposure (4% of variation) as significant predictors (Table 4). For *Cystophora* spp. small-scale factors had a stronger influence than large-scale factors. All three spatial scales were included in the DISTLM accounting for 22% (Adj R²) of variation in traits and included height on shore (14% of variation), wave exposure (4% of variation), and latitude (3% of variation) (Table 4).

Table 4. DISTLM models for individual habitats (*Hormosira banksii*, Coralline, *Sargassum* spp. and *Cystophora* spp.) investigating the influence of spatial variables (latitude, wave exposure, vertical shore height on all habitats, and latitude² on *H. banksii* and Coralline) on multivariate algal traits (biomass, frond length, patch area, percentage cover). The best model for each habitat is shown with variables in order of contribution to the model. Models were selected using the AIC with the step-wise selection criteria.

Variable	AIC	SS(trace)	Pseudo-F	P	Prop.	Cumul. R ²
<i>H. banksii</i>						
Exposure	-158.35	8.22	18.46	0.001	0.09	0.09
Latitude	-160.04	1.61	3.67	0.031	0.02	0.10
Latitude ²	-181.27	9.48	24.15	0.001	0.10	0.20
<i>Coralline</i>						
Shore height	-86.984	3.51	5.42	0.012	0.03	0.03
Latitude ²	-87.409	1.54	2.40	0.092	0.01	0.04
Latitude	-92.612	4.48	7.19	0.003	0.03	0.07
<i>Sargassum</i> spp.						
Shore height	103.34	27.49	8.91	0.003	0.09	0.09
Exposure	100.84	13.23	4.46	0.035	0.04	0.14
<i>Cystophora</i> spp.						
Shore height	62.252	27.18	12.55	0.001	0.14	0.14
Exposure	60.469	7.79	3.73	0.029	0.04	0.18
Latitude	59.089	6.65	3.28	0.036	0.03	0.22

Abiotic drivers

There were only weak correlations with traits and abiotic variables for the summer survey in Australia. Sea surface temperature (SST) was the most important variable overall and was included in the BEST model for all habitats, followed by ambient air temperature, although neither were statistically significant (Table 5). For *Hormosira banksii* none of the variables were significant but when modelled individually SST accounted for 20% of variation and maximum air temperature accounted for 13% of variation (Table 5). *Sargassum* spp. also had non-significant correlations with SST (41%) and maximum air temperature (7%). The models for Coralline were not significant, but selected the variables SST (11%) and minimum air temperature (2%) as the best predictors (Table 5).

Table 5. DISTLM models for Australian habitats (*Hormosira banksii*, Coralline, and *Sargassum* spp.), investigating the influence of abiotic variables (Sea Surface Temperature, Maximum Temperature (°C), Minimum Temperature (°C), Rainfall (mm), and Daily Global Solar Exposure (MJ/m*m)) on multivariate algal traits (biomass, frond length, patch area). The variables that were selected in the best model for each habitat are shown with variables in order of contribution to the model. Models were selected using the AICc with the BEST selection criteria.

Variable	SS(trace)	Pseudo-F	P	R ²
<i>H. banksii</i>				
Sea surface temperature	143.71	2.008	0.136	0.20
Maximum temperature	90.96	1.164	0.324	0.13
<i>Coralline</i>				
Sea surface temperature	173.75	0.896	0.411	0.11
Minimum temperature	25.86	0.120	0.909	0.02
<i>Sargassum</i> spp.				
Sea surface temperature	437.30	3.504	0.125	0.41
Maximum temperature	70.01	0.353	0.616	0.07

Discussion

The morphological traits of four intertidal algal habitats varied across multiple spatial scales. More specifically algal morphology varied among patches separated by 1-10's of metres, sites along latitudinal gradients spanning hundreds of kilometres, and continents separated by thousands of kilometres. The patterns for each habitat were idiosyncratic, with *H. banksii* and Coralline correlating most strongly with large-scale gradients, *Cystophora* spp. correlating with multiple spatial scales and *Sargassum* spp. correlating with small spatial scales. The results highlight the complexity of how interspecific morphological traits can vary with spatially distributed environmental conditions, but importantly indicate some similarity in the relationships of the study habitats with spatial scale (e.g. site, latitude) and abiotic drivers (e.g. sea surface temperature). Differences among countries for the habitats inhabiting both Australia and New Zealand were weaker than expected, and despite the large distance, the greatest scale of variation was generally among sites within countries (with *H. banksii* traits showing no significant variation at the country scale). For the three brown algal habitats, linear models of spatial proxies (e.g. latitude, wave exposure, shore height) accounted for 14-22% of multivariate trait variation indicating important relationships with spatial drivers, however, the turfing red algae showed very weak spatial variation (Table 4).

The most striking pattern was the comparative size distribution of patterns at corresponding latitudes in Australia and New Zealand (Fig 2). This suggests that the macrophytes were varying similarly with large-scale environmental conditions and provides evidence for some similarity in macro-algal trait distributions across countries and habitats. Most biogeographic patterns related to size predict a gradient from small to large sizes with latitude (e.g. in the biomass of trees; Murphy et al. 2006), but as a general pattern in this study there were smaller sizes at the centre of the shared distribution including at the centre of *H. banksii* and Coralline distributions, the southern end of *Sargassum* spp. distribution and northern end of *Cystophora* spp. distribution (Fig 2). It is possible that the patterns observed are

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related to large-scale physical variables including biogeographic barriers and oceanographic processes rather than gradients in climatic conditions. Indeed, the region where small sizes occurred corresponded with major biogeographic barriers in both countries including Bass Strait in Australia and Cook Strait in New Zealand, both situated at approximately -40 degrees latitude. Biogeographic barriers have historically been identified as a major contributor to large-scale ecological patterns, with both historical and contemporary processes affecting distribution patterns. Previous research has similarly found Bass Strait to have an influence on biogeographic patterns with contemporary patterns of genetics, abundances and distributions found to be a reflection of physical barriers including ocean currents that limit dispersal, as well as species historical distributions that naturally occurred further south prior to the submersion of the Bassian Isthmus (Pleistocene land bridge) (Waters 2008, Waters et al. 2010, Lloyd et al. 2012, Miller et al. 2013).

Sea surface temperature and air temperature (max monthly temperature or minimum monthly temperature) were consistent predictors of multivariate trait patterns in the abiotic data models, though the models for all habitats were weak (Table 5). Macro-algal traits (biomass and length) respond to temperature particularly in summer when higher water temperatures are associated with lower growth and productivity (Kalvas and Kautsky 1993, Bearham et al. 2013). Although the predictive models were not strong, the abiotic data acquired was limited in scope as it was only collected during the summer period and for Australian sites. The Bureau of Meteorology data were from weather stations that were sometimes >20 km away from the sites. Site specific data may have led to stronger predictive models, although the large area of the study should have reduced spatial bias to some extent. Nevertheless, these models provide an indication for further study on specific abiotic drivers (e.g. temperature) affecting the morphology of intertidal macro-algae.

Wave exposure was a significant predictor of multivariate traits in the three brown algal habitats in the models for spatial drivers (Table 4). Wave exposure is one of the

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most recognised factors influencing algal morphology and greater exposure is generally observed to lead to smaller overall sizes (Blanchette 1997, Blanchette et al. 2000). However, when observed at larger spatial scales, reported patterns are contradictory and are inconsistent when multiple traits and abiotic variables are considered (Fowler-Walker et al. 2005a, Wernberg and Thomsen 2005, Wernberg and Vanderklift 2010). For example, the influence of exposure on *Ecklonia radiata* was inconsistent across the southwest coast of Australia. Individual traits had independent patterns, and local processes (e.g. grazing, sediment, nutrient levels etc.) confounded the predicted trait patterns (e.g. stunted size) to exposure (Wernberg and Thomsen 2005). In Australia, *H. banksii* and *Sargassum* spp. conformed to a generalised pattern of small size on exposed shores (albeit weakly). However, for sites in New Zealand the patterns were in the opposite direction with *H. banksii* and *Cystophora* spp. having larger biomass on exposed shores. In contrast to Australia, New Zealand platforms tended to have wider vertical shorelines (distance from low to high tide) (Lloyd personal observation), this may have reduced the influence of wave exposure somewhat as its strength would interact more strongly with the height of the patch on the shoreline. Vertical shore height was a significant factor driving multivariate patterns for all habitats except for *H. banksii* (Table 4). This pattern was strongest for *Sargassum* spp. with biomass greater lower on the shore. *Cystophora* spp. was also larger lower on the shore, however, Coralline had the opposite pattern with smaller biomass in low tidal areas. Previous research on Coralline has shown that these species are generally larger lower on the shore (Kelaher 2003), however, high biomass at Bonny Hills, the most northern location in Australia (Fig 2b), may have driven some inconsistency in the pattern. Furthermore, shore height was a very weak predictor in this model, consequently, this pattern should be viewed with caution.

Morphological variation differed spatially among seasons, though the season of greatest variation was not consistent across all habitats. For *H. banksii* and Coralline variation between sites was greatest during summer, whereas for *Sargassum* spp. and *Cystophora* spp. variation between sites was greatest in winter (Table 3). As

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mentioned above macro-algal traits generally show greater variation in summer as higher water temperatures inhibit growth and productivity (Kalvas and Kautsky 1993, Bearham et al. 2013). Morphological variation in *Sargassum* spp. may contrast with this pattern as this taxa is deciduous with seasonal growth patterns and therefore may respond differently to seasonal stressors than the other study habitats (Edgar 2008). *Cystophora* spp. on the other hand does not have seasonal growth patterns. However, *Cystophora* spp. was sampled throughout New Zealand. In contrast to Australia, limiting seasonal conditions in New Zealand are more likely to be associated with cold temperatures. Therefore, extreme cold may have led to a negative relationship with *Cystophora* spp. growth and winter. Though these results indicate temporal variation in traits, replication across seasons would be required to make more specific conclusions about the influence season.

While variation occurred at multiple spatial scales for all habitats, the strength of the models varied between habitats. Correlations were strong for the three brown algal habitats (accounting for 14-22% of variation in multivariate traits). However, the same models only accounted for 7% of variation in Coralline (Table 4). Trait patterns for Coralline were harder to quantify than other habitats due to its small size and turf like structure. Other studies have successfully quantified trait patterns in Coralline (e.g. Kelaher 2003). However, the methods in this study for measuring algal traits may have been better suited to larger furoid seaweed. Due to inconsistent results and low R^2 for some models, conclusions about the results for this alga should be viewed with some caution. The scales that were most important in the spatial models were also not consistent among habitats. The size of the distribution sampled for each habitat may have influenced the scale at which variation was most evident. For example, *H. banksii* was present throughout the study area and had a strong correlation with Latitude², whereas *Sargassum* spp., which was only sampled in mainland Australia, correlated most strongly with the smallest scale; shore height (Table 4). Potential bias can occur in the detection of ecological patterns as a consequence of using arbitrarily defined scales that may not be biologically relevant to the study species (i.e. not covering their total

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distribution). However, these issues are more evident in meta-analyses as the study design and data collection is not specific to the study at hand (Anderson et al. 2005b, Fowler-Walker et al. 2005b, Rahbek 2005).

Although individual traits were not correlated with each other, univariate and multivariate data had similar spatial patterns. Wernberg et al. (2003) similarly found that the traits of the macro-alga, *Ecklonia radiata*, were generally not correlated. Instead, they found that traits were independent and correlated with different spatial conditions. For example, lamina length was related to site level wave exposure, and lateral spinosity to regional scale grazing pressure. Though there is a large body of work on biogeographic adaptations of specific macrophyte traits e.g. larger leaves in rainforest ecosystems (Schlichting 1986), the majority is related to terrestrial plants. To reconcile inconsistency in the biogeographic patterns of macro-algae, further research is needed on the advantages of specific algal traits to spatially distributed environmental conditions (Wernberg et al. 2003, Wernberg and Vanderklift 2010).

The spatial variation in the morphology of habitat patches in this study highlights the complexity of species relationships with spatially distributed abiotic conditions. The overall results show that local scale variation tends to be habitat specific, whereas patterns at the large scale tend to be more consistent across taxa including correlations with large-scale physical (e.g. biogeographic barriers) and climatic (e.g. sea surface temperature) conditions. Small-scale drivers of algal morphology (i.e. wave exposure, shore height) influenced traits. However, the correlations of some habitats with local scale factors were not as strong as predicted, and may have been masked by interactions between these drivers at different spatial scales (see discussion above), or were responding to factors not measured. Trait distribution patterns did not consistently conform to ecological theory (e.g. patterns along exposure and tidal gradients were inconsistent). My findings suggest that the strength of predicted patterns is contextual (with respect to concomitant abiotic conditions). Therefore, predictions for ecological patterns derived from small-scale

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studies may not apply in the context of large scale gradients in environmental conditions (Wernberg and Thomsen 2005).

My findings show that macro-algae correlate with abiotic conditions across multiple spatial scales. As macro-algae are the dominant foundation species on rocky shores, these results suggest that abiotic conditions operating across multiple spatial scales are likely to have consequences for the capacity of macro-algae to fulfil their roles in habitat provision and primary production. Therefore, spatially explicit research considering how multiple driving forces contribute to trait patterns is required to make predictions about how macro-algae may respond to future environmental change.

CHAPTER THREE

*Intercontinental patterns in the biodiversity in intertidal
biogenic habitats*

Introduction

Determining the relative importance of the drivers of biodiversity in their ecological context is vital to understanding the conditions that promote biodiversity (Whittaker et al. 2001). As many of the key determinants of biodiversity are spatially distributed, observing variation in communities across multiple spatial scales is a valuable tool for determining the hierarchical contribution of both biotic and abiotic conditions to biodiversity patterns (Ricklefs 1987, Whittaker et al. 2001). In terrestrial ecosystems, both large and local scale processes influence biodiversity. For example, bird species richness corresponds with climate (large scale variation) and habitat niche (small scale variation) (Rahbek 2005). In marine systems, there is a strong focus on identifying the processes underpinning diversity by experimentally isolating factors at local scales. This work has identified a number of important mechanisms that can alter diversity levels (Underwood et al. 2000) e.g. tidal height (Underwood and Chapman 1998, Bertness et al. 2001), site exposure (Blanchette 1997, Blanchette et al. 2000). Biogeographic studies complement these findings by identifying how the strength of those drivers vary throughout species' distributions with respect to natural variation in the organisms themselves and associated environmental conditions (Sagarin et al. 2006, Lloyd et al. 2012).

Habitat heterogeneity (both within and between habitat-forming species) and latitudinal gradients in biotic and abiotic factors are two of the dominant drivers of biodiversity patterns at local and large scales, respectively. Biogenic habitats facilitate high levels of biodiversity by increasing structural complexity in the local environment and subsequently providing a refuge from predation, surfaces for colonisation and reducing environmental stress (Bruno and Bertness 2001, Gribben and Wright 2006, Hastings et al. 2007). Latitudinal gradients can result from several factors including climate, the strength of biotic processes, and historical biogeography (Hillebrand 2004, Rahbek 2005, Schemske et al. 2009). The effects of habitat and latitude on biodiversity are typically studied independently as they occur at different spatial scales, and there is some disparity between experimental

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ecology and macroecology (see reviews by Ricklefs 2004, Crain and Bertness 2006). However, local and regional processes are not isolated in natural systems, and spatially exclusive research fails to account for the influence of factors that act at different scales on diversity (e.g. small-scale habitat availability vs. large-scale climate conditions). Thus, little is known about the relative contribution of large and small scales to biodiversity patterns.

The role of habitat provisioning in biodiversity facilitation in intertidal systems is generally determined at small scales (Underwood et al. 2000). However, traits (e.g. morphology, biomass) of habitat-forming species that are important determinants of associated community structure can vary over large scales (Hastings et al. 2007, Bishop et al. 2012, Bishop et al. 2013). Thus, we may expect habitat and spatial scales to interact to control biodiversity. For example, Kelaher (2003) demonstrated that variation in the frond length of red turf algae at different tidal heights on rocky shores led to changes in the diversity of gastropod communities. To identify the key processes that lead to high biodiversity we must consider how diversity facilitation within habitats varies with respect to changing habitat morphology at multiple spatial scales (Crain and Bertness 2006). However, we know little about how variation in specific habitat traits across broad spatial scales contributes to large-scale patterns in biodiversity.

Spatially explicit studies are useful for understanding of how various scales influence ecological communities. For example, Anderson et al. (2013) found an interaction between fish diversity across latitude and depth on the North American Pacific coast, with stronger depth gradients in diversity at lower latitudes compared to higher latitudes, as the gradient in temperature is stronger closer to the equator. The importance of the depth gradient to diversity may not have been recognised had the study only been conducted in an area of high latitude. Similarly, employing a hierarchical design across three spatial scales (treatment, site and region) and 32° latitude in the USA, Freestone et al. (2011) showed that the strength of predation pressure on sessile marine invertebrates was greater at lower latitudes compared to

higher latitudes, demonstrating that the significance of key diversity drivers can be spatially variable. In addition, multiple spatial scales can also contribute to patterns of diversity. For example, Connell and Irving (2008) found that both regional scale (e.g. urchin herbivory) and local scale processes (e.g. abiotic disturbance) negatively affected the diversity and distribution patterns of sub-tidal macro-algae. Clearly, spatially explicit designs are a powerful, yet surprisingly under-utilised, tool for identifying the spatial structure of ecological communities.

In intertidal ecosystems, the biodiversity associated with biogenic habitats can be spatially variable with regard to a range of habitat traits e.g. algal patch size and shape (Airoldi 2003a), frond length (Kelaher 2003), holdfast volume (Anderson et al. 2005b), frond density, interstitial space, fractal geometry (Kovalenko et al. 2012), macrophyte canopy cover (Wernberg et al. 2011b) and mussel structure and density (Palomo et al. 2007). In addition, habitat heterogeneity is also an important driver of community structure through the creation of habitat niches, which in turn promote recruitment of more species with larger range of body sizes. Habitats with high heterogeneity can also increase the diversity of functional groups (e.g. filter feeders, detritivores) by increasing resource availability via processes such as sedimentation and increased nutrients (Kovalenko et al. 2012). The creation of microhabitats subsequently leads to a decoupling of trophic interactions and stabilisation of the food web (Kovalenko et al. 2012). While habitat heterogeneity is often quantified by using a single trait as a proxy for habitat space (i.e. a species-area relationship), there is increasing evidence that a combination of traits can contribute to biodiversity levels (Kovalenko et al. 2012). Facilitation in intertidal rocky shores has largely focussed on how individual habitat-forming species determine communities at local scales (but see; Dijkstra et al. 2012). However, intertidal rocky shores have a high diversity of biogenic habitats that can co-occur over large spatial scales. One expectation is that different co-occurring habitat-formers will consistently house the same communities at multiple spatial scales. However, little is known about whether the traits of co-occurring habitat-formers and their associated communities, will vary similarly or differently across multiple spatial scales (but see Kelaher et al.

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2004, Anderson et al. 2005b, Kelaher et al. 2007). Therefore, conservation strategies that aim to protect key habitats and associated high biodiversity must consider intraspecific trait variation and spatial scale to be effective.

Large-scale interspecific studies provide a powerful method for understanding the response of communities to spatially distributed environmental conditions. As extensive field studies are hampered by cost and effort required this research often takes a meta-analytic approach (for example to identify global patterns in marine herbivore/primary producer interactions results were combined from 613 small scale experiments; Poore et al. 2012). However, specifically designed biogeographic studies are not limited by inconsistencies in methods or temporal confounding and therefore provide a sound case for ecological generality (Anderson et al. 2005b). Here, I utilise a rocky intertidal system with the aim of providing one of the most comprehensive assessments investigating how marine invertebrate communities vary with changes in biogenic habitats from local to intercontinental scales, throughout temperate New Zealand and Australia. This system is amenable to such studies because the east coast of Australia and New Zealand both have extensive coastlines that overlap in latitude with comparable environmental conditions including abundant rocky reef habitat, and similar biogenic habitats. These similarities allow for direct comparison of patterns at the continental scale. This system also covers a large latitudinal distribution and is limited to a narrow band along the coastline making it easier to quantify latitudinal patterns (Sagarin et al. 2006).

In this study, I quantified changes in invertebrate communities within four biogenic habitats, across two continents. My aim was to identify the relative importance of spatially distributed environmental conditions to biodiversity patterns. Biodiversity patterns were related to diversity drivers across multiple spatial scales including, biogenic habitat type, habitat traits, vertical shore height, site exposure, and latitude and longitude. By looking at interspecific habitat patterns across replicate coastlines,

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I intend to provide a strong basis for the detection of generalised ecological patterns.

Specifically I investigated the following hypotheses:

1. Individual habitats will house specific associated communities, but biodiversity patterns will respond to variation in the morphology of habitat-forming organisms across multiple spatial scales.
2. Biodiversity patterns within algal habitats will vary across small-scale (site exposure, vertical shore height) and large-scale (country, latitude) abiotic gradients.

Methods

Field Survey

Building on Chapter 2, here I documented the communities inhabiting each of the biogenic habitats to identify how habitat traits and spatial scale interacted to determine biodiversity patterns. Biodiversity was determined from four habitats in 18 sites in Australia (n=10) and New Zealand (n=8) during the summer sampling period from January to early April 2012. Habitats sampled include *Hormosira banksii* and Coralline in both countries, and *Sargassum* spp. and *Cystophora* spp. in Australia and New Zealand, respectively. Descriptions of the study period, area, habitat, as well as the sampled distribution of each habitat are provided in Chapter 2. Biodiversity was determined from invertebrates within replicate patches (n=6 patches/habitat/site) of each habitat. These were the same patches used to measure algal morphology (methods outlined in Chapter 2). The first core collected for algal biomass (see Chapter 2) was used to determine biodiversity. Samples were rinsed in 1 mm sieves to trap macroscopic invertebrates. Seaweed biomass and large debris were removed and macrophyte fronds were searched by hand to remove trapped animals (Kelaher and Castilla 2005). In addition, I determined invertebrate diversity in a single quadrat (25 x 25 cm) in each algal patch to better capture larger species that may not be captured in cores. All animals from the same patch (core + quadrat) were placed in a labelled plastic bag and later fixed in 7% formalin (minimum 1 week) and subsequently washed and transferred to 80% ethanol for preservation.

Species identification

Animals were identified and counted under a dissecting microscope at the Australian Museum. The dominant taxa present included molluscs, crustaceans, polychaetes, echinoderms, anthozoa, and foraminifera (see Results). Within these groups, molluscs and polychaetes were identified to family level, crustaceans to class or subclass, echinoderms to class, Anthozoa to order and foraminifera to phyla. The level of taxonomic identification was prioritised according to the

taxonomic group's dominance among samples, as well as the condition of the samples required for fine scale identification. For example, although amphipods were a dominant group the identifying features of these animals commonly degraded and finer scale identification could not be achieved. Including a range of taxonomic groups identified to family level or higher was preferred over having a smaller range of taxa identified to species level as this ensured a more complete picture of biodiversity in this system was maintained and that important habitat-diversity associations would not be excluded (Anderson et al. 2005a). The use of higher taxonomic groups is also more appropriate for biogeographic studies as it reduces noise (high variability) at small scales that can mask biodiversity patterns at large scales (Anderson et al. 2005a). The sampling procedure did not capture all invertebrate taxa, therefore some groups including barnacles, tube dwelling polychaetes, and colonial species including sponges and bryozoans, were excluded from the dataset (Kelaher and Castilla 2005). However, field observations suggested that these were not a large component of fauna in macro-algae due to an absence of bare rock they need for colonisation (Edgar 2008).

Data analysis

Do biogenic habitats house specific associated communities?

I used multivariate analyses to determine whether individual habitats housed specific associated communities (hypothesis 1), and whether biodiversity patterns within algal habitats varied across small and large-scale abiotic gradients (hypothesis 2). I analysed diversity among habitats at the site and country scale. Multivariate analysis of variance by permutation (PERMANOVA) was used to determine the influence of Habitat (fixed factor; three levels: *H. banksii*, Coralline, and Frondose), Sites (random factor nested within Country) and Country (fixed factor; two levels, Australia, and New Zealand) on community structure. *Sargassum* spp. and *Cystophora* spp. were combined into a single habitat for this analysis (referred to as 'Frondose') to test the hypothesis that structurally similar habitats (i.e. frondose fucales) with different identities would house functionally similar

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communities in their respective ecosystems. Because of significant interactions (see Results) I ran reduced models investigating the effects of Habitat identity at each Site, and for the effect of Country and Site (Country) on individual habitats (*H. banksii*, Coralline, and Frondose). Variance components were calculated for random factors and pair-wise tests were conducted for fixed factors in order to determine the contribution of each factor to community patterns. Coles Bay was excluded from these analyses as there was only one habitat sampled at this site. *Sargassum* spp. and *Cystophora* spp. were analysed separately for the remaining analyses.

To further explore the community patterns detected in the spatial models I ran a 2-way SIMPER (Similarity Percentages) analysis. This was conducted in PRIMERV6 for the factors Habitat (four levels; *H. banksii*, Coralline, *Sargassum* spp. and *Cystophora* spp.) and Country. Results were used to identify the taxa driving differences between habitats.

What variables explain spatial patterns in habitat-community associations?

Here I used distance based linear models (DISTLM) for each habitat separately (*H. banksii*, Coralline, *Sargassum* spp. and *Cystophora* spp.) to identify specific conditions within habitats that influence biodiversity. Models were used to determine the contribution of individual habitat traits (biomass, frond length, patch area, percentage cover), localised variables (site exposure and height of patches on the shore) and large-scale variables (latitude and longitude) (see Chapter 2 for collection of data) to multivariate diversity patterns. Models were selected using the Akaike Information Criterion (AIC) with the step-wise selection criteria (analyses were conducted in the PRIMERV6 add-on PERMANOVA+).

Results

Do biogenic habitats house specific associated communities?

High abundances and diversity of invertebrates were observed throughout the study, with 10's–100's of individuals collected in each habitat patch, and 81 taxonomic groups found across the study area. In Australia, abundances and diversity per core ranged from 1-2059 and 1-16, respectively. In New Zealand abundances and diversity per core ranged from 3-1851 and 2-14, respectively. The highest abundances in Australia were recorded at Bonny Hills and the lowest abundances were recorded at Coles Bay (Fig. 3 a, c, e). Pearl Beach had the highest diversity in Australia and Coles Bay had the lowest (Fig. 4 a, c, e) (Coles Bay only had one site, despite this, abundances and diversity were proportionally low). In New Zealand the highest abundances were recorded at Shag Point and the lowest abundances were recorded at Cooks Beach (Fig. 3 b, d, f). Aramoana had the highest diversity and Leigh had the lowest (Fig. 4 b, d, f). Coralline had the highest average abundances and diversity across all sites (Fig. 3 c, d and 4 c, d). The lowest average abundances and diversity was in *Hormosira banksii* (Fig. 3 a, b and 4 a, b). *Cystophora* spp. had similar abundances to Coralline, but had much lower diversity (Fig. 3f and 4f). *Sargassum* spp. had higher diversity than *Cystophora* spp., but much lower abundances (Fig. 3e and 4e).

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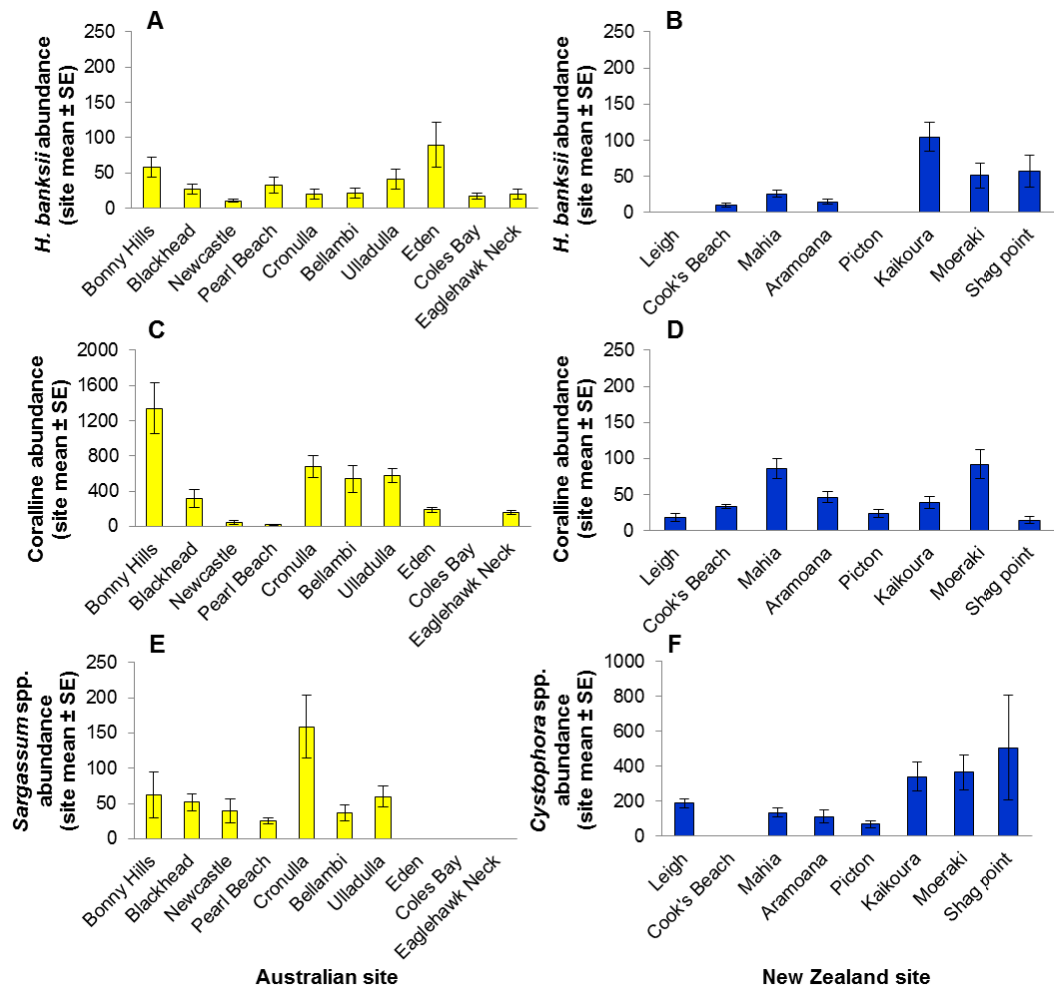


Figure 3. Invertebrate abundance (site mean \pm SE) within each habitat *Hormosira banksii* (a, b), Coralline (c, d), *Sargassum* spp. (e) and *Cystophora* spp. (f), at each site in Australia (n=10; left panel) and New Zealand (n=8; right panel). The Y-axis scale is different for Coralline in Australia and *Cystophora* spp. in New Zealand due to high abundances.

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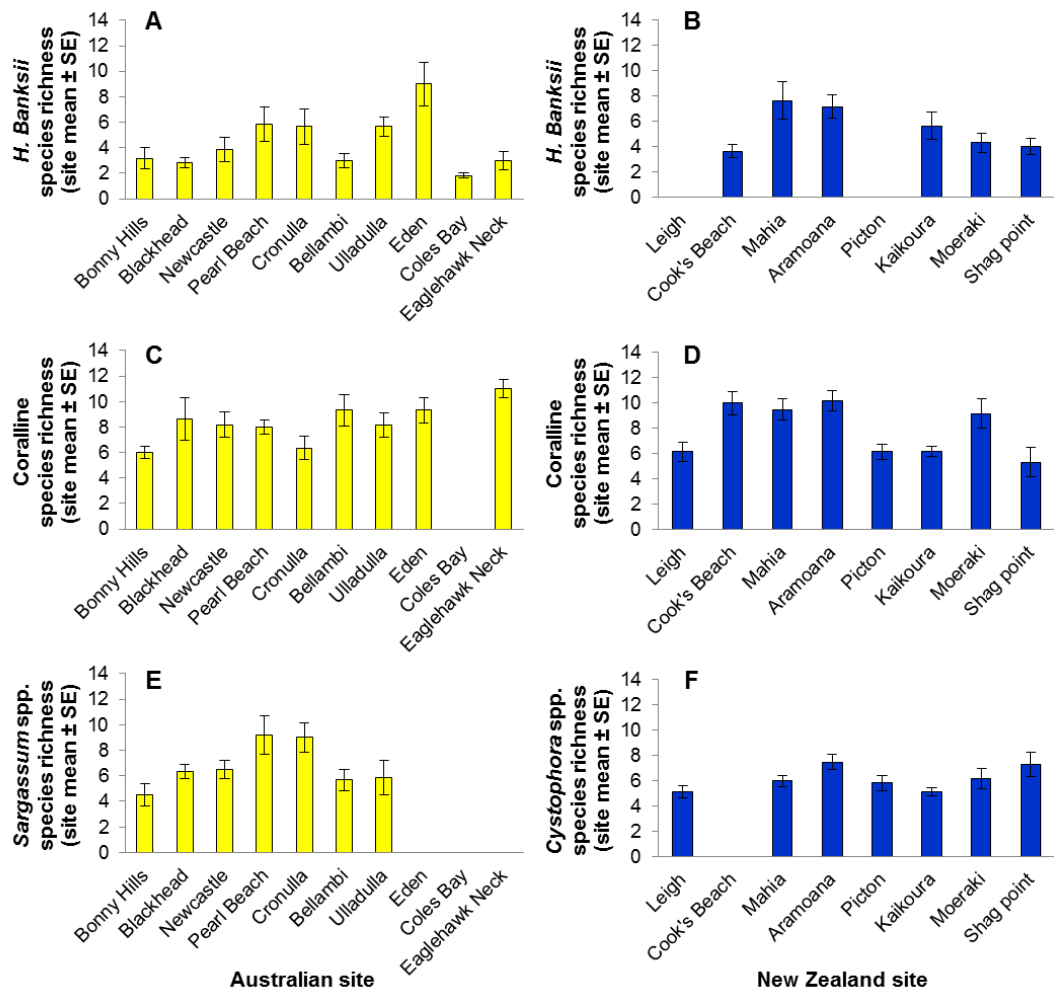


Figure 4. Invertebrate species richness (site mean \pm SE) within each habitat *Hormosira banksii* (a, b), Coralline (c, d), *Sargassum* spp. (e) and *Cystophora* spp. (f), at each site in Australia (n=10; left panel) and New Zealand (n=8; right panel).

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There were significant Country x Habitat and Site (Country) x Habitat interactions on invertebrate communities (Table 6). At all 17 Sites, communities differed among Habitat (Appendix 3) as predicted. Pair-wise comparisons revealed significant differences among all Habitats within all Sites except *H. banksii* and Coralline at Mahia in New Zealand ($t = 1.1, P = 0.27$) (Appendix 4). At Australian sites where all three habitats were present (7 sites); qualitatively, the greatest differences were between Coralline and *Sargassum* spp., except for Pearl Beach where the greatest difference was between Coralline and *H. banksii* ($t = 2.8$). At New Zealand sites where all three habitats were present (5 sites); qualitatively, the greatest differences were between Coralline and *Cystophora* spp. (Appendix 4). Differences between Coralline and other habitats were due to higher abundances and diversity of species in Coralline habitat (see SIMPER results below). *Hormosira banksii* communities had the largest overlap with communities in other habitats (see SIMPER results), and were less distinct than other habitats in the pairwise comparisons in the PERMANOVA (Appendix 4).

Table 6. PERMANOVA of the full spatial model showing significant interactions between Country and Habitat and, Site (Country) and Habitat on multivariate community assembly. Followed by reduced models for Australia and New Zealand showing significant interactions between Site and Habitat. Significant factors are highlighted in bold.

Source	df	SS	MS	Pseudo-F	P(perm)
<i>Full spatial model</i>					
Country	1	103190	10319	8.69	0.001
Habitat	2	113800	56900	9.52	0.001
Site (Country)	16	179040	11190	9.56	0.001
Country*Habitat	2	41739	20870	3.83	0.001
Site (Country)*Habitat	25	136120	5445	4.65	0.001
Residual	235	275160	1171		
Total	281	849050			
<i>Australia</i>					
Site	9	113880	12653	10.66	0.001
Habitat	2	90843	45422	7.57	0.001
Site*Habitat	14	83958	5997	5.05	0.001
Residual	130	154290	1187		
Total	155	442970			
<i>New Zealand</i>					
Site	7	75346	10764	9.35	0.001
Habitat	2	54514	27257	5.75	0.001
Site*Habitat	11	52158	4742	4.12	0.001

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Residual	105	120870	1151
Total			

For individual habitats, there were significant differences in communities between Countries and among Sites (Country) (Table 7). Sites within Countries accounted for between 32-35% of variation in the modelled variance components for each of the Habitats. Percentage variance components could not be calculated for the fixed factor Country. However, the results of the estimate of variance components indicated that differences in Sites within Countries were much greater than differences between Countries for *H. banksii*, differences in Sites within Countries and between Countries were equivalent for Coralline, whereas differences between Countries were slightly greater than differences within Countries for the frondose habitats (Table 7).

Australian communities (35.34% similarity) overall had high abundances of Galeommatidae (dominated by the small bivalve *Lasaea australis*) and amphipods, whereas New Zealand (40.09% similarity) had high abundances of amphipods, isopods and Nereididae (polychaetes). Differences in Australian and New Zealand communities were driven by higher abundances of Galeommatidae (*L. australis*) (27%) in Australia and higher numbers of amphipods (34%) in New Zealand communities; the countries were on average 79.57% dissimilar. Coralline communities had the greatest taxonomic diversity of the habitats, sharing 37.04% similarity and were composed primarily of Galeommatidae (*L. australis* bivalves) (24%), Nereididae (polychaetes) (12%), amphipods (10%), and Acanthochitonidae (chitons) (7%). *Hormosira banksii* communities shared 31.27% similarity across the study and were dominated by amphipods (50%). *Sargassum* spp. communities (36.68% similarity) were dominated by Trochidae (gastropods) (35%), but also housed amphipods (15%), whereas *Cystophora* spp. communities (55.04% similarity) predominantly housed amphipod (37%) and isopod (18%) crustaceans and had less diverse communities overall (Appendix 5). The taxa driving differences between *H. banksii* and Coralline were high numbers of Galeommatidae (13% contribution) in Coralline and high numbers of amphipods (9%) in *H. banksii*. Differences between

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H. banksii and *Sargassum* spp. were driven by high numbers of amphipods (11%) in *H. banksii* and Trochidae (11%) in *Sargassum* spp. Differences between Coralline and *Sargassum* spp. were driven by Galeommatidae (18%) in Coralline and amphipods (7%) in *Sargassum* spp. *H. banksii* and *Cystophora* spp., as well as Coralline and *Cystophora* spp. were differentiated by higher numbers of amphipods (15%, 11% respectively) and Eatoneliidae (gastropods) (11%, 9% respectively) in *Cystophora* spp. (Appendix 6).

Table 7. Results of PERMANOVA for individual habitats (*Hormosira banksii*, Coralline and Frondose), investigating the influence of Country (fixed factor; 2 levels Australia and New Zealand), and Site (Country) (random factor) on multivariate community assembly. Coles Bay was excluded as there was only one habitat at this site. Significant factors are highlighted in bold.

Source	df	SS	MS	Pseudo-F	P(perm)	% Variation	Estimate of variance components
<i>Hormosira banksii</i>							
Country	1	31517	31517.0	3.80	0.001	n/a*	515.9
Site (Country)	14	116200	8299.7	5.36	0.001	35	1125.1
Residual	80	123940	1549.3			49	1549.3
Total	95	271660					3190.3
<i>Coralline</i>							
Country	1	62400	62400.0	7.93	0.001	n/a	1073.0
Site (Country)	15	118020	7867.7	7.00	0.001	34	1124.1
Residual	85	95485	1123.4			34	1123.4
Total	101	275900					3320.5
<i>Frondose</i>							
Country	1	54179	54179.0	8.34	0.001	n/a	1135.3
Site (Country)	12	77963	6496.9	8.16	0.001	33	950.1
Residual	70	55734	796.2			28	796.2
Total	83	187880					2881.6

*Variance components should not be calculated for fixed factors so percentage variation was not calculated for Country (Quinn and Keough 2002).

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What variables explain spatial patterns in habitat-community associations?

Processes acting at large and small-scales were significant predictors of community structure for all habitats except *Sargassum* spp. communities, which were only driven by habitat traits (Table 8). Variables included in the linear model for *H. banksii* communities included the large-scale variables; longitude (11% of variation) and latitude (3.0 % of variation) and the small-scale variables biomass (6.7% of variation) and exposure (4.1% of variation) and (overall $R^2 = 0.25$). The linear model for Coralline included seven variables and accounted for 41% of variation. Longitude and latitude contributed most to the model accounting for 20% and 7.7% respectively. Site exposure accounted for 4.5% of variation and habitat traits including biomass, percentage cover, frond length and patch area collectively contributed a further 8.2% to the model. For *Sargassum* spp. the linear model accounted for 21% of variation and included the morphological variables biomass and percentage cover. For *Cystophora* spp. the linear model included five variables accounting for 55% of variation. Site exposure was the most important predictor of communities accounting for 17% of variation, followed by the large-scale predictors; longitude and latitude, which accounted for 14% and 12% respectively. The morphological trait variables biomass, frond length and patch area collectively accounted for a further 14.4% (Table 8).

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Table 8. DISTLM models for individual habitats (*Hormosira banksii*, Coralline, *Sargassum* spp. and *Cystophora* spp.), investigating the influence of individual habitat traits (biomass, frond length, patch area, percentage cover) and spatial variables (latitude, longitude site exposure and vertical shore height) on multivariate community assembly. The best model for each habitat is shown with variables in order of contribution to the model. Models were selected using the AIC with the step-wise selection criteria.

Variable	AIC	SS(trace)	Pseudo-F	P	Prop. R ²	Cumul. R ²
<i>Hormosira banksii</i>						
Longitude	755.44	30821	12.03	0.001	0.11	0.11
Biomass	749.80	18434	7.71	0.001	0.07	0.18
Exposure	746.45	12059	5.27	0.001	0.04	0.23
Latitude	744.55	8361	3.77	0.002	0.03	0.26
Coralline						
Longitude	786.07	57878	26.55	0.001	0.21	0.21
Latitude	777.61	21264	10.70	0.001	0.08	0.29
Exposure	772.94	12454	6.62	0.001	0.05	0.33
Biomass	771.51	6084	3.31	0.002	0.02	0.35
% cover	770.02	6006	3.35	0.001	0.02	0.38
Length	768.48	5869	3.35	0.001	0.02	0.40
Area	767.52	4757	2.77	0.001	0.02	0.41
<i>Sargassum</i> spp.						
Biomass	318.30	13714	7.35	0.001	0.16	0.16
% cover	317.42	4937	2.76	0.015	0.06	0.21
<i>Cystophora</i> spp.						
Exposure	289.38	7790	8.31	0.001	0.17	0.17
Longitude	283.51	6415	8.04	0.001	0.14	0.31
Latitude	276.84	5798	8.71	0.001	0.13	0.44
Biomass	273.41	3069	5.11	0.001	0.07	0.51
Length	271.41	2018	3.59	0.006	0.04	0.55
Area	270.32	1438	2.68	0.015	0.03	0.59

Discussion

Biodiversity patterns were evident from local to continental scales and varied with changes in (1) habitat identity, (2) habitat morphology, and (3) spatially distributed environmental conditions. The results were consistent with the ecological literature as biodiversity correlated with known drivers of diversity patterns (e.g. habitat traits, site exposure) (Blamey and Branch 2009). However, the strength of predicted patterns and the order of importance of each scale to biodiversity were particular to each habitat.

As predicted, habitat identity was the strongest predictor of biodiversity. Each algal habitat housed specific communities representing a range of taxonomic groups and differing levels of diversity. Coralline had the most complex morphological trait structure and the highest diversity of taxa, supporting my prediction that increased habitat heterogeneity would yield higher levels of diversity. This supports other research (e.g. Badano and Cavieres 2006), including studies on Coralline habitats that found strong relationships between diversity and habitat traits (e.g. Kelaher et al. 2001, Kelaher and Castilla 2005). Communities in the brown algae varied with the distribution of patches on the shore (e.g. *H. banksii* occurs highest on the platform), and differences in morphological trait structure. *Hormosira banksii* had simple communities, likely a reflection of its homogenous trait structure. Although it was predicted *Sargassum* spp. and *Cystophora* spp. would house similar taxa in their respective ecosystems (both being brown, frondose fucoid's with a low shore distribution), the communities within them were different. *Sargassum* spp. supported amphipods and a high proportion of gastropods that likely consumed the alga and were also facilitated by its frondose structure and low shore distribution (Edgar 2008). *Cystophora* spp. also housed amphipods, but rather than gastropods, supported crustaceans adapted to the low shore (e.g. Flabelliferan isopods) (Jones and Morgan 1994). These results demonstrate that conserving habitat diversity is important for maintaining the overall biodiversity in intertidal ecosystems.

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Although Habitat was the most important factor in determining biodiversity (Appendix 3), interactions of Habitat with Site and Country in the spatial models indicated that their effect on biodiversity varied throughout the study area (Table 6). Within habitats, differences in Sites within Countries (i.e. at the local and latitudinal scale) were the greatest source of variation (Table 7). In rocky shore communities the greatest level of variation in species is at the scale of 10's of metres, attributed to small-scale heterogeneity in environmental conditions (Underwood and Chapman 1998, Fraschetti et al. 2005, Smale et al. 2010). Country effects were weaker than Site effects for *H. banksii* communities, equivalent for Coralline communities, and only marginally greater for the frondose habitats (Table 7). However, this is likely driven by a combination of Country (e.g. species pools, evolutionary histories) and differences in facilitation (i.e. differences in structure of fronds, and possibly herbivore preference) between *Sargassum* spp. and *Cystophora* spp. The strong variation in Sites within Countries (Table 7) is likely due to a combination between localised and latitudinal variation (Table 8). The results support previous work on rocky shores highlighting the importance of local scales to diversity, but show that the variation does not preclude mechanisms that occur at large spatial scales.

Habitat traits, and spatial variables were significant predictors of biodiversity for all species (Table 8) except *Sargassum* spp., which was only driven by traits. However, there were differences in the order of importance across habitats. Habitat traits were the most important predictor of biodiversity overall and accounted for between 6 and 21% of variation in communities. Several morphological traits drove invertebrate communities including biomass, frond length, percentage cover and patch area. More traits drove communities in habitats with complex morphological trait structures than those in simpler habitats. Communities in Coralline, were driven by all habitat traits, whereas, communities in *H. banksii*, were only driven by biomass. This pattern is likely a reflection of habitat heterogeneity (Table 8). Habitat heterogeneity is a positive driver of biodiversity as increased complexity in morphological traits leads to greater surface area and habitat space (Hastings et al.

2007), this is particularly true in rocky intertidal systems where space is limited (Dayton 1971).

In addition to habitat heterogeneity, latitudinal variation is one of the most important scales influencing diversity patterns globally (Kraft et al. 2011). For the species that occurred in both countries (Coralline and *H. banksii*) differences within countries were equivalent or greater than differences between countries, indicating potential generality in spatial patterns between the two countries (Table 7). However, in the linear models, longitude (i.e. country) was a stronger predictor of diversity patterns than latitude (Table 8). Longitude in this model is essentially an effect of country (Australia vs. New Zealand), rather than representing a continuous gradient with longitude. The importance of latitude varied between species. For *Cystophora* spp. latitudinal variation was strong accounting for 12% of variation in communities. For Coralline the strength of latitude was only surpassed by longitude (i.e. country) in the model. For *H. banksii* the influence of latitude was analogous to longitudinal (i.e. country) and local scale effects. There was no effect of latitude on *Sargassum* spp. communities (Table 8). As latitude was a significant predictor variable for most of these species there is some support in the results for shared latitudinal generality across the two countries, however, the strength of this gradient was weaker than expected. The latitudinal diversity gradient is defined as a gradual decline in diversity from the equator to the poles (Hillebrand 2004). This biogeographic theory is generally studied across climate gradients (e.g. transitions between tropical and temperate plant diversity; Kraft et al. 2011). As the observations in this study were within the distributions of temperate habitats, climate variability in the study area may not have been strong enough to detect this pattern clearly (Freestone et al. 2011). Furthermore, latitude was analysed across the full dataset in the linear model to aim to detect latitudinal generality across the two countries (i.e. not accounting for the effect of country). Therefore, interactions at the country level may have weakened the predictive capacity of latitude in this model.

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For *H. banksii* and Coralline longitude was included as a proxy for differences between countries and differences. However, longitude was also important for *Cystophora* spp. in New Zealand (Table 8). In contrast to Australia, New Zealand has a less vertical coastline, and there was seven (decimal) degrees of longitude between study sites (Fig. 1, Table 1). This response to longitude indicates that regional scale processes within New Zealand are also an important determinant of community patterns in *Cystophora* spp. This supports other studies which show longitudinal variation is an important driver of the diversity of sub-tidal kelp, with algal diversity related to regional differences between biogeographic provinces (e.g. strength of herbivory) (Connell and Irving 2008). Consistent responses to latitude and longitude indicate that there are differences in the species pool between Australia and New Zealand, as well as some shared latitudinal generality in biodiversity patterns.

Exposure has strong effects on population processes in rocky shore ecosystems and can influence size, distribution and diversity patterns (Dayton 1971, Burrows et al. 2008). At the local scale exposure was a key driver of community patterns and explained between and 4-17% of variation within habitats (excepting *Sargassum* spp.) (Table 8). Exposure had an equivalent predictive power to latitude in the spatial models (Table 8), indicating that both large (biogeographic) and small-scale (local) forces were acting upon diversity throughout the study area. The height of patches on the shore was not significant in any of the models despite the fact that diversity is variable across this scale (Kelaher et al. 2001). Interactions with shore height and other spatial proxies may have altered its significance. For example, the intensity of conditions related to shore height are likely to be influenced by site exposure and subsequent wave force (Blamey and Branch 2009). Furthermore, 'shore height' was relative to the distributions of these habitats (i.e. the study organisms do not occur at the upper tidal range at any site), so a narrower range was covered than is usually incorporated into studies specifically testing diversity patterns along tidal gradients (Kelaher et al. 2001, Ingolfsson 2005).

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Similar factors drove diversity patterns in all habitats, except *Sargassum* spp. However, the order of importance was species' specific. The two habitats sampled throughout the full latitudinal range of the study and across both countries (*H. banksii* and Coralline) had similar proportional responses to spatial scales, with longitude most important (a proxy for differences across countries), followed by traits, then latitude and exposure. Conversely, *Cystophora* spp., which was present throughout the New Zealand study area, related almost evenly to the four drivers; exposure, longitude, latitude and morphology. For all three habitat-forming species latitude, exposure, and morphology (traits combined) contributed similar power to their respective models, suggesting that the influence of key diversity drivers are additive (Table 8) (Williams et al. 2013). The community in *Sargassum* spp. did not show a response to spatial drivers and were only predicted by traits (Table 8). As this study was not able to cover the wide ranging distribution of the *Sargassum* genus (it was only sampled throughout NSW, Australia), the study area may not have been large enough to detect broad scale variation within this habitat (Rahbek 2005, Edgar 2008). This emphasises the value of large-scale ecological studies for detecting biogeographic patterns across species' distributions.

The level of taxonomic identification may have also affected the scales at which biodiversity patterns were detected. Anderson et al. (2005a) investigated how differing levels of taxonomic identification (species through to phyla) altered spatial patterns in biodiversity. The study found that using higher taxonomic identification (family to phyla) led to better identification of large-scale patterns and a reduction in small-scale (sample level) variability. Using high taxonomic levels in this study may have strengthened the detection of large-scale patterns and reduced the noise resulting from endemic species in Australia and New Zealand. However, the use of coarse taxonomic resolution did not inhibit the detection of biodiversity patterns at local scales. Other processes not considered in the study may have led to inconsistency in large-scale patterns e.g. geomorphological characters of rocky substrata (Liversage et al. 2012), local currents and other factors determining recruitment (Rule and Smith 2005) among others.

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Furthermore, it is not known whether the influence of habitat heterogeneity on biodiversity is dependent or independent of latitude. Though there was no collinearity detected in the linear models, the morphological traits of the habitats was variable throughout the study. Therefore, there may be additive effects of latitude on habitat morphology and subsequent biodiversity. Consequently, the importance of latitude may be reflected in the strong response of species to habitat traits. However, more research is needed to disentangle these dependent effects.

The influence of multiple spatial scales on biodiversity in this study highlights the complexity of factors contributing to high biodiversity. Small-scale heterogeneity in environmental conditions is frequently cited as the primary source of ecological variation in coastal systems (Fraschetti et al. 2005, Smale et al. 2010). However, my findings suggest that biodiversity varies with processes at multiple spatial scales. Indeed, diversity patterns within most habitats varied strongly with large-scale gradients (i.e. longitude, latitude). There is a growing body of work revealing heterogeneity in diversity patterns at small spatial scales, which are nested within generalised patterns at large scales (Anderson et al. 2005a, Fowler-Walker et al. 2005b, Connell and Irving 2008). Advances in our understanding of the conditions that promote biodiversity will be aided by research that determines whether the causes of localised diversity patterns are purely at small scales, or if they are rooted within a hierarchy of regional and global scale processes (Ricklefs 1987, Gaston 2000, Ricklefs 2004).

CHAPTER FOUR

General Discussion

Discussion

Thesis overview

The tremendous diversity of earth means we are unlikely to ever identify all species, particularly when we consider that diversity is constantly changing through extinction, speciation, range shifts etc. (Millennium Ecosystem Assessment 2005). Therefore, advances in biodiversity research are better directed towards understanding the processes that underpin it (Beck et al. 2012). A powerful approach for identifying these conditions is through the observation of ecological patterns across multiple spatial scales (Whittaker et al. 2001), as ecological patterns are a reflection of species relationships with biotic and abiotic conditions throughout their distribution. This thesis describes patterns in the morphology of important intertidal habitats, and patterns in their associated biodiversity on the temperate east coasts of Australia and New Zealand. The study aimed to determine how biogenic habitats facilitate the biodiversity of intertidal invertebrates across multiple spatial scales.

The first chapter described the morphological trait patterns of intertidal macro-algae from local to intercontinental scales. The macro-algae surveyed included four conspicuous algal habitats with extensive distributions, along the east coasts of Australia and New Zealand. My findings revealed significant relationships with morphological traits and abiotic conditions across large and small spatial scales. However, interspecific trait patterns across each spatial scale were inconsistent. The second chapter of this thesis built on these patterns by determining how invertebrate biodiversity associated with habitat-formers depended on changes in habitat traits, and how communities varied with abiotic conditions. Biodiversity correlated strongly with habitat identity, habitat morphology, and abiotic conditions. The importance of large vs. small scales to morphology and biodiversity varied among habitats. This suggests that the relationship of habitat-forming species with environmental conditions is idiosyncratic.

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A comparison of spatial patterns in macro-algae and biodiversity revealed interesting patterns. Biodiversity in each habitat corresponded with similar spatial scales as the morphology of their associated habitat. Patterns in *H. banksii* morphology and communities were always strongest along geographic gradients (e.g. latitude). Additionally, *H. banksii* communities also correlated with biomass. In the spatial models for diversity, the independent variables biomass and latitude were not correlated (based in tests for collinearity). However, as a parabolic pattern was detected in *H. banksii* traits, there may be a non-linear relationship between these two variables and their role in facilitating biodiversity. Patterns in Coralline morphology and communities were also strongest at large scales. For *Cystophora* spp. morphology and communities there was a consistent pattern of large scales being more important than small scales. In contrast, *Sargassum* spp. was only driven by local scale variables; morphology correlated with shore height and exposure, and communities with habitat traits. The significance of localised variables on *Sargassum* spp. traits, and subsequently traits on associated communities, indicate that the effects of habitat morphology on biodiversity are dependent on local abiotic conditions i.e. local conditions indirectly control biodiversity by controlling the traits of *Sargassum* spp. Within individual habitats, morphology and biodiversity corresponded to the same spatial scales. For example, Coralline morphology and diversity varied with large scales and *Sargassum* spp. morphology and diversity with small scales. However, the spatial models generally included different variables for morphology and communities, for instance, *Sargassum* spp. traits varied with physical gradients, but diversity to morphology. This suggests that the responses of biodiversity to abiotic conditions are dependent on habitat morphology. This information highlights potential for further research on dependent effects between abiotic conditions, habitat morphology and biodiversity.

Conservation applications

Environmental managers are faced with the challenge of managing diversity at regional scales, in the face of large scale impacts like urbanisation and population

growth (Crain and Bertness 2006, Shokri et al. 2008). Therefore, identifying spatial structure in biodiversity is increasingly advocated in ecology. This is particularly relevant in light of global change as altered conditions (e.g. increased temperature, sea level rise, more frequent and intense storm events) are likely to impact diversity and species' distributions (Pitt et al. 2010). The results of this thesis demonstrated that biogenic habitat traits and their associated biodiversity varied with a range of spatially distributed abiotic conditions. Yet, the importance of large vs. small scales varied between habitat types. This indicates that management strategies focussed on the conservation of key habitats will need to consider the influence of both large and small-scale environmental conditions on biodiversity, and the responses of specific habitats to those same conditions (e.g. *Sargassum* spp. to small scale conditions, and Coralline to large).

Additionally, identifying the spatial structure of ecological patterns can provide the baseline information needed to develop conservation strategies (Crain and Bertness 2006, Ackerly et al. 2010). For example, the traits of macro-algae were important drivers of biodiversity throughout the study. Therefore, environmental effects on macro-algal morphology may have negative consequences for biodiversity. For example, ocean acidification poses a serious threat to the ability of Coralline algae to secrete calcium carbonate to form its rigid thallus (Kuffner et al. 2008). Coralline housed the highest abundances and diversity throughout the study area covering over 2,000 kilometres of coastline. Therefore, morphological degradation in this species may result in significant declines in the biodiversity of rocky shores. In addition, temperature conditions are harsh in this system and increases in ocean and ambient temperature may negatively affect the morphology of brown algae. For example, Bearham et al. (2013) found that high temperatures and light exposure negatively affected the growth of kelp (*Ecklonia radiata*). Furthermore, Bell (1995) demonstrated the importance of the morphology of intertidal algae (e.g. thallus thickness and branching structure) for protecting against the negative effects of temperature and desiccation. Therefore, any impact on the growth and size of algae from increased temperatures is likely to exacerbate the increased temperature and

desiccation stress already predicted in intertidal systems. Additionally, sedimentation as a result of human activities threatens to degrade the structural quality of algal habitats (Airoldi 2003b). Sediment accumulation has negative effects on the morphology of furoid algae (Airoldi 2003b). Biodiversity in brown algae varied with a range of traits (biomass, frond length, percentage cover, patch area), therefore predicted declines in algal growth with increased temperatures and sedimentation are likely to have a significant impact on biodiversity. I suggest that changes to the substratum in rocky intertidal ecosystems and associated changes to the morphology of brown seaweed, and biogenic habitats more broadly, should be monitored (Airoldi 2003b).

Climate change presents a unique threat in intertidal ecosystems. Not only are intertidal species limited in their longitudinal distribution, any potential southward range shifts in response to increasing temperatures would be limited by biogeographic barriers e.g. the south east (Peronian) and southern (Maugean) biogeographical regions of Australia (Waters and Roy 2003), Cook Strait in New Zealand (Ayers and Waters 2005) and of course by the southern limits of both continents. Therefore, species' distributions are predicted to contract poleward and southern regions are expected to form refuges for temperate species (Waters 2008, Pitt et al. 2010, Wernberg et al. 2011a). The southeast corner of Australia is a climate change hot spot and the region has experienced coastal warming higher than most of the southern hemisphere. This area also has the highest population in the country and subsequently biodiversity faces additional pressures including pollution, overfishing, and development. Wernberg et al. (2011a) predicted that hundreds of algal species may go extinct due to increasing temperatures and subsequent range contractions in the next half century. The loss of species is expected to be particularly severe on the east coast of Australia, which houses a quarter of the world's macroalgae (Wernberg et al. 2011a). Baseline information, such as the data in this thesis that identifies the conditions that alter diversity patterns is valuable for predicting how species' may respond to predicted threats (Poloczanska et al. 2007).

Our understanding of biodiversity is limited due to its inherent complexity. Biodiversity surrogates can be used to unravel this complexity by identifying species whose presence can be used as a proxy for other ecological components, such as the presence of high diversity, or a specific associated community (Caro and O'Doherty 1999). The development of surrogates is a continually developing area, and in this early stage needs to be supplemented by detailed field studies (Mumby et al. 2008). The results found in this thesis provide valuable information for the development of biodiversity surrogates on rocky shores as biodiversity varied strongly with the potential surrogates; habitat identity and habitat traits. This indicates that habitat-forming species on rocky shores may be used to predict associated biodiversity (e.g. bivalves in Coralline, gastropods in *Sargassum* spp., isopods in *Cystophora* spp.). To date many studies have incorporated surrogate species as representatives of a co-occurring community or indicators of site quality e.g. in predicting bird co-occurrences (Cushman et al. 2010), or the response of endangered fish to runoff (Wenger 2008). Though habitats are an implicit consideration in conservation planning, there are few studies that explicitly test the predictive power of using biogenic habitats as biodiversity surrogates. However, Mumby et al. (2008) tested the utility of several levels of a tropical reef ecosystem as potential diversity surrogates and found that coral habitat was the best surrogate for diversity in comparison to concomitant fish and benthic species. The habitats in this study similarly displayed strong relationships with biodiversity. As communities varied with habitat identity and individual habitat traits, intertidal systems are likely to be amenable to predictive research regarding habitat characteristics as indicators of biodiversity. Further research should combine my spatial results with the mechanistic understanding of habitat traits from local-scale manipulative studies replicated across large scales e.g. disentangling biotic (trophic) and abiotic (structure) facilitation using mimics (Palomo et al. 2007), to develop a predictive understanding of the habitat characteristics that promote biodiversity.

Determining the interactions between habitat-facilitation, localised conditions and geographic variation is important for furthering our understanding of the processes

behind biodiversity. Previous research has demonstrated the importance of biogenic habitats to biodiversity, thus these species are increasingly being advocated as important conservation management tools (Byers et al. 2006, Crain and Bertness 2006). My findings confirm this, as the four habitats in the study supported different levels of biodiversity and represented specific taxonomic groups, indicating that the conservation of habitat diversity is likely to promote overall diversity, and increase ecosystem function. However, the role of habitat identity in facilitating biodiversity varied throughout the study area with respect to changes in habitat structure and abiotic conditions. Therefore, biodiversity conservation should consider the trait distribution patterns of valuable biogenic habitats, and the additive influence of large and small-scale abiotic processes when predicting diversity patterns. As management strategies that apply a generalised conservation value to specific habitats may not be effective (Crain and Bertness 2006).

Spatially explicit hierarchical studies are useful for detecting generality in ecology by considering how interacting factors drive biodiversity patterns in the natural context of species distributions (Hewitt et al. 2007, Anderson et al. 2013). The results of this thesis suggest that multiple driving forces, from local to intercontinental scales, determine community structure in rocky intertidal habitats. However, the strength of predicted patterns is dependent on habitat identity, and also additive effects of environmental conditions on habitat morphology. Advances in our understanding of the conditions that promote high biodiversity will develop from a better understanding of (1) the hierarchical structure of biodiversity patterns, (2) interactions between environmental conditions operating at different spatial scales, and (3) whether the influence of abiotic conditions on biodiversity is dependent or independent of habitat traits.

LITERATURE CITED

- Ackerly, D. D., S. R. Loarie, W. K. Cornwell, S. B. Weiss, H. Hamilton, R. Branciforte, and N. J. B. Kraft. 2010. The geography of climate change: implications for conservation biogeography. *Diversity and Distributions* **16**:476-487.
- Airoldi, L. 2003a. Effects of patch shape in intertidal algal mosaics: roles of area, perimeter and distance from edge. *Marine Biology* **143**:639-650.
- Airoldi, L. 2003b. The effects of sedimentation on rocky coast assemblages. *Oceanography and Marine Biology* **41**:161-236.
- Anderson, M. J., S. D. Connell, B. M. Gillanders, C. E. Diebel, W. M. Blom, J. E. Saunders, and T. J. Landers. 2005a. Relationships between taxonomic resolution and spatial scales of multivariate variation. *Journal of Animal Ecology* **74**:636-646.
- Anderson, M. J., C. E. Diebel, W. M. Blom, and T. J. Landers. 2005b. 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**:35-56.
- Anderson, M. J., R. N. Gorley, and K. R. Clarke. 2005c. PERMANOVA. Permutational multivariate analysis of variance, a computer program. . Department of Statistics, University of Auckland **24**.
- Anderson, M. J., and C. J. F. Ter Braak. 2003. Permutation tests for multi-factorial analysis of variance. *Journal of Statistical Computation and Simulation* **73**:85-113.
- Anderson, M. J., N. Tolimieri, and R. B. Millar. 2013. Beta Diversity of Demersal Fish Assemblages in the North-Eastern Pacific: Interactions of Latitude and Depth. *PLoS ONE* **8**:e57918.
- Australian Government Bureau of Meteorology. 2013. Climate classification maps: Köppen major classes.
- Ayers, K. L., and J. M. Waters. 2005. Marine biogeographic disjunction in central New Zealand. *Marine Biology* **147**:1045-1052.

- Badano, E. I., and L. A. Cavieres. 2006. Ecosystem engineering across ecosystems: do engineer species sharing common features have generalized or idiosyncratic effects on species diversity? *Journal of Biogeography* **33**:304-313.
- Bearham, D., M. A. Vanderklift, and J. R. Gunson. 2013. Temperature and light explain spatial variation in growth and productivity of the kelp *Ecklonia radiata*. *Marine Ecology Progress Series* **476**:59-70.
- Beck, J., L. Ballesteros-Mejia, C. M. Buchmann, J. Dengler, S. A. Fritz, B. Gruber, C. Hof, F. Jansen, S. Knapp, H. Kreft, A.-K. Schneider, M. Winter, and C. F. Dormann. 2012. What's on the horizon for macroecology? *Ecography* **35**:673-683.
- Bell, E. C. 1995. Environmental and morphological influences on thallus temperature and desiccation of the intertidal alga *Mastocarpus papillatus* Kutzing. *Journal of Experimental Marine Biology and Ecology* **191**:29-55.
- Berke, S. K. 2012. Biogeographic variability in ecosystem engineering: patterns in the abundance and behavior of the tube-building polychaete *Diopatra cuprea*. *Marine Ecology Progress Series* **447**:1-13.
- Bertness, M., D. S. Gaines, D. and M. Hay, E, editors. 2001. *Marine community ecology*. Sinauer Associates, Inc., Sunderland.
- Bishop, M. J., J. E. Byers, B. J. Marcek, and P. E. Gribben. 2012. Density-dependent facilitation cascades determine epifaunal community structure in temperate Australian mangroves. *Ecology* **93**:1388-1401.
- Bishop, M. J., J. Fraser, and P. E. Gribben. 2013. Morphological traits and density of foundation species modulate a facilitation cascade in Australian mangroves. *Ecology* **94**:1927-1936.
- Blackburn, T., M, and B. Hawkins, A. 2004a. Bergmann's rule and the mammal fauna of northern North America. *Ecography*:715-724.
- Blackburn, T., M, and B. Hawkins, A. 2004b. Bergmann's rule and the mammal fauna of northern North America. *Ecography* **27**:715-724.
- Blackburn, T. M., and K. J. Gaston. 1996. Spatial patterns in the body sizes of bird species in the New World. *Oikos*:436-446.

- Blackburn, T. M., K. J. Gaston, and N. Loder. 1999. Geographic gradients in body size: a clarification of Bergmann's rule. *Diversity and Distributions*:165-174.
- Blamey, L. K., and G. M. Branch. 2009. Habitat diversity relative to wave action on rocky shores: implications for the selection of marine protected areas. *Aquatic Conservation: Marine and Freshwater Ecosystems* **19**:645-657.
- Blanchette, C. A. 1997. Size and survival of intertidal plants in response to wave action: a case study with *Fucus gardneri*. *Ecology* **79**:1563-1578.
- Blanchette, C. A., C. Thornber, and S. Gaines, D. 2000. Effects of wave exposure on intertidal furoid algae. *Proceedings of the California Islands Symposium*:347-355.
- Brown, J. H., and A. K. Lee. 1968. Bergmann's rule and climatic adaptation in woodrats (*Neotoma*). *Evolution*:329-338.
- Bruno, J. F., and M. D. Bertness. 2001. Habitat modification and facilitation in benthic marine communities. *in* M. D. Bertness, S. D. Gaines, and M. E. Hay, editors. *Marine Community Ecology*. Sinauer Associates, Inc., Massachusetts.
- Burrows, M. T., R. Harvey, and L. Robb. 2008. Wave exposure indices from digital coastlines and the prediction of rocky shore community structure. *Marine Ecology Progress Series* **353**:1-12.
- Byers, J. E., K. Cuddington, C. G. Jones, T. S. Talley, A. Hastings, J. G. Lambrinos, J. A. Crooks, and W. G. Wilson. 2006. Using ecosystem engineers to restore ecological systems. *Trends in Ecology & Evolution* **21**:493-500.
- Campbell, N. A., J. B. Reece, M. R. Taylor, and E. J. Simon, editors. 2006. *Biology: concepts and connections*. 5th edition. Benjamin Cummings, San Francisco.
- Caro, T., M., and G. O'Doherty, O. 1999. On the use of surrogate species in conservation biology. *Conservation Biology* **13**:805-814.
- Chapman, M. G., J. People, and D. Blockley. 2005. Intertidal assemblages associated with natural corallina turf and invasive mussel beds. *Biodiversity and Conservation* **14**:1761-1776.

- Cole, V. J., and C. D. McQuaid. 2011. Broad-scale spatial factors outweigh the influence of habitat structure on the fauna associated with a bioengineer. *Marine Ecology Progress Series* **442**:101-109.
- Connell, S. D., and A. D. Irving. 2008. Integrating ecology with biogeography using landscape characteristics: a case study of subtidal habitat across continental Australia. *Journal of Biogeography* **35**:1608-1621.
- Crain, C., M., and M. Bertness, D. 2006. Ecosystem engineering across environmental gradients: implications for conservation and management. *Bioscience* **56**:211-218.
- Cruz-Motta, J., J. P. Miloslavich, G. Palomo, K. Iken, B. Konar, G. Pohle, T. Trott, L. Benedetti-Cecchi, C. Herrera, A. Hernandez, A. Sardi, A. Bueno, J. Castillo, E. Klein, E. Guerra-Castro, J. Gobin, D. Gomez, I. R. Riosmena-Rodriguez, A. Mead, G. Bigatti, A. Knowlton, and Y. Shirayama. 2010. Patterns of spatial variation of assemblages associated with intertidal rocky shores: a global perspective. *PLoS ONE* **5**:1-10.
- Cushman, S. A., K. S. McKelvey, B. R. Noon, and K. McGarigal. 2010. Use of abundance of one species as a surrogate for abundance of others. *Conservation biology : the journal of the Society for Conservation Biology* **24**:830-840.
- Dayton, P., K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecological Monographs* **41**:351-389.
- Dayton, P. K. 1972. Toward an understanding of community resilience and the potential effects of enrichments to the benthos at McMurdo Sound, Antarctica. In: Parker BC (Ed). *Proceedings of the colloquium on conservation problems in Antarctica*. Lawrence, KS: Allen Press.
- Dijkstra, J. A., J. Boudreau, and M. Dionne. 2012. Species-specific mediation of temperature and community interactions by multiple foundation species. *Oikos* **121**:646-654.
- Dyer, L. A., M. S. Singer, J. T. Lill, J. O. Stireman, G. L. Gentry, R. J. Marquis, R. E. Ricklefs, H. F. Greeney, D. L. Wagner, H. C. Morais, I. R. Diniz, T. A. Kursar,

- and P. D. Coley. 2007. Host specificity of Lepidoptera in tropical and temperate forests. *Nature* **448**:696-699.
- Edgar, G., J. 2008. Australian marine life: the plants and animals of temperate waters. 2nd edition. New Holland Publishers, Sydney.
- Ellison, A. M., M. S. Bank, B. D. Clinton, E. A. Colburn, K. Elliott, C. R. Ford, D. R. Foster, B. D. Kloeppel, J. D. Knoepp, G. M. Lovett, J. Mohan, D. A. Orwig, N. L. Rodenhouse, W. V. Sobczak, K. A. Stinson, J. K. Stone, C. M. Swan, J. Thompson , B. Von Holle, and J. R. Webster. 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology* **3**:479-486.
- Fowler-Walker, M. J., S. D. Connell, and B. M. Gillanders. 2005a. To what extent do geographic and associated environmental variables correlate with kelp morphology across temperate Australia? *Marine and Freshwater Research* **56**:877-887.
- Fowler-Walker, M. J., S. D. Connell, and B. M. Gillanders. 2005b. Variation at local scales need not impede tests for broader scale patterns. *Marine Biology* **147**:823-831.
- Fraschetti, S., A. Terlizzi, and L. Benedetti-Cecchi. 2005. Patterns of distribution of marine assemblages from rocky shores: evidence of relevant scales of variation. *Marine Ecology Progress Series* **296**:13-29.
- Freestone, A., L. R. Osman, W. G. Ruiz, M, and M. Torchin, E. 2011. Stronger predation in the tropics shapes species richness patterns in marine communities. *Ecology* **92**:983-993.
- Gaston, K. J. 2000. Global patterns in biodiversity. *Nature* **405**:220-227.
- Gestoso, I., C. Olabarria, and J. S. Troncoso. 2013. Selection of habitat by a marine amphipod. *Marine Ecology*.
- Gilman, S. 2005. A test of Brown's principle in the intertidal limpet *Collisella scabra* (Gould, 1846). *Journal of Biogeography* **32**:1583-1589.
- Gribben, P. E., J. E. Byers, J. T. Wright, and T. M. Glasby. 2013. Positive versus negative effects of an invasive ecosystem engineer on different components of a marine ecosystem. *Oikos* **122**:816-824.

- Gribben, P. E., and J. Wright, T. 2006. Invasive seaweed enhances recruitment of a native bivalve: roles of refuge from predation and the habitat choice of recruits. *Marine Ecology Progress Series* **318**:177-185.
- Gwyther, J., and P. G. Fairweather. 2002. Colonisation by epibionts and meiofauna of real and mimic pneumatophores in a cool temperate mangrove habitat. *Marine Ecology Progress Series* **229**:137-149.
- Hastings, A., J. E. Byers, J. A. Crooks, K. Cuddington, C. G. Jones, J. G. Lambrinos, T. S. Talley, and W. G. Wilson. 2007. Ecosystem engineering in space and time. *Ecology Letters* **10**:153-164.
- Hewitt, J., E. S. Thrush, F. P. Dayton, K. and E. Bonsdorff. 2007. The effect of spatial and temporal heterogeneity on the design and analysis of empirical studies of scale-dependent systems. *American Naturalist* **169**:398-408.
- Hillebrand, H. 2004. On the generality of the latitudinal diversity gradient. *American Naturalist* **163**:192-211.
- Hobday, A., T. Okey, E. Poloczanska, T. Kunz, and A. Richardson. 2006a. Impacts of climate change on Australian marine life: Part B. Technical Report. Canberra, Australia.
- Hobday, A. J., T. A. Okey, E. S. Poloczanska, T. J. Kunz, and A. J. Richardson. 2006b. Impacts of climate change on Australian marine life: Part C. Literature Review. Canberra, Australia.
- Hubbell, S., P. 2005. The neutral theory of biodiversity and biogeography and Stephen Jay Gould. *Paleobiology* **31**:122-132.
- Ingolfsson, A. 2005. Community structure and zonation patterns of rocky shores at high latitudes: an interocean comparison. *Journal of Biogeography* **32**:169-182.
- Jones, C., G. J. Lawton, H, and M. Shachak. 1994. Organisms as ecosystem engineers. *Oikos* **69**:373-386.
- Jones, C., G. J. Lawton, H, and M. Shachak. 1997. Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* **78**:1946-1957.
- Jones, D., and G. Morgan. 1994. A field guide to crustaceans of Australian waters. 2nd edition. Reed New Holland.

- Kalvas, A., and L. Kautsky. 1993. Geographic variation in *Fucus vesiculosus* morphology in the Baltic and North Seas. *European Journal of Phycology* **28**:85-91.
- Kelaher, B., P. 2003. Effects of frond length on diverse gastropod assemblages in Coralline turf. *Journal of the Marine Biological Association of the United Kingdom* **83**:159-163.
- Kelaher, B., P., J. Castilla, C., and R. Seed. 2004. Intercontinental test of generality for spatial patterns among diverse molluscan assemblages in Coralline algal turf. *Marine Ecology Progress Series* **271**:221-231.
- Kelaher, B. P., and J. C. Castilla. 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**:155-165.
- Kelaher, B. P., J. C. Castilla, L. Prado, P. York, E. Schwindt, and A. Bortolus. 2007. Spatial variation in molluscan assemblages from Coralline turfs of Argentinean Patagonia. *Journal of Molluscan Studies* **73**:139-146.
- Kelaher, B. P., M. G. Chapman, and A. J. Underwood. 2001. Spatial patterns of diverse macrofaunal assemblages in coralline turf and their associations with environmental variables. *Journal of the Marine Biological Association of the United Kingdom*:917-930.
- Kerr, J., T. H. Kharouba, M., and D. Currie, J. 2007. The macroecological contribution to global change solutions. *Science* **316**:1581-1584.
- Kerswell, A., P. 2006. Global biodiversity patterns of benthic marine algae. *Ecology* **87**:2479-2488.
- Kirkman, H. 1989. Growth, density and biomass of *Ecklonia radiata* at different depths and growth under artificial shading off Perth, Western Australia. *Australian Journal of Marine and Freshwater Research* **40**:169-177.
- Kovalenko, K. E., S. M. Thomaz, and D. M. Warfe. 2012. Habitat complexity: approaches and future directions. *Hydrobiologia* **685**:1-17.
- Kraft, N. J. B., L. S. Comita, J. M. Chase, N. J. Sanders, N. G. Swenson, T. O. Crist, J. C. Stegen, M. Vellend, B. Boyle, M. J. Anderson, H. V. Cornell, K. F. Davies, A. L. Freestone, B. D. Inouye, S. P. Harrison, and J. A. Myers. 2011.

- Disentangling the drivers of diversity along latitudinal and elevational gradients. *Science* **333**:1755-1758.
- Kuffner, I. B., A. J. Andersson, P. L. Jokiel, K. S. Rodgers, and F. T. Mackenziem. 2008. Decreased abundance of crustose coralline algae due to ocean acidification. *Nature Geoscience* **1**:114-117.
- Kylafis, G., and M. Loreau. 2011. Niche construction in the light of niche theory. *Ecology Letters* **14**:82-90.
- Liversage, K., V. J. Cole, C. D. McQuaid, and R. A. Coleman. 2012. Intercontinental tests of the effects of habitat patch type on the distribution of chitons within and among patches in intertidal boulder field landscapes. *Marine Biology* **159**:2777-2786.
- Lloyd, H. B., B. R. Murray, and P. E. Gribben. 2012. Trait and abundance patterns of two marine molluscs: the influence of abiotic conditions operating across multiple spatial scales. *Marine Ecology Progress Series* **463**:205-214.
- López-Bucio, J., A. Cruz-Ramírez, and L. Herrera-Estrella. 2003. The role of nutrient availability in regulating root architecture. *Current Opinion in Plant Biology* **6**:280-287.
- Mabin, C. J. T., P. E. Gribben, A. Fischer, and J. T. Wright. 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.
- Martínez, B., R. M. Viejo, F. Carreño, and S. C. Aranda. 2012. Habitat distribution models for intertidal seaweeds: responses to climatic and non-climatic drivers. *Journal of Biogeography* **39**:1877-1890.
- Menge, B., A. 1976. Organization of the New England rocky intertidal community: role of predation, competition, and environmental heterogeneity. *Ecological Monographs* **46**:355-393.
- Millennium Ecosystem Assessment. 2005. Ecosystems and human well-being: biodiversity synthesis. World Resources Institute, Washington.
- Miller, A. D., V. L. Versace, T. G. Matthews, S. Montgomery, and K. C. Bowie. 2013. Ocean currents influence the genetic structure of an intertidal mollusc in

- southeastern Australia - implications for predicting the movement of passive dispersers across a marine biogeographic barrier. *Ecology and Evolution* **3**:1248-1261.
- Mumby, P. J., K. Broad, D. R. Brumbaugh, C. P. Dahlgren, A. R. Harborne, A. Hastings, K. E. Holmes, C. V. Kappel, F. Micheli, and J. N. Sanchirico. 2008. Coral reef habitats as surrogates of species, ecological functions, and ecosystem services. *Conservation Biology* **22**:941-951.
- Murphy, H. T., J. VanDerWal, and J. Lovett-Doust. 2006. Distribution of abundance across the range in eastern North American trees. *Global Ecology and Biogeography* **15**:63-71.
- Paine, R., T. 2010. Macroecology: does It ignore or can it encourage further ecological syntheses based on spatially local experimental manipulations? *American Naturalist* **176**:385-393.
- Paine, R. T. 1976. Size-limited predation: an observational experiemental approach with the *Mytilus Pisaster* interaction. *Ecology* **57**:858-873.
- Palomo, M. G., J. People, M. G. Chapman, and A. J. Underwood. 2007. Separating the effects of physical and biological aspects of mussel beds on their associated assemblages. *Marine Ecology Progress Series* **344**:131-142.
- Perelman, S., B, S. Burkart, E, and R. Leon, J, C. 2003. The role of a native tussock grass (*Paspalum quadrifarium* Lam.) in structuring plant communities in the flooding Pampa grasslands, Argentina. *Biodiversity and Conservation* **12**:225-238.
- Pitt, N., R, E. Poloczanska, S, and A. Hobday, J. 2010. Climate-driven range changes in Tasmanian intertidal fauna. *Marine and Freshwater Research* **61**:963-970.
- Pollock, L. J., W. K. Morris, and P. A. Vesk. 2012. The role of functional traits in species distributions revealed through a hierarchical model. *Ecography* **35**:716-725.
- Poloczanska, E., S , R. Babcock, C, A. Butler, A. Hobday, J , O. Hoegh-Guldberg, T. Kunz, J , R. Matear, D. Milton, A, T. Okey, A , and A. Richardson, J. 2007. Climate change and Australian marine life. *Oceanography and Marine Biology* **45**:407-478.

- Poore, A. G. B., A. H. Campbell, R. A. Coleman, G. J. Edgar, V. Jormalainen, P. L. Reynolds, E. E. Sotka, J. J. Stachowicz, R. B. Taylor, M. A. Vanderklift, J. Emmett Duffy, and S. Navarrete. 2012. Global patterns in the impact of marine herbivores on benthic primary producers. *Ecology Letters* **15**:912-922.
- Quinn, G., P. and M. Keough, J. 2002. *Experimental design and data analysis for biologists*. Cambridge University Press, Melbourne.
- Rahbek, C. 2005. The role of spatial scale and the perception of large-scale species-richness patterns. *Ecology Letters* **8**:224-239.
- Rangel, T. F., J. A. F. Diniz-Filho, and L. M. Bini. 2010. SAM: a comprehensive application for Spatial Analysis in Macroecology. *Ecography* **33**:46-50.
- Ricklefs, R. E. 1987. Community diversity: relative roles of local and regional processes. *Science* **235**:167-171.
- Ricklefs, R. E. 2004. A comprehensive framework for global patterns in biodiversity. *Ecology Letters* **7**:1-15.
- Rule, M. J., and S. D. A. Smith. 2005. Spatial variation in the recruitment of benthic assemblages to artificial substrata. *Marine Ecology Progress Series* **290**:67-78.
- Sagarin, R. D., and S. D. Gaines. 2002. The 'abundant centre' distribution: to what extent is it a biogeographical rule? *Ecology Letters* **5**:137-147.
- Sagarin, R. D., S. D. Gaines, and B. Gaylord. 2006. Moving beyond assumptions to understand abundance distributions across the ranges of species. *Trends in Ecology & Evolution* **21**:524-530.
- Schemske, D. W., G. G. Mittelbach, H. V. Cornell, J. M. Sobel, and K. Roy. 2009. Is there a latitudinal gradient in the importance of biotic interactions? *Annual Review of Ecology and Systematics* **40**:245-269.
- Schlichting, C. D. 1986. The evolution of phenotypic plasticity in plants. *Annual Review of Ecology, Evolution, and Systematics* **17**:667-693.
- Serisawa, Y., H. Akino, K. Matsuyama, M. Ohno, J. Tanaka, and Y. Yokohama. 2002. Morphometric study of *Ecklonia cava* (Laminariales, Phaeophyta) sporophytes in two localities with different temperature conditions. *Phycological Research* **50**:193-199.

- Shokri, M. R., W. Gladstone, and A. Kepert. 2008. Annelids, arthropods or molluscs are suitable as surrogate taxa for selecting conservation reserves in estuaries. *Biodiversity and Conservation* **18**:1117-1130.
- Smale, D. A., G. A. Kendrick, and T. Wernberg. 2010. Assemblage turnover and taxonomic sufficiency of subtidal macroalgae at multiple spatial scales. *Journal of Experimental Marine Biology and Ecology* **384**:76-86.
- Smith, F. A., and J. L. Betancourt. 2006. Predicting woodrat (*Neotoma*) responses to anthropogenic warming from studies of the palaeomidden record. *Journal of Biogeography* **33**:2061-2076.
- Stevens, G. C. 1989. The latitudinal gradient in geographical range: how so many species coexist in the tropics. *American Naturalist* **133**:240-256.
- Tam, J. C., and R. A. Scrosati. 2011. Mussel and dogwhelk distribution along the north-west Atlantic coast: testing predictions derived from the abundant-centre model. *Journal of Biogeography* **38**:1536-1545.
- Terlizzi, A., M. J. Anderson, S. Bevilacqua, S. Fraschetti, M. Włodarska-Kowalczyk, and K. E. Ellingsen. 2009. Beta diversity and taxonomic sufficiency: do higher-level taxa reflect heterogeneity in species composition? *Diversity and Distributions* **15**:450-458.
- Thrush, S. F., M. Chiantore, V. Asnagi, J. Hewitt, D. Fiorentino, and R. Cattaneo-Vietti. 2011. Habitat–diversity relationships in rocky shore algal turf infaunal communities. *Marine Ecology Progress Series* **424**:119-132.
- Underwood, A. J., and M. G. Chapman. 1998. Spatial analyses of intertidal assemblages on sheltered rocky shores. *Australian Journal of Ecology* **23**:138-157.
- Underwood, A. J., M. G. Chapman, and S. D. Connell. 2000. Observations in ecology: you can't make progress on processes without understanding the patterns. *Journal of Experimental Marine Biology and Ecology*:97-115.
- Virgós, E., R. Kowalczyk, A. Trua, A. de Marinis, J. G. Mangas, J. M. Barea-Azcón, and E. Geffen. 2011. Body size clines in the European badger and the abundant centre hypothesis. *Journal of Biogeography* **38**:1546-1556.

- Waters, J., M. 2008. Marine biogeographical disjunction in temperate Australia: historical landbridge, contemporary currents, or both? *Diversity and Distributions* **14**:692-700.
- Waters, J., M., and M. Roy, S. 2003. Marine biogeography of southern Australia: phylogeographical structure in a temperate sea-star. *Journal of Biogeography* **30**:1787-1796.
- Waters, J. M., T. Wernberg, S. D. Connell, M. S. Thomsen, G. C. Zuccarello, G. T. Kraft, J. C. Sanderson, J. A. West, and C. F. D. Gurgel. 2010. Australia's marine biogeography revisited: Back to the future? *Austral Ecology* **35**:988-992.
- Wenger, S. J. 2008. Use of surrogates to predict the stressor response of imperiled species. *Conservation Biology* **22**:1564-1571.
- Wernberg, T., M. Coleman, A. Fairhead, S. Miller, and M. Thomsen. 2003. Morphology of *Ecklonia radiata* (Phaeophyta: Laminariales) along its geographic distribution in south-western Australia and Australasia. *Marine Biology* **143**:47-55.
- Wernberg, T., B. D. Russell, M. S. Thomsen, C. F. Gurgel, C. J. Bradshaw, E. S. Poloczanska, and S. D. Connell. 2011a. Seaweed communities in retreat from ocean warming. *Current Biology* **21**:1828-1832.
- Wernberg, T., and M. S. Thomsen. 2005. The effect of wave exposure on the morphology of *Ecklonia radiata*. *Aquatic Botany* **83**:61-70.
- Wernberg, T., M. S. Thomsen, F. Tuya, and G. A. Kendrick. 2011b. Biogenic habitat structure of seaweeds change along a latitudinal gradient in ocean temperature. *Journal of Experimental Marine Biology and Ecology* **400**:264-271.
- Wernberg, T., and M. A. Vanderklift. 2010. Contribution of Temporal and Spatial Components to Morphological Variation in the Kelp *Ecklonia* (Laminariales)1. *Journal of Phycology* **46**:153-161.
- Whittaker, R., J. K. Willis, J. and R. Field. 2001. Scale and species richness: towards a general, hierarchical theory of species diversity. *Journal of Biogeography* **28**:453-470.

- Williams, S. L., M. E. S. Bracken, and E. Jones. 2013. Additive effects of physical stress and herbivores on intertidal seaweed biodiversity. *Ecology* **94**:1089-1101.
- Wright, J. P., and C. G. Jones. 2004. Predicting effects of ecosystem engineers on patch-scale species richness from primary productivity. *Ecology* **85**:2071-2081.

APPENDIX

Appendix 1. Pearson correlation between biomass samples weighed in the field (wet weight) and oven-dried in the lab (dry weight). Correlations > 0.90 are highlighted in bold.

	<i>H. banksii</i> wet weight	<i>Sargassum</i> spp. wet weight	Coralline wet weight
<i>H. banksii</i> dry weight	0.98	-	-
<i>Sargassum</i> spp. dry weight	0.13	0.91	-
Coralline dry weight	0.39	-0.07	0.92

Appendix 2. PERMANOVA of individual habitats showing significant interactions between Season and Site (Country) on univariate habitat traits for *Hormosira banksii* biomass and Coralline biomass, and Season and Site on univariate habitat traits for *Sargassum* spp. biomass and *Cystophora* spp. frond length. Significant factors are highlighted in bold.

Source	df	SS	MS	F	P(perm)
<i>H. banksii</i> - biomass					
Country	1	6.94	6.94	2.50	0.129
Season	1	1.97	1.97	8.34	0.015
Site(Country)	15	44.22	2.95	35.01	0.001
Country*Season	1	0.40	0.40	1.71	0.187
Season*Site(Country)	14	3.30	0.24	2.80	0.001
Residual	165	13.89	0.08		
Total	197	71.14			
<i>Coralline</i> - biomass					
Country	1	9.98	9.98	9.62	0.008
Season	1	19.78	19.78	22.95	0.002
Site(Country)	15	15.56	1.04	8.14	0.001
Country*Season	1	0.11	0.11	0.13	0.729
Season*Site(Country)	15	12.93	0.86	6.76	0.001
Residual	170	21.67	0.13		
Total	203	80.28			
<i>Sargassum</i> spp. - biomass					
Season	1	0.90	0.90	2.03	0.21
Site	7	8.29	1.18	13.24	0.001
Season*Site	6	2.66	0.44	4.95	0.001
Residual	75	6.71	0.09		
Total	89	18.21			
<i>Cystophora</i> spp. - length					
Season	1	0.48	0.48	1.07	0.371
Site	6	3.76	0.63	8.84	0.001
Season*Site	5	2.27	0.45	6.40	0.001
Residual	65	4.60	0.07		
Total	77	11.67			

Appendix 3. PERMANOVA of individual habitats showing significant interactions between Season and Site (Country) on multivariate habitat traits for *Hormosira banksii* and Coralline, and Season and Site on multivariate habitat traits for *Sargassum* spp. and *Cystophora* spp. Significant factors are highlighted in bold.

Source	df	SS	MS	Pseudo-F	P(perm)
<i>H. banksii</i>					
Country	1	719.92	719.92	2.41	0.114
Season	1	122.27	122.27	6.27	0.006
Site(Country)	15	4753.80	316.92	26.82	0.001
Country*Season	1	37.52	37.52	1.92	0.185
Season*Site(Country)	14	273.13	19.51	1.65	0.035
Residual	165	1949.70	11.82		
Total	197	7779.80			
<i>Coralline</i>					
Country	1	883.05	883.05	4.66	0.013
Season	1	1091.00	1091.00	17.27	0.001
Site(Country)	15	2841.60	189.44	10.75	0.001
Country*Season	1	124.09	124.09	1.96	0.138
Season*Site(Country)	15	947.62	63.18	3.59	0.001
Residual	170	2995.00	17.62		
Total	203	8868.10			
<i>Sargassum</i> spp.					
Season	1	174.06	174.06	12.97	0.001
Site	7	1340.30	191.47	14.26	0.001
Season*Site	6	400.97	66.83	4.98	0.001
Residual	75	1006.80	13.42		
Total	89	2926.90			
<i>Cystophora</i> spp.					
Season	1	60.84	60.84	6.94	0.003
Site	6	377.22	62.87	7.17	0.001
Season*Site	5	104.40	20.88	2.38	0.010
Residual	65	569.57	8.76		
Total	77	1127.40			

Appendix 4. Results of PERMANOVA showing the influence of Habitat (fixed factor, three levels; *Hormosira banksii*, Coralline, *Sargassum* spp. in Australia, and *H. banksii*, Coralline, *Cystophora* spp. in New Zealand) on multivariate community assembly at Sites in Australia and New Zealand (n=17). Coles Bay was excluded as there was only one habitat at this site. Significant factors are highlighted in bold.

Source	df	SS	MS	Pseudo-F	P(perm)
Australia					
<i>Bonny Hills</i>					
Habitat	2	30399	15200.00	19.33	0.001
Residual	15	11796	786.43		
Total	17	42196			
<i>Blackhead</i>					
Habitat	2	23651	11826.00	9.65	0.001
Residual	15	18375	1225.00		

Total	17	42026			
Newcastle					
Habitat	2	19351	9675.50	7.22	0.001
Residual	15	20104	1340.20		
Total	17	39455			
Pearl Beach					
Habitat	2	18123	9061.40	6.69	0.001
Residual	15	20317	1354.40		
Total	17	38439			
Cronulla					
Habitat	2	15862	7931.10	5.82	0.001
Residual	15	20444	1362.90		
Total	17	36306			
Bellambi					
Habitat	2	28615	14307.00	15.62	0.001
Residual	15	13736	915.71		
Total	17	42351			
Ulladulla					
Habitat	2	19131	9565.50	7.66	0.001
Residual	15	18732	1248.80		
Total	17	37863			
Eden					
Habitat	1	5721.3	5721.30	5.06	0.004
Residual	10	11310	1131.00		
Total	11	17031			
Eaglehawk Neck					
Habitat	1	13948	13948.00	14.47	0.003
Residual	10	9642.5	964.25		
Total	11	23591			
New Zealand					
Leigh					
Habitat	1	13809	13809.00	8.87	0.002
Residual	10	15570	1557.00		
Total	11	29379			
Cooks Beach					
Habitat	1	10846	10846.00	5.22	0.001
Residual	10	20762	2076.20		
Total	11	31608			
Mahia					
Habitat	2	13317	6658.40	6.58	0.001
Residual	15	15175	1011.70		
Total	17	28492			
Aramoana					
Habitat	2	14309	7154.40	8.25	0.001
Residual	15	13012	867.47		
Total	17	27321			
Picton					
Habitat	1	13561	13561.00	16.84	0.003
Residual	10	8054.6	805.46		
Total	11	21615			
Kaikoura					

Habitat	2	14526	7263.00	7.63	0.001
Residual	15	14274	951.60		
Total	17	28800			
Moeraki					
Habitat	2	15758	7878.90	8.11	0.001
Residual	15	14578	971.90		
Total	17	30336			
Shag Point					
Habitat	2	10547	5273.50	4.07	0.001
Residual	15	19444	1296.30		
Total	17	29991			

Appendix 5. Pair-wise comparisons from PERMANOVA for the influence of Habitat (fixed factor, three levels; *Hormosira banksii*, Coralline, *Sargassum* spp. in Australia, and *H. banksii*, Coralline, *Cystophora* spp. in New Zealand) on multivariate community assembly at Sites in Australia and New Zealand (n=17). Coles Bay was excluded as there was only one habitat at this site. Significant factors are highlighted in bold.

Groups	t	P(perm)
Australia		
Bonny Hills		
<i>H. banksii</i> , Coralline	5.00	0.002
<i>H. banksii</i> , <i>Sargassum</i> spp.	2.74	0.001
Coralline, <i>Sargassum</i> spp.	5.19	0.002
Blackhead		
<i>H. banksii</i> , Coralline	3.33	0.002
<i>H. banksii</i> , <i>Sargassum</i> spp.	2.45	0.003
Coralline, <i>Sargassum</i> spp.	3.38	0.002
Newcastle		
<i>H. banksii</i> , Coralline	2.76	0.006
<i>H. banksii</i> , <i>Sargassum</i> spp.	2.38	0.007
Coralline, <i>Sargassum</i> spp.	2.90	0.003
Pearl Beach		
<i>H. banksii</i> , Coralline	2.88	0.002
<i>H. banksii</i> , <i>Sargassum</i> spp.	2.74	0.007
Coralline, <i>Sargassum</i> spp.	1.86	0.002
Cronulla		
<i>H. banksii</i> , Coralline	2.40	0.001
<i>H. banksii</i> , <i>Sargassum</i> spp.	2.00	0.003
Coralline, <i>Sargassum</i> spp.	3.06	0.005
Bellambi		
<i>H. banksii</i> , Coralline	3.83	0.005
<i>H. banksii</i> , <i>Sargassum</i> spp.	4.28	0.003
Coralline, <i>Sargassum</i> spp.	3.67	0.003
Ulladulla		
<i>H. banksii</i> , Coralline	2.91	0.005
<i>H. banksii</i> , <i>Sargassum</i> spp.	1.95	0.006
Coralline, <i>Sargassum</i> spp.	3.51	0.003
Eden		
<i>H. banksii</i> , Coralline	2.25	0.004
Eaglehawk Neck		

<i>H. banksii</i> , Coralline	3.45	0.004
New Zealand		
Leigh		
Coralline, <i>Cystophora</i> spp.	2.98	0.006
Cooks Beach		
<i>H. banksii</i> , Coralline	2.29	0.003
Mahia		
<i>H. banksii</i> , Coralline	1.11	0.278
<i>H. banksii</i> , <i>Cystophora</i> spp.	2.61	0.002
Coralline, <i>Cystophora</i> spp.	4.27	0.003
Aramoana		
<i>H. banksii</i> , Coralline	1.78	0.010
<i>H. banksii</i> , <i>Cystophora</i> spp.	2.58	0.003
Coralline, <i>Cystophora</i> spp.	5.07	0.004
Picton		
Coralline, <i>Cystophora</i> spp.	4.10	0.003
Kaikoura		
<i>H. banksii</i> , Coralline	2.57	0.004
<i>H. banksii</i> , <i>Cystophora</i> spp.	2.74	0.004
Coralline, <i>Cystophora</i> spp.	3.01	0.003
Moeraki		
<i>H. banksii</i> , Coralline	2.70	0.003
<i>H. banksii</i> , <i>Cystophora</i> spp.	2.04	0.005
Coralline, <i>Cystophora</i> spp.	3.76	0.003
Shag Point		
<i>H. banksii</i> , Coralline	1.99	0.005
<i>H. banksii</i> , <i>Cystophora</i> spp.	1.68	0.003
Coralline, <i>Cystophora</i> spp.	2.24	0.004

Appendix 6. Results of SIMPER analysis showing the average similarity of communities in Habitat groups (*Hormosira banksii*, Coralline, *Sargassum* spp. and *Cystophora* spp.) across all country groups, and Country groups (Australia and New Zealand) across all habitat groups. The top 50% of taxa contributing to assemblages are presented.

Species	Average Abundance	Average Similarity	Similarity/SD	Contribution %	Cumulative %
<i>Hormosira banksii</i>					
<i>Average similarity: 31.27</i>					
Amphipoda	1.44	15.87	0.89	50.75	50.75
Coralline					
<i>Average similarity: 37.04</i>					
Galeommatidae (<i>L. australis</i>)	1.85	9.21	0.71	24.86	24.86
Nereididae	0.88	4.71	0.81	12.72	37.58
Amphipoda	0.71	3.83	0.60	10.34	47.92
Acanthochitonidae	0.61	2.66	0.59	7.19	55.12
<i>Sargassum</i> spp.					
<i>Average similarity: 36.68</i>					
Trochidae	1.50	13.01	1.79	35.47	35.47
Amphipoda	1.11	5.85	0.54	15.94	51.41
<i>Cystophora</i> spp.					
<i>Average similarity: 55.04</i>					
Amphipoda	2.96	20.79	2.45	37.76	37.76
Isopoda	1.38	9.98	2.06	18.13	55.89
Australia					
<i>Average similarity: 35.34</i>					
Galeommatidae (<i>L. australis</i>)	1.70	9.54	0.75	26.99	26.99
Amphipoda	0.90	8.57	0.56	24.25	51.24
New Zealand					
<i>Average similarity: 40.09</i>					

Amphipoda	1.90	13.66	1.23	34.08	34.08
Isopoda	0.85	4.62	0.77	11.51	45.59
Nereididae	0.71	4.47	0.72	11.15	56.75

Appendix 7. Results of SIMPER analysis showing the average dissimilarity of communities among Habitat groups (*Hormosira banksii*, Coralline, *Sargassum* spp. and *Cystophora* spp.) across all country groups. The top 50% of taxa contributing to differences in assemblages are presented. There is no comparison between *Sargassum* spp. and *Cystophora* spp. as there are no pairs of groups with samples.

Species	Average Abundance	Average Abundance	Average Dissimilarity	Dissimilarity/SD	Contribution %	Cumulative %
<i>H. banksii</i> & Coralline	<i>H. banksii</i>	<i>Coralline</i>				
<i>Average dissimilarity</i> = 76.77						
Galeommatidae (<i>L. australis</i>)	0.71	1.85	10.26	0.91	13.37	13.37
Amphipoda	1.44	0.71	7.16	1.27	9.33	22.70
Trochidae	0.53	0.55	4.16	1.05	5.42	28.11
Turbinidae	0.35	0.63	3.91	0.99	5.10	33.21
Nereididae	0.29	0.88	3.89	0.99	5.07	38.28
Acanthochitonidae	0.11	0.61	3.88	0.93	5.05	43.33
Syllidae	0.26	0.66	3.79	1.02	4.94	48.27
Mytilidae	0.22	0.55	3.30	0.83	4.29	52.56
<i>H. banksii</i> & <i>Sargassum</i> spp.	<i>H. banksii</i>	<i>Sargassum</i> spp.				
<i>Average dissimilarity</i> = 76.08						
Amphipoda	1.44	1.11	8.87	1.19	11.66	11.66
Trochidae	0.53	1.50	8.55	1.44	11.24	22.90
Galeommatidae (<i>L. australis</i>)	0.71	0.49	7.16	1.12	9.41	32.31
Litiopidae	0.09	0.86	6.15	1.08	8.08	40.39
Columbellidae	0.06	0.79	5.19	1.11	6.82	47.21
Turbinidae	0.35	0.59	4.89	0.92	6.42	53.64
Coralline & <i>Sargassum</i> spp.	<i>Coralline</i>	<i>Sargassum</i> spp.				
<i>Average dissimilarity</i> = 78.61						

Galeommatidae (<i>L. australis</i>)	1.85	0.49	14.11	1.43	17.94	17.94
Amphipoda	0.71	1.11	5.49	0.96	6.98	24.93
Acanthochitonidae	0.61	0.05	4.45	1.26	5.65	30.58
Trochidae	0.55	1.50	4.31	1.25	5.48	36.06
Litiopidae	0.18	0.86	3.75	1.16	4.77	40.84
Mytilidae	0.55	0.46	3.63	1.06	4.61	45.45
Columbellidae	0.09	0.79	3.51	1.16	4.46	49.91
Syllidae	0.66	0.11	3.45	1.10	4.39	54.30
<i>H. banksii</i> & <i>Cystophora</i> spp.						
<i>Average dissimilarity</i> = 63.56	<i>H. banksii</i>	<i>Cystophora</i>	<i>spp.</i>			
Amphipoda	1.44	2.96	9.73	1.41	15.31	15.31
Eatoniellidae	0.21	1.52	7.20	1.32	11.32	26.64
Trochidae	0.53	1.44	6.16	1.25	9.69	36.33
Anthozoa Actiniaria	0.25	1.07	5.92	1.08	9.31	45.64
Isopoda	0.23	1.38	5.73	1.43	9.01	54.65
<i>Coralline</i> & <i>Cystophora</i> spp.						
<i>Average dissimilarity</i> = 75.48	<i>Coralline</i>	<i>Cystophora</i>	<i>spp.</i>			
Amphipoda	0.71	2.96	8.86	1.49	11.74	11.74
Eatoniellidae	0.28	1.52	6.61	1.35	8.75	20.49
Trochidae	0.55	1.44	6.11	1.43	8.09	28.58
Nereididae	0.88	0.19	5.16	1.69	6.84	35.42
Isopoda	0.41	1.38	5.10	1.45	6.76	42.18
Anthozoa Actiniaria	0.28	1.07	4.90	0.96	6.49	48.67
Tanaidacea	0.11	0.79	3.97	0.82	5.26	53.93