Interactions between subtidal coralline turf and associated small mobile invertebrates

Anna Kate Berthelsen

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Frontispiece: Small mobile invertebrates found amongst subtidal coralline turf.

Abstract

This thesis investigates interactions between small (1 to 8 mm) mobile invertebrates and coralline turfs in shallow coastal rocky reefs in northeastern New Zealand. The effects of host species identity and spatial variability were examined on animals inhabiting subtidal coralline algal turfs, by comparing the assemblages of small mobile invertebrates associated with five coralline turf species across a number of subtidal rocky reefs in northeastern New Zealand. Coralline turf fauna were abundant (average of 16,000 to 80,000 ind.m^{-2}) and diverse (129 taxa in total), with assemblages dominated by arthropods, gastropods and polychaetes. Despite substantial differences in the morphologies of the coralline turf species, host identity had little effect on total abundance and richness of the fauna, and a moderate effect on taxonomic composition. Spatial variation at the scale of 10^2–10^3 m had a stronger influence than host identity on all three assemblage-level properties, with wave exposure and depth having the most explanatory power of the environmental factors measured. Host-specificity was low, probably due to the close taxonomic relatedness of the host algal species and their inedibility (with consequent lack of dietary specialisation by fauna). These results justify the common practice of lumping coralline turf species in ecological studies with regard to the description of the total abundance and richness of the associated fauna, but not the taxonomic composition of the fauna.

The principle that biological traits relating to the behaviour, morphology and life-history of organisms can influence ecological functioning is becoming increasingly used to examine the functional response of communities to natural and anthropogenic variation in environmental factors. The taxonomic composition and biological traits of fauna were examined along an environmental gradient ranging from (1) relatively deep, wave-exposed sites with short turf containing a low proportion of fine sediment to (2) shallow wave-sheltered sites with taller turf containing a higher proportion of fine sediment. The most common traits of fauna were small size, globose shape, calcareous exterior, detritus/deposit feeding, omnivorous diet and low larval mobility. Total abundances of animals were higher at the wave-exposed sites. The animal assemblage as a whole more clearly reflected the environmental gradient when the assemblage was described in terms of taxonomic composition than in terms of biological traits. Only 3 out of 23 traits (suspension feeding, detritus/deposit feeding and vermiform shape) were at least moderately correlated with the overall gradient, although stronger relationships were present between some of the traits and individual environmental variables. Overall, the biological traits of turf-dwelling faunal assemblages were less sensitive to an environmental gradient than taxonomic composition, indicating that functioning can persist despite taxonomic change.

Benthic primary producers such as seaweeds and seagrasses are often inhabited by high densities of small arthropods, but little is known about the impact of these animals on their hosts, which could be positive if they keep them free of fouling epiphytes. The impact of small arthropods on algal epiphytes growing on coralline algal turf in a shallow, wave-exposed, rocky reef in warm temperate northeastern New Zealand were assessed. Plaster blocks impregnated with the insecticide carbaryl were used to reduce arthropod densities (by 96% relative to unmanipulated controls in the case of amphipods). By the end of the ~3.5 mo experiment total epiphyte cover was 88% when arthropods were excluded compared to 38% in unmanipulated controls, a 2.3-fold increase. Brown (*Colpomenia* spp.), green (*Ulva* spp.) and ‘filamentous and microscopic’ algal epiphyte taxa were responsible for the increase, while the cover of red foliose algal epiphytes decreased slightly. Hyalid amphipods (*Protohyale* spp.) were likely responsible for suppressing the epiphytes, as they were the most abundant arthropod mesograzer taxon and ate both *Colpomenia* spp. and *Ulva* spp. in a laboratory no-choice feeding assay. During the field experiment 2 large storms removed most of the epiphytes that had grown in the mesograzer exclusion treatment. Overall, these results indicate that the amphipods prevented overgrowth of the turf by epiphytes during calm periods. These results provide the first *in situ* cageless example of arthropod mesograzer-exerted control on the abundance and composition of primary producers on a subtidal rocky reef.

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Name	Nature of Contribution
Richard (RB) Taylor	Manuscript editing
Judi (JE) Hewitt	Manuscript editing

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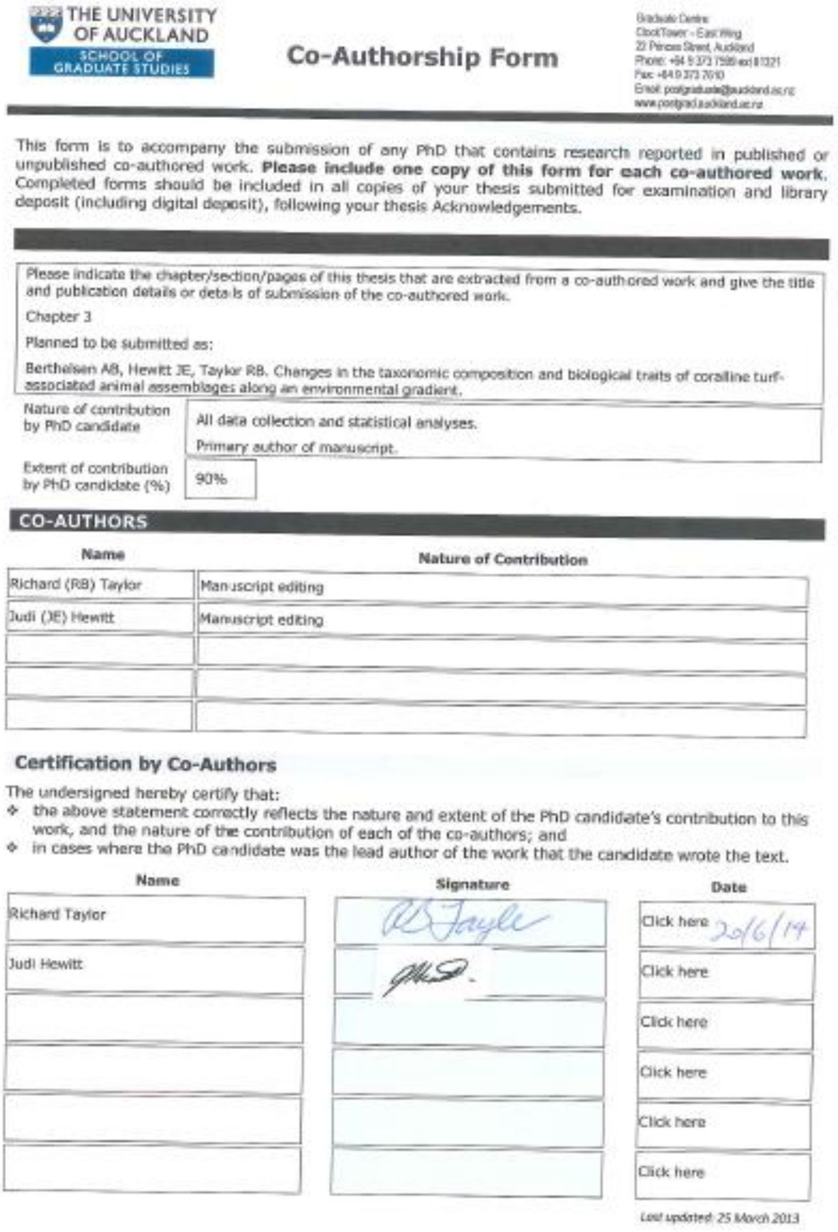

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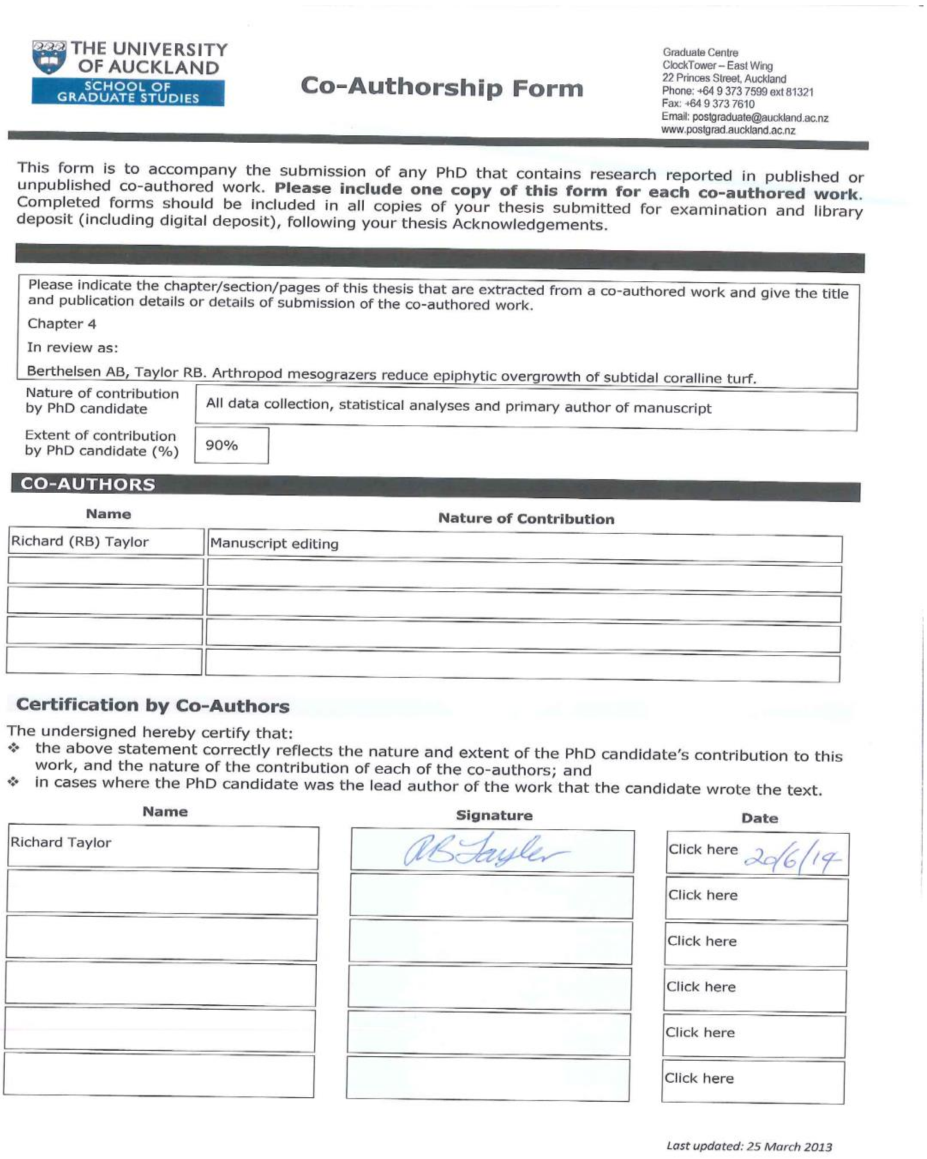

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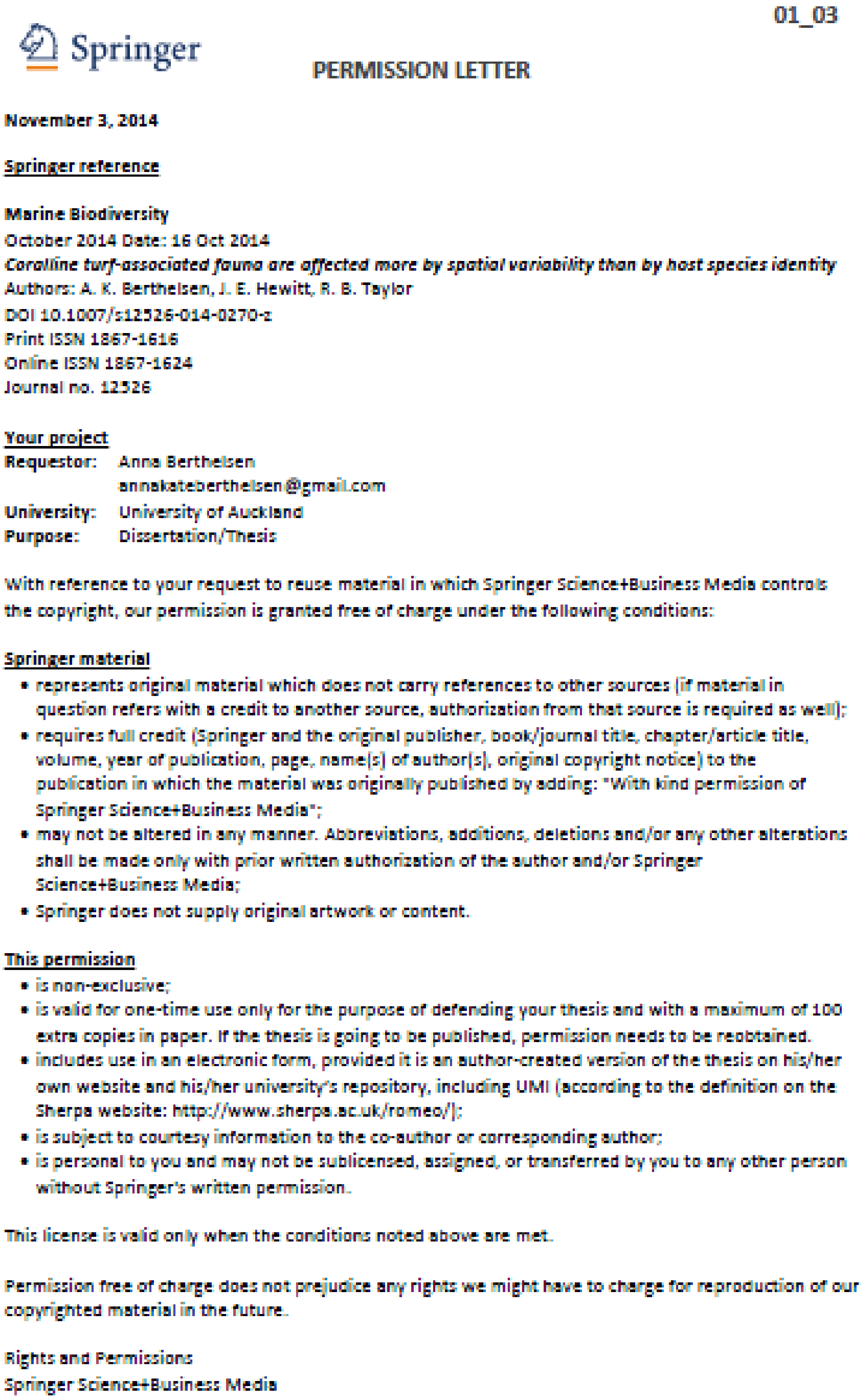

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Your project
Requestor: Anna Berthelsen
annakateberthelsen@gmail.com
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Chapter 1. General Introduction

1.1. Small mobile invertebrates and their interactions with marine macrophytes

Small (< 10 mm) mobile invertebrates are ubiquitous in shallow coastal habitats (Cowles et al. 2009). They are taxonomically diverse, with peracarid crustaceans (e.g., amphipods and isopods), molluscs and polychaetes being numerically dominant (Russo 1997, Brawley 1992, Taylor & Steinberg 2005). On temperate rocky reefs, small mobile invertebrates comprise > 95% of animal individuals in some habitats, and contribute significantly to secondary productivity (Edgar & Moore 1986, Taylor 1998). They play a number of important ecological roles, one of which is linking primary producers to higher trophic levels such as fish (Pomeroy 1979, Edgar & Moore 1986). Small mobile invertebrates dominate the diets of most small fishes, including juveniles of larger species (Jones 1988, Holbrook & Schmitt 1988). Small mobile invertebrates are also important as nutrient regenerators (Taylor & Rees 1998) and consumers (Brawley 1992), and can structure algal communities through herbivory (Poore et al. 2012).

Small animals often use plants for food and shelter, so the physical structure and food value of plants has a strong influence on the distribution, abundance and diversity of their associated fauna (Macarthur & Macarthur 1961, Bell et al. 1991). Marine macrophytes, which include both seaweeds and seagrasses, are used as a living space by many small mobile invertebrates (Hacker & Steneck 1990). They gain protection from predators (Coull & Wells 1983, Holmlund et al. 1990) and environmental stressors such as wave disturbance (Hagerman 1966, Fenwick 1976, Caine 1977). Seaweeds and seagrasses present a diverse array of shapes and sizes and can differ greatly in surface area and complexity. Many studies have investigated the relationships between phytal-living small invertebrates and morphological features of marine macrophytes, and often those that are more finely-structured, i.e. more complex, are found to support high densities (e.g., Edgar 1990, Russo 1990, Duffy & Hay 2000), and diversities (e.g., Chemello & Milazzo 2002) of small invertebrates. Ecological theory suggests that morphologically similar macrophyte taxa can be classified into functional groups that provide similar habitat for animals (Steneck & Dethier 1994), and that closely-related macrophyte taxa are more likely to perform similar functions. However some studies have found little evidence for this in regards to small mobile invertebrate assemblages on seaweeds (e.g., Bates 2009) and seagrasses (e.g., Hamilton et al. 2012). Habitat structure also indirectly influences animals by affecting other factors important for their survival. For example, algal epiphytes and detritus associated with macrophyte hosts are important food sources for invertebrates (Edgar & Moore 1986, Duffy 1990) and hosts that are more finely-structured may provide a larger surface area for algal epiphytes to grow (Edgar 1991a) and are more likely to trap detritus amongst their fronds (Hicks 1986).

Invertebrates living on marine macrophytes are also strongly influenced by the physical environment (Edgar & Moore 1986), which can impact them directly, e.g., dislodgment by waves (Dommasnes 1968, Tararam & Wakabara 1981) or smothering by sediment (Huff & Jarett 2007). Environmental variables may also affect macrophyte-dwelling invertebrates indirectly by altering other factors, such as food availability. For example, epiphytic algae are a less productive food source in deeper water where light levels are lower (Edgar 1991b) and the rate of supply of food in the water column, utilised by suspension feeders, is a function of water motion (Hagerman 1966, Fenwick 1976, Caine 1977). Interactions between these variables and the morphology of the host macrophyte are complex and can modify suitability of the macrophyte as a habitat for animals. For example, fine sediments are more likely to accumulate in wave-sheltered habitats and within the branches of finely-structured macrophytes (Prathep et al. 2003).

The impacts of small animals on marine macrophytes are still poorly understood (Poore et al. 2009). They may be negative if the animals feed directly on the host tissue (Duffy 1990, Poore et al. 2014), or positive if they assist with host spore dispersal (Buschmann & Santelices 1987), feed on algal epiphytes (Duffy 1990), or provide nitrogen through their faeces (Bracken & Nielsen 2004). Marine benthic herbivores strongly affect primary productivity (Poore et al. 2012). However, most research has focussed on larger animals such as fish and urchins (e.g., Leighton 1966, Andrew & Jones 1990, Taylor & Schiel 2010). Small invertebrates living amongst marine macrophytes can eat the tissue of their hosts, although it is more common for them to instead feed on algal epiphytes associated with their host (Bell 1991). The reduction of algal epiphytes through herbivory may benefit the host, as epiphytes can compete with the host for resources such as light and/or nutrients (van Montfrans et al. 1984), and also increase the risk of frond breakage (D’Antonio 1985). The overgrowth of marine macrophytes by algal epiphytes is becoming increasingly common in shallow coastal habitats due to anthropogenic impacts such as elevated nutrient levels from land run-off (Myers & Heck 2013). The ability of mesograzers to control the growth of algal epiphytes on marine macrophytes is important as this could benefit the health of the macrophytes (Reynolds et al. 2014). Evidence is emerging that mesograzers often exert strong grazing pressure on marine macrophytes (Poore et al. 2012). This evidence is derived from field observations (e.g., Tegner & Dayton 1987), mesocosm experiments (e.g., Duffy & Hay 2000, Newcombe & Taylor 2010) and field experiments (e.g., Brawley & Fei 1987, Davenport & Anderson 2007, Cook et al. 2011, Poore et al. 2014, Whalen et al. 2013).

1.2. Coralline turf

Algal turfs are widespread on tropical and temperate rocky reefs and shores, and often form conspicuous mats (Connell et al. 2014) that are structurally complex and comprise tightly packed thalli that trap sediment (Stewart 1989) (Fig. 1.1). In many places worldwide algal turfs are becoming more prevalent, likely due to anthropogenic impacts (Connell et al. 2014). Algal turfs can be composed of articulated, or geniculate, coralline algae (Phylum Rhodophyta, order Corallinales) (Nelson 2009), as well as other foliose species. Coralline turfs play an important role in the global carbon cycle by depositing calcium carbonate (Nelson 2009). Coralline turfs, as well as the bacterial films attached to their fronds, are also important as settlement cues for many invertebrates (Huggett et al. 2008, Williams et al. 2008). However, one of their most important roles is as ecosystem engineers (Nelson 2009), with their three-dimensional structure providing a habitat for many small animals. Coralline turf species can be morphologically plastic in response to their environment (Dommasnes 1968). This feature, as well as their ability to be present in a variety of forms (e.g., turfs and crusts) has meant that the taxonomic identity of many coralline turf species is uncertain (Akioka et al. 1999).

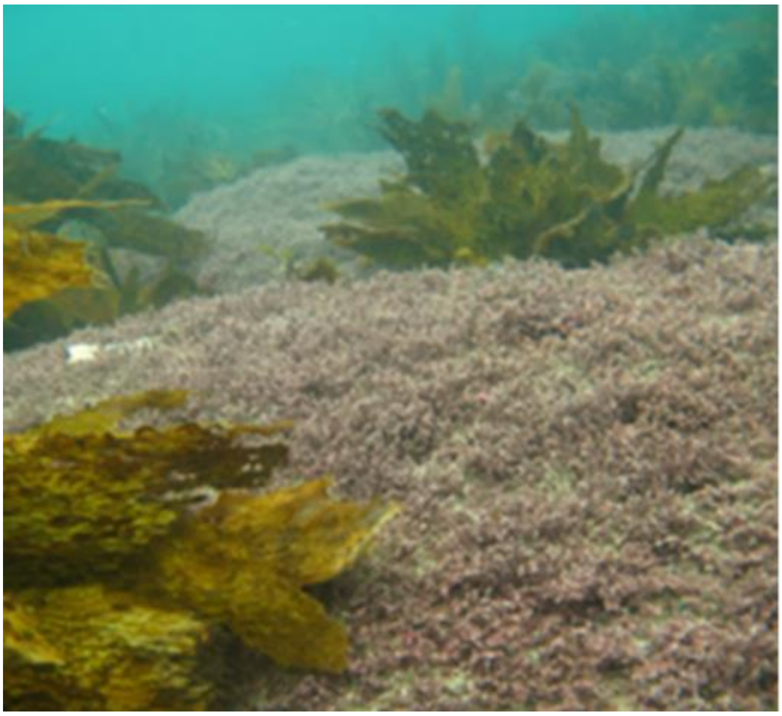

Figure 1.1 Subtidal *Corallina officinalis* turf in northeastern New Zealand.

1.3. Turf as a host for small mobile invertebrates

Coralline turfs are host to an extremely abundant assemblage of small invertebrates (Akioka et al. 1999, Grahame & Hanna 1989, Kelaher & Castilla 2005), whose densities can exceed 2 x 10^5 ind.m^{-2} (Choat & Kingett 1982). Out of 34 coastal habitats in northeastern New Zealand, subtidal coralline turf held the highest densities of small mobile invertebrates (Cowles et al. 2009). These invertebrates are diverse and inhabit not only the fronds of the turf (epifauna) (Fig. 1.2) but also the sediment within the turf (infauna) (Kelaher et al. 2001). The invertebrate assemblages of intertidal coralline turfs are well studied (e.g., Akioka et al. 1999, Kelaher et al. 2001, Kelaher & Castilla 2005), but relatively little attention has been paid to the fauna in subtidal coralline turfs (but see Dommasnes 1968, Choat & Kingett 1982, Taylor 1998, Cowles et al. 2009, Cowles 2010).

In common with other finely-structured macrophytes, coralline turfs protect animals from stresses such as predation (Coull & Wells 1983) and water movement (Dommasnes 1968, Fretter & Manly 1977), and also provide a platform from which invertebrates can suspension feed (Hicks 1971). Although the calcareous coralline fronds are unpalatable to most small invertebrates (Taylor & Steinberg 2005), the turfs are likely to provide them with food sources such as algal epiphytes growing on the fronds (Stewart 1982, Akioka et al. 1999), as well as detritus trapped amongst the turf matrix (Hines 1982, Crisp & Mwaiseje 1989). Turf morphology has a strong influence on the richness, diversity and density of small invertebrate assemblages within intertidal coralline turfs (e.g., Grahame & Hanna 1989, Bussell et al. 2007).

Besides the turf structure, environmental variables also strongly influence the distribution of small invertebrates within intertidal coralline turfs (Kelaher et al. 2001, Kelaher & Castilla 2005). Coralline turfs can trap large quantities of sediment within their matrix and occupy sites varying greatly in wave-exposure, with these two physical factors particularly influential on invertebrate communities within coralline turfs (e.g., Dommasnes 1968, Huff & Jarett 2007). As with other macrophytes, it is likely that complex interactions occurring between environmental variables and the turf structure can modify the turf habitat for invertebrates. Therefore coralline turfs, which can comprise coralline species that differ morphologically (Padilla 1984) and occupy sites subject to varying environmental factors (Kelaher & Castilla 2005), are likely to present differing habitats for small invertebrates. The relative effects of host algal species and site-related environmental variables on habitat suitability for small invertebrates within subtidal coralline turf, is currently unknown. One reason for this is that in ecological studies, taxonomic uncertainty often necessitates the lumping of coralline species to the broad level of ‘coralline turf’ (e.g., Connell et al. 2014).

A method that may offer new insight into relationships between small invertebrates, their coralline turf hosts and the physical environment involves describing invertebrate communities by their biological traits. This is because the biological traits, such as those relating to morphology, behaviour and life history, of organisms can either directly or indirectly influence ecosystem function (Diaz & Cabido 2001). As the biological traits exhibited by different organisms cannot necessarily be predicted by taxonomic relatedness, they have the potential to provide greater insight into community functioning than can be inferred from the taxonomic composition of the community (Bremner et al. 2003, Frid et al. 2008). Biological traits analysis (BTA) was originally developed for freshwater (e.g., Townsend & Hildrew 1994, Doledec et al. 1999) and terrestrial ecosystems (e.g., Olff et al. 1994, McIntyre et al. 1995). The focus of BTA in marine systems has largely been on soft-sediment fauna (e.g., Bremner et al. 2003, Hewitt et al. 2008, Oug et al. 2012), with studies often investigating anthropogenic impacts such as fishing (e.g.,Tillen at al. 2006) and dredging (e.g., Bolam 2014). Comparatively little attention has been paid to hard substrate habitats (but see Munari 2013), including the fauna living amongst seaweeds attached to these substrates (but see Thrush et al. 2011, Törnroos et al. 2013).

1.4. The impact of small mobile invertebrates on turf

Differences in palatability between macrophyte hosts and their epiphytes can strongly influence the outcome of interactions between mesograzers and their hosts (Duffy 1990, Poore 1994). Although little is known about the impacts of small animals on coralline turf it is likely that negative effects from the direct consumption of coralline tissue are probably negligible due to the unpalatability of turf fronds for many mesograzers (Taylor & Steinberg 2005, Taylor & Brown 2006). It is therefore likely that mesograzers instead feed on other sources of primary productivity within the turf. This could include algal epiphytes, which commonly grow on turf fronds (Stewart 1982, Kelaher et al. 2001) and are important food items for mesograzers in other habitats (Brawley & Fei 1987, Edgar 1993, Jernakoff & Nielsen 1998). If mesograzers can control the abundance of epiphytes growing on the turf, it is possible that the relationship between these and their host coralline is mutualistic, as the mesograzers would derive food in the form of algal epiphytes, along with shelter from predators (Coull & Wells 1983) and wave action (Dommasnes 1968), while the turf would be kept free of fouling organisms (Duffy 1990, Hay et al. 2004).

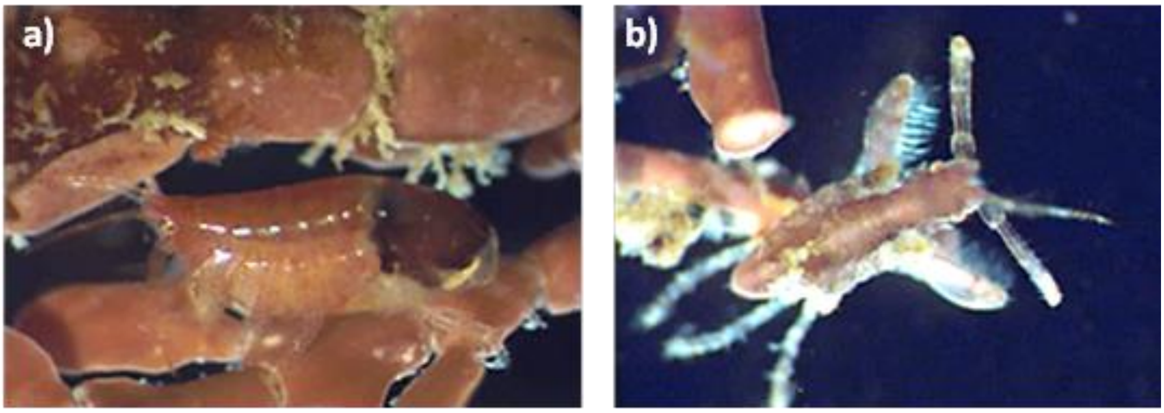

Figure 1.2 Small mobile invertebrates interacting with coralline turf fronds a) ischyrocerid amphipod, b) podocerid amphipod.

1.5. Aims

This thesis aims to elucidate interactions between small mobile invertebrates and subtidal coralline turfs on shallow reefs in warm-temperate northeastern New Zealand. These interactions involve the influence of the turf structure and environmental factors on invertebrate communities, and also the impact of the invertebrates on the turf. The structure of small mobile invertebrate assemblages is quantified and compared between different coralline host species and sites, while both the taxonomic composition and biological traits of assemblages are compared along an environmental gradient. Densities of small arthropods are experimentally reduced in order to determine their impact on the abundance and composition of epiphytes growing on the turf.

The objectives of this thesis are to:

Determine whether coralline turf is a homogeneous habitat for small mobile invertebrates (Chapter 2). A recently published taxonomic guide to coralline algae in northern New Zealand by Farr et al. (2009) allows a closer investigation of the impacts of coralline host identity on fauna. The faunal assemblages of five coralline turf species are sampled from several sites, with more than one coralline species sampled from most individual sites, in order to determine the relative and interactive effects of coralline species and spatial variation on faunal assemblages.

Examine variation in the taxonomic composition and biological traits of faunal assemblages in subtidal coralline turf along an environmental gradient (Chapter 3). The relative sensitivities of biological traits and taxonomic composition to an environmental gradient (driven by wave exposure, depth and sediment) are determined for coralline turf-dwelling fauna.

Determine the impacts of fauna on subtidal coralline turf (Chapter 4). Small arthropods are excluded *in situ* from subtidal coralline turf for over 100 days using a cageless method. The resulting impacts of arthropod exclusion on the abundance and composition of algal epiphytes growing on the turf are quantified.

Chapter 2. Faunal Assemblages in Relation to Coralline Host Identity and Spatial Variation in Environmental Factors

2.1. Introduction

Coralline algal turfs are inhabited by a diverse and highly abundant community of small mobile invertebrates (Cowles et al. 2009, Kelaher & Castilla 2005) that make a major contribution to reef-wide secondary production (Taylor 1998) and are an important food source for higher trophic levels such as fishes (Choat & Kingett 1982, Wellenreuther & Connell 2002). It is important, therefore, to understand the factors influencing variation in turf-dwelling fauna. At any one site coralline turf habitat can comprise a number of algal species (e.g., Hicks 1971, Kelaher et al. 2001) that may vary considerably in morphological properties relevant to associated fauna (Dommasnes 1968, Grahame & Hanna 1989). Together, frond height, width, and biomass per unit area influence the amount of surface area available for epiphytic algal food to grow on (Edgar 1993), the suitability of the turf as a platform from which to suspension feed (Hicks 1971), and the degree of refuge provided from wave action (Dommasnes 1968) and predators (Coull & Wells 1983). The morphology of the turf is also likely to affect its propensity to trap detritus, which is another potential food source (Hicks 1986), and inorganic sediment, which provides an additional habitat for infauna (Kelaher et al. 2001). Spatial variation in environmental factors may modify the effects of these algal properties on fauna. For example, epiphytic algae are a less productive food source in deeper waters where light levels are lower (Edgar 1991), suspension feeders are often more numerous at wave-exposed sites (Fenwick 1976), and fine sediments inhabited by infauna tend to accumulate more at wavesheltered sites (Prathep et al. 2003). Lumping of coralline algal species in ecological studies is common, often necessitated by difficulties with distinguishing individual taxa (Johansen & Womersley 1986, Connell et al. 2014). However, this practice potentially overlooks important differences in the value of turf species as habitat for fauna. Knowing whether it is possible to generalise about faunal assemblages inhabiting different turf species will be particularly important in the future, as turfs are expanding globally (Connell et al. 2014). I took advantage of recent taxonomic work on the New Zealand flora (Farr et al. 2009) to examine variation in fauna across five well defined coralline turf species found on subtidal rocky reefs in northeastern New Zealand. By sampling each coralline turf species from several sites, and sampling more than one coralline turf species from most individual sites, I was able to determine the relative and interactive effects of coralline species and spatial variation on the fauna.

2.2. Materials and Methods

2.2.1 Sites and sampling

Study sites were situated on the moderately wave-exposed, shallow rocky reefs between Okakari Point and Cape Rodney (36° 16’S, 174° 47’E) in temperate northeastern New Zealand (Fig. 2.1). Sites were chosen for the presence of as many coralline turf species as possible. The other major features at the sites were stands of brown macroalgae, dominated by *Ecklonia radiata* (C. Agardh) J. Agardh and/or *Carpophyllum flexuosum* (Esper) Grev. Five coralline turf species were sampled: *Amphiroa anceps* (Lam.) Decne., *Corallina officinalis* L., “*Corallina* sp. 1” of Farr et al. (2009), *Jania rosea* (Lam.) Decne. (“feather form” sensu Farr et al. 2009), and *Jania sagittata* (J.V. Lamour.) Blainv. (Fig. 2.2). Each species was sampled at three sites (except for *Jania rosea*, sampled at two sites). A total of seven sites were sampled as not all coralline species were present at the same three sites. Depths ranged from 0.7 - 7.2 m depth below chart datum (~extreme low water spring). Samples were collected during autumn 2011. Turf and associated fauna were scraped from within a haphazardly-selected 78.5-cm^2 area of turf using the suction sampler of Taylor et al. (1995) with 0.2-mm mesh sampling bag (n = 4 samples per coralline turf species-site combination). In association, sediment samples (n = 3) were collected by sliding a knife under a 13.9-cm^2 container pushed into the turf down to the underlying rock, collecting any remaining sediment with a syringe, and placing the overall sample in a ziploc bag. Turf frond height was measured *in situ* next to each sample with a ruler (n = 3). The relative wave exposure of each site was estimated by summing fetch values (to a maximum of 300 km) at 10° intervals.

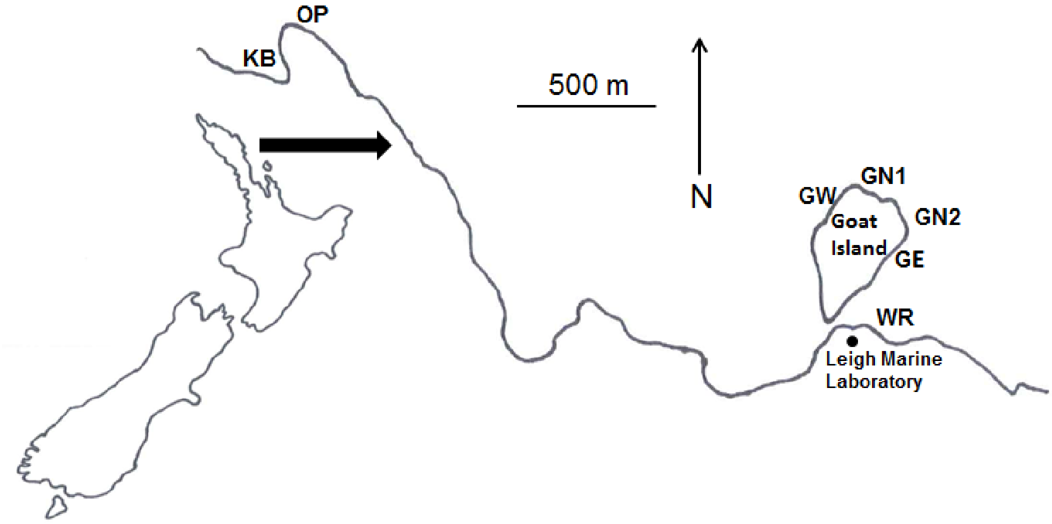

Figure 2.1 Sites around Goat Island in northeastern New Zealand from which coralline turf-dwelling small mobile invertebrates were sampled. Full site names are Kempts Bay (KB), Okakari Point (OP), Goat Island east (GE), Goat Island north 1 (GN1), Goat Island north 2 (GN2), Goat Island west (GW) and Waterfall Reef (WR).

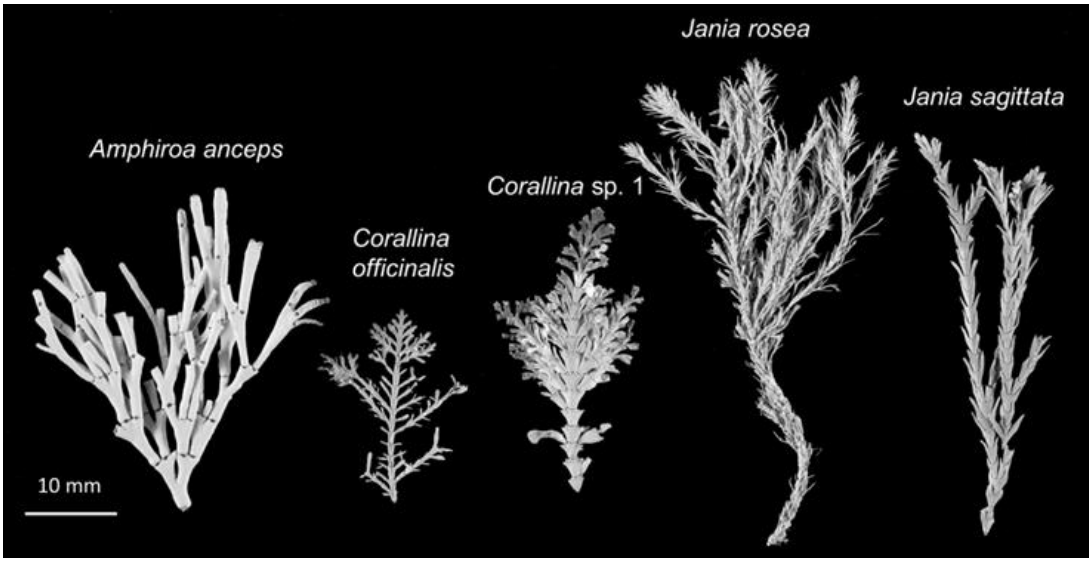

Figure 2.2 Coralline turf species examined in this study (from northeastern New Zealand).

2.2.2 **Laboratory analyses**

After collection, faunal and sediment samples were preserved in GLYO-FIXX (Titford & Horenstein 2005) and 70% isopropyl alcohol respectively. Faunal samples were later washed with tap water to separate fauna from the coralline fronds over an 8-mm, and then 1-mm, sieve. All mobile invertebrates retained on the 1-mm sieve were identified as far as possible (see Gordon 2009, 2010 for taxonomic authorities) and counted. The few individuals retained on the 8-mm sieve, usually consisting of hermit crabs, nereid polychaetes and ophiuroids, were discarded. Turf thallus width was estimated by measuring the widths of ten thalli haphazardly chosen from one frond from each sediment sample, and pooling the resulting values to obtain an overall mean (e.g., Taylor & Cole 1994). To quantify algal biomass, all coralline turf fragments were picked out of each sediment sample and then oven-dried to a constant weight at 60°C. To quantify sediment, all sediment was wet-sieved into three size fractions; coarse (> 1 mm), medium (0.5-1 mm) and fine (0.125-0.5 mm), and oven-dried as above.

2.2.3 **Statistical analyses**

Significant differences in the morphology (frond height, thallus width, algal biomass) of the different coralline species were determined using one-way ANOVA and Holm-Sidak Pairwise comparisons, with data log-transformed to meet assumptions when required. Faunal richness and evenness were calculated as the total number of taxa and the proportional abundance of the most abundant taxon (Berger & Parker 1970), respectively. Relationships between abundance, richness and evenness and physical/turf structural variables were determined using Pearson correlations (r) based on replicate data. Differences in the abundance, richness and evenness of faunal assemblages from different coralline species at different sites were tested for with a two-factor, mixed-model (with 'coralline species' as a fixed factor and 'site' nested within 'coralline species'), permutation-based, analysis of variance (ANOVA) (Anderson et al. 2008) using Euclidean distance matrices based on square-root transformed data (Clarke & Gorley 2006).

Differences in the composition of faunal assemblages (with numbers of individual taxa standardised to a proportion of total abundance) were tested for with non-parametric permutational multivariate analysis of variance (PERMANOVA), run on Bray-Curtis dissimilarity matrices based on fourth-root transformed data. Fourth-root transformation was used to down-weight the importance of abundant fauna (Clarke & Gorley 2006) as the main purpose of multivariate analyses was to determine patterns in the taxonomic composition, rather than in the abundance (which was analysed separately as a univariate statistic), of fauna. A two-factor fixed PERMANOVA design was used to compare between the groups of coralline species present at > 1 sites (i.e., *Jania sagittata* and *Jania rosea* at Goat Island north 2 and Okakari Point, and *Amphiroa anceps* and *Corallina* sp. 1 at Goat Island east and west and Waterfall Reef). A mixed-model PERMANOVA (with 'coralline species' as a fixed factor and 'site' nested within 'coralline species') was used to compare the faunal assemblages between all coralline species and all sites. Faunal assemblage patterns based on the data above were visualised using Principal Coordinates Analysis (PCO). Vectors were used to display highly correlated (vector length ≥ 0.75) faunal taxa, and all environmental variables, to the above assemblage patterns. Vector lengths (= $\sqrt{}$(PC12 + PC22) (Anderson et al. 2008) were based on Pearson correlations of mean ($n = 4$) proportional faunal abundance (data fourth-root transformed) and mean ($n = 3$) environmental variable (data normalised) with mean PC1 and PC2 values calculated from the above PCO.

A DistLM (distance-based linear model) (Anderson et al. 2008) was conducted to determine the ability of factors relating to the physical environment and coralline morphology to explain patterns in faunal assemblages. In order to run this analysis, replicate numbers were balanced by removing all faunal replicates that were not paired with an environmental replicate (so that $n = 3$, rather than 4). The environmental variable 'percentage of coarse sediment' was excluded prior to DistLM analysis as it was very strongly correlated ($r = -0.96$) with 'percentage of fine sediment' (Clarke & Gorley 2006). The DistLM model used a stepwise selection procedure and adjusted r^2 selection criterion, and was based on Bray-Curtis resemblance matrices from fourth-root proportional faunal abundance data, and normalised environmental/turf morphology data. As a draftsman plot indicated that the fetch data was skewed, it was log-transformed prior to DistLM in order to stabilise the variance (Clarke & Gorley 2006). All multivariate analyses (and permutation-based ANOVAs) were conducted using the software package PRIMER v.6 (Clarke & Gorley 2006) and its add-on PERMANOVA+ (Anderson et al. 2008).

2.3. Results

2.3.1 Coralline turf morphology and environmental variables

Mean (pooled across sites) frond heights for each coralline species ranged from 15.6 ± 2.1 SE mm (*Corallina officinalis*) to 59.2 ± 5.5 mm (*Jania rosea*) and were significantly different ($F_4 = 28.2$, $p < 0.001$ pairwise comparisons not shown for this and subsequent analyses) (Fig. 2.3a). Mean (pooled across sites) thallus widths ranged from 0.33 ± 0.04 SE mm (*J. rosea*) to 1.34 ± 0.05 mm (*Corallina* sp. 1) and were significantly different between all species except for *Corallina* sp. 1 and *Amphiroa anceps* ($F_4 = 85.0$, $p < 0.001$) (Fig. 2.3b).

Mean (pooled across sites) algal biomass ranged from 0.50 ± 0.09 SE kg.m^{-2} (*C. officinalis*) to 1.56 ± 0.39 kg.m^{-2} (*A. anceps*) and was significantly different between *C. officinalis* and all other species ($F_4 = 6.8$, $p < 0.001$) (Fig. 2.3c). Sites differed considerably in exposure to wave action, with fetch values ranging from 133 km (Kempts Bay) to 2609 km (Goat Island north 1) (Fig. 2.3d). Mean depth (pooled across coralline species) ranged from 0.93 ± 0.12 SE (Kempts Bay) to 5.1 ± 0.47 m (Goat Island east) (Fig. 2.3e). Mean total sediment (pooled across coralline species) ranged from 281.4 ± 132 SE g.m^{-1} (Goat Island north 1) to 2676.4 ± 940.7 SE g.m^{-1} (Goat Island east) (Fig. 2.3f). Although percentages of fine, medium and coarse sediment were variable within sites, mean values per site ranged from 14.7% (Goat Island north 1) to 62.6% (Kempts Bay) for fine sediment, 11.2% (Okakari Point) to 20% (Waterfall Reef) for medium sediment, and 24.1% (Kempts Bay) to 71.6% (Goat Island north 2) for coarse sediment (Fig. 2.3g).

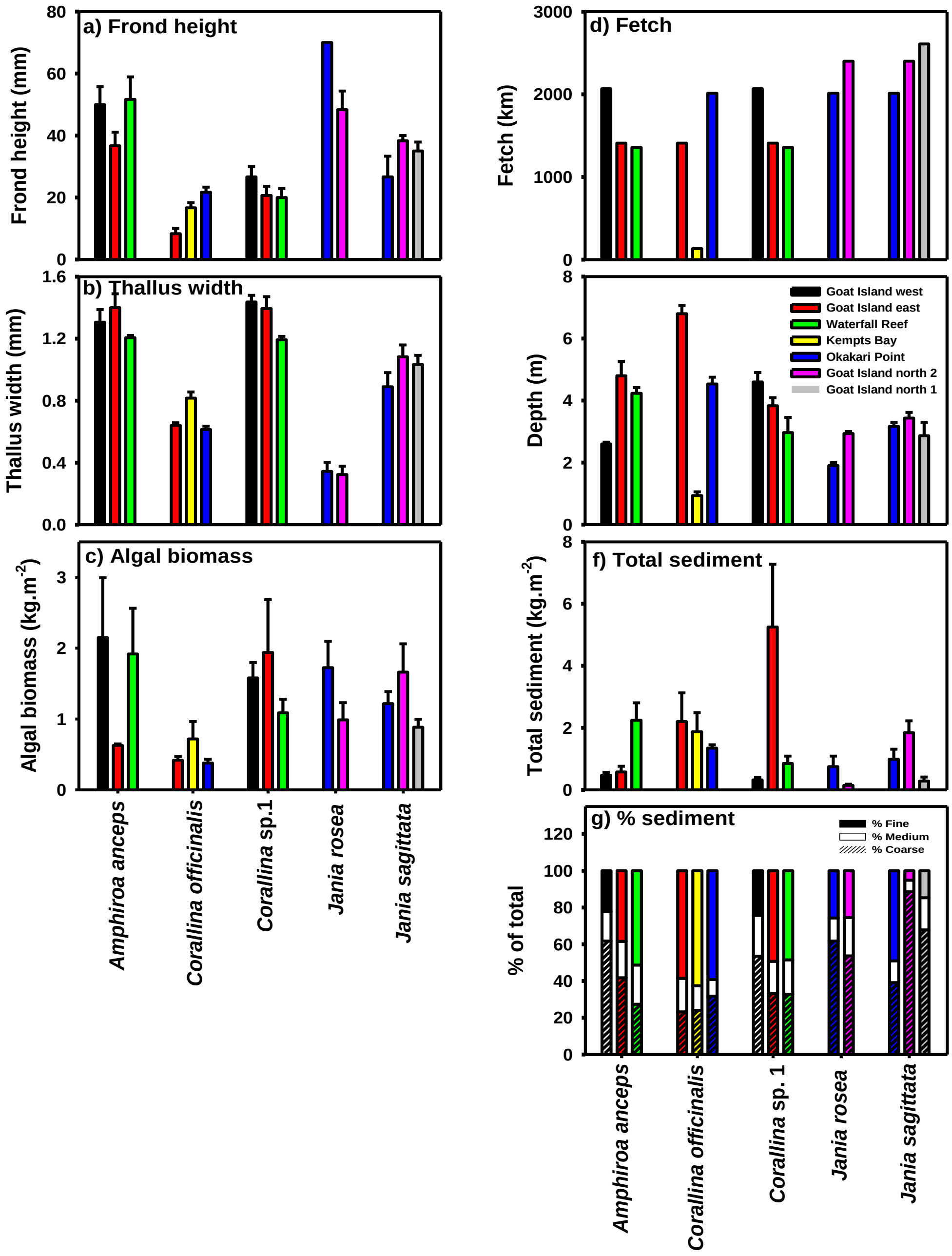

Figure 2.3 Features of the morphological structure of five coralline species (a-c) and physical site-related factors (d-h) in subtidal coralline turf on shallow rocky reefs in northeastern New Zealand (mean + SE, n = 3 for graphs with error bars).

2.3.2 **Abundance, richness and evenness**

Mean (per site/coralline species combination) total animal abundance ranged from 16,173 ± 858 (SE) to 80,069 ± 5877 ind.m^{-2} and differed significantly between sites ($F_9 = 7.4$, $p = 0.001$) but not between coralline species ($F_4 = 1.0$, $p > 0.5$) (Fig. 2.4a). Mean (per site/coralline species combination) richness ranged from 24.3 ± 0.48 (SE) to 41.5 ± 2.6 taxa and also differed significantly with site ($F_9 = 6.18$, $p = 0.001$) but not between coralline species ($F_4 = 0.51$, $p > 0.5$) (Fig. 2.4b). The mean proportion of the total fauna comprised of the most abundant taxon (i.e., evenness) ranged from 15 ± 2.7% (SE) to 42 ± 2.6% and did not significantly differ between coralline species ($F_4 = 3.2$, $p > 0.05$) or sites ($F_9 = 2.1$, $p = 0.05$) (Fig. 2.4c). 129 taxa were recorded, including 60 arthropods (of which 29 were amphipods), 48 gastropods, 13 polychaetes, 6 echinoderms, 1 nematode and 1 nemertean (Appendix 2.1). Amphipods, molluscs (mostly gastropods) and polychaetes were the most abundant groups, comprising 43%, 20% and 15% of individuals across all sites and coralline species (Fig. 2.4d).

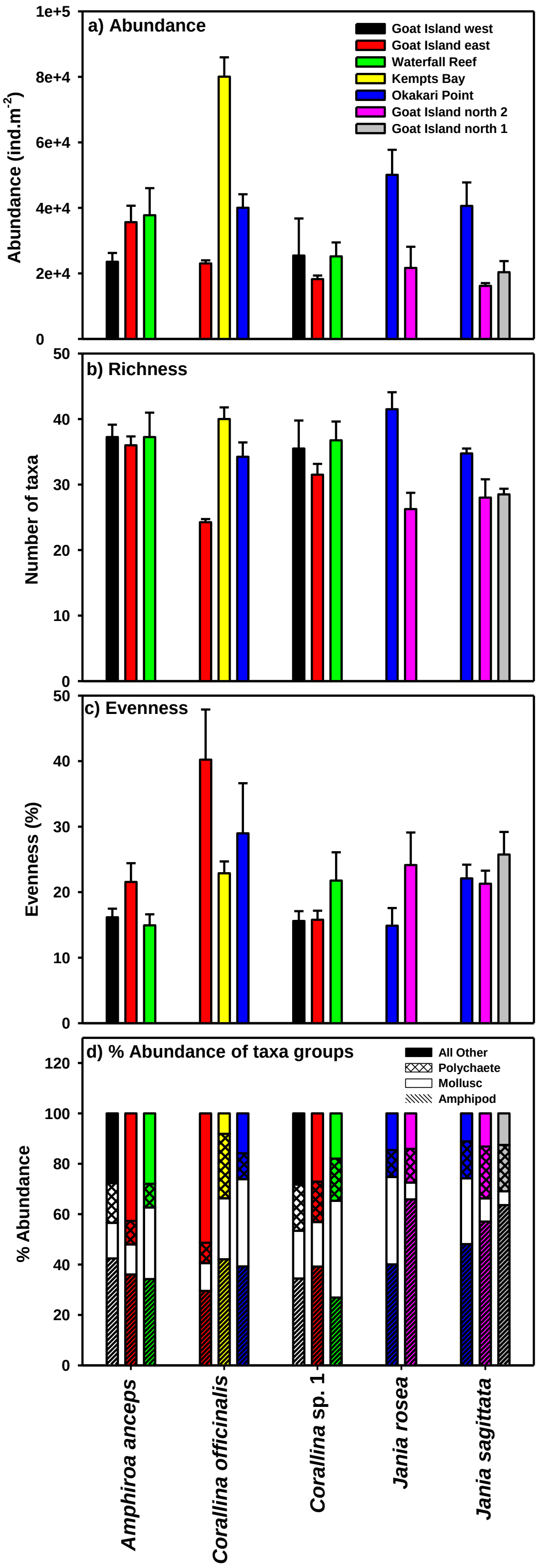

Figure 2.4 The mean (n = 4, + SE for graphs with error bars) abundance (a), richness (b), evenness (c) and % composition of taxa groups (d) of small (1-8 mm) mobile invertebrates inhabiting different subtidal coralline turf species at different sites in northeastern New Zealand. See Fig. 2.1 for full site names.

2.3.3 **Composition of faunal assemblages**

For each coralline species/site combination, the ten most abundant faunal taxa comprised 64-82% of total individuals (Fig. 2.5). Rankings of these top ten taxa (39 in total) showed few consistent patterns across either coralline species or sites. Of the total number of taxa, 63 (49%) taxa were considered common (> 20 individuals sampled) while 66 (51%) were rare (< 20 individuals sampled in total). There was a general lack of host specificity, with all common taxa occurring on two or more host coralline turf species and with 49 (78%) of these found on all five coralline species. Site specificity was also low, with all common taxa occurring at two or more sites and with 53 (84%) of these found at five or more sites. The most frequently occurring taxa (each found in ≥ 95% of samples) were *Nereis falcaria* and Syllidae (polychaetes) and *Podocerus karu* and *Gammaropsis* sp. (amphipods).

Strong differences in assemblage composition were detected by the fully-crossed site/species combination PERMANOVA (e.g., *A. anceps* vs *Corallina* sp. 1, and *J. rosea* vs *J. sagittata*), as the main effects of these were all significant with significant interactions also occurring between site and species (Table 2.1a,b). Overall, a mixed-model PERMANOVA, which included faunal assemblages from all species and all sites (nested within species), showed that site (32.2%) explained more of the variation in faunal assemblages than did coralline turf species (13.2%) (Table 2.1c). Patterns existed in multivariate space with faunal assemblages (based on proportional abundance) clustering loosely together in regards to both coralline turf species and site (Fig. 2.6a,b).

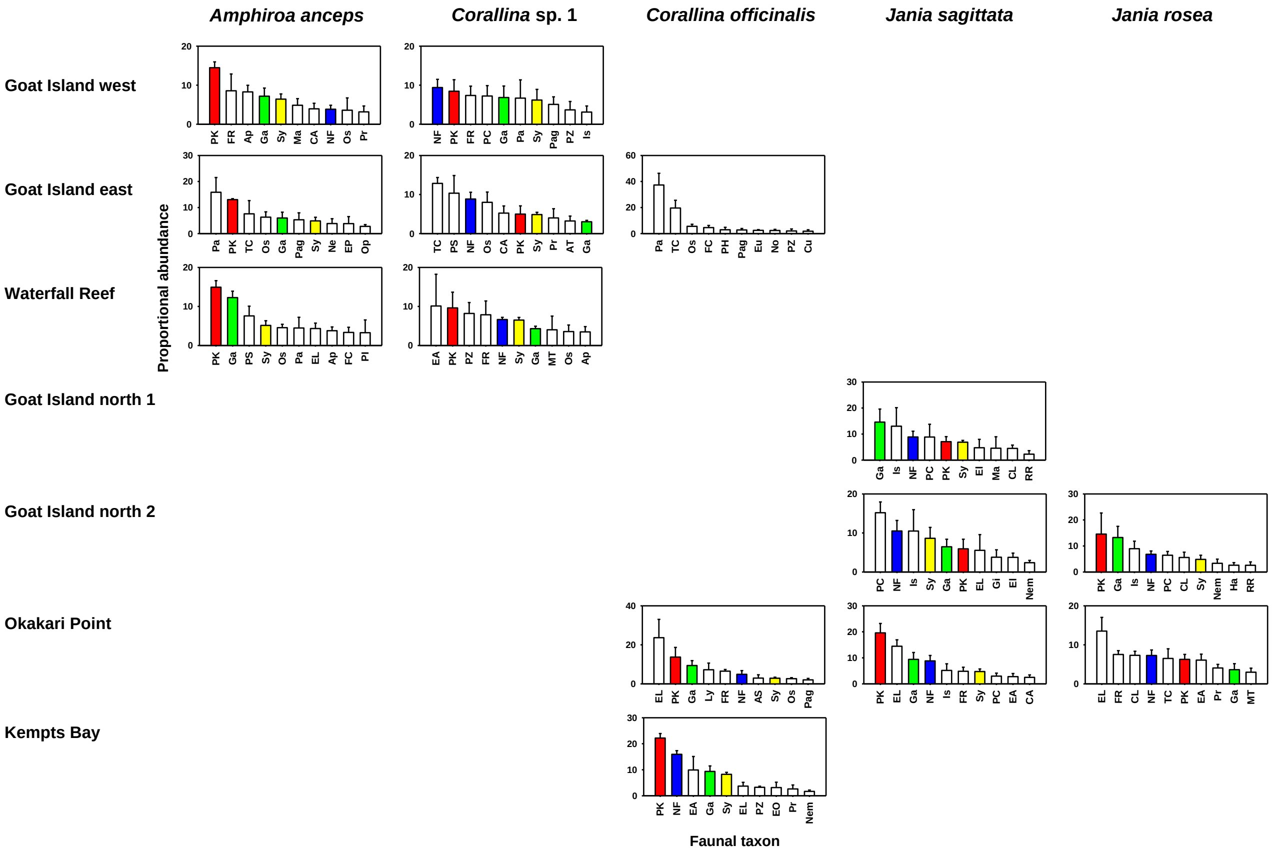

Figure 2.5 The ten most proportionally abundant faunal taxa (mean, n = 4 + SE) found at different coralline species/site combinations on shallow subtidal reefs in northeastern New Zealand. Frequently occurring (≥ 10 times amongst the coralline/site combinations) taxa are coloured: *Podocerus karu* (PK) = red, *Gammaropsis* sp. (Ga) = green, Syllidae (Sy) = yellow, *Nereis falcaria* (NF) = blue. All of the rest are white: Apseudidae (Ap), *Amphipholis squamata* (AS), *Aora typica* (AT), *Cassidinopsis admirabilis* (CA), *Caprellina longicollis* (CL), Cumacea (Cu), *Eatoniella albocolumella* (EA), *Eatoniella limbata* (EL), *Elasmopus* spp. (El), *Eatoniella olivacea* (EO), *Ericthonius pugnax* (EP), *Eunice* sp. (Eu), *Fictonoba rufolactea* (FR), *Fictonoba carnosa* (FC), *Gitanopsis* sp. (Gi), *Halicarcinus* spp. (Ha), Ischyroceridae (Is), Lysianassidae (Ly), *Maera* sp. (Ma), *Merelina taupoensis* (MT), *Neastacilla* sp. (Ne), Nematoda (Nem), *Nothria* sp. (No), Ophiuroidea (Op), Ostracoda (Os), *Pagurapseudes* sp. (Pa), Paguridae (Pag), *Parapherusa crassipes* (PC), *Paradexamine houtete* (PH), *Pisinna olivacea impressa* (PI), *Protohyale* spp. (Pr), *Pisinna semiplicata* (PS), *Pisinna zosterophila* (PZ), *Raumahara rongo* (RR), *Tetradeion crassum* (TC).

Table 2.1 PERMANOVA results comparing the faunal assemblage composition (1-8 mm) of different coralline turf species, on shallow reefs in northeastern New Zealand.

a) *Amphiroa anceps* and *Corallina* sp. 1 (coralline species) and Goat Island east and west and Waterfall Reef (sites): two-factor fixed design.

	df	MS	Pseudo-F	P(perm)	% variation
Coralline	1	2451.9	2.8	0.001	8.7
Site	2	2669.2	3.0	0.001	14.8
Coralline x site	2	1964.9	2.2	0.001	17.9
Residual	18	884.7			58.6
Total	23				

b) *Jania rosea* and *Jania sagittata* (coralline species) and Okakari Point and Goat Island north 2 (sites): two-factor fixed design.

	df	MS	Pseudo-F	P(perm)	% variation
Coralline	1	697.7	1.0	0.43	0.3
Site	1	5328.1	7.9	0.001	45.6
Coralline x site	1	754.6	1.1	0.33	1.6
Residual	12	671.5			52.6
Total	15				

c) All coralline species (x 5) (fixed) at all sites (x 7) (nested) - two-factor mixed model design.

	df	MS	Pseudo-F	P(perm)	% variation
Coralline	4	4715.7	1.8	0.043	13.2
Site (coralline)	9	2611.7	3.6	0.001	32.2
Residual	42	778.1			54.6
Total	55				

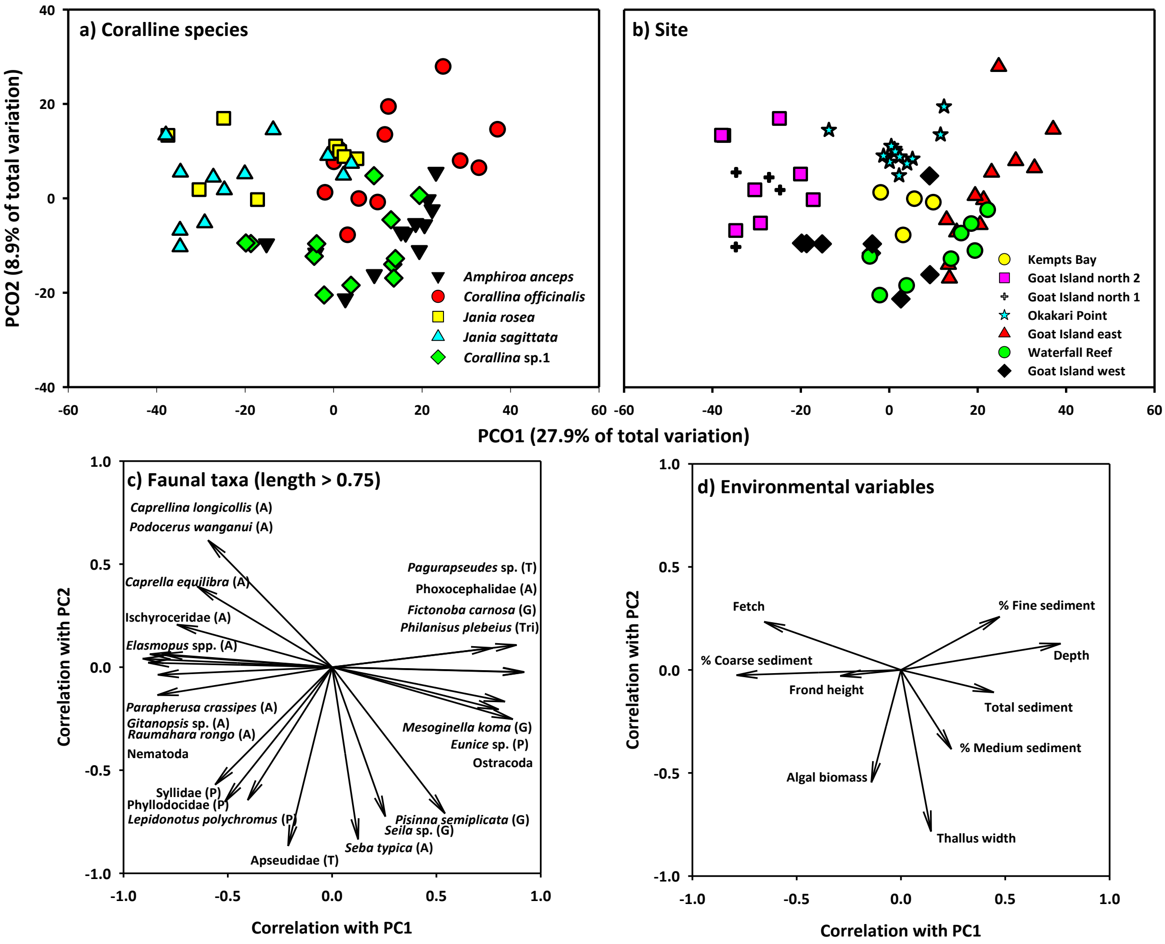

Figure 2.6 **Principal coordinates analysis (PCO) of faunal assemblages (1-8 mm) based on proportional abundance from five coralline turf species at different sites (n = 4 per coralline/site combination) colour-coded by coralline species (a) and site (b), with correlation vectors for fauna (vector length ≥ 0.75) (c) and environmental variables (all vectors) (d) - see methods for details.**

2.3.4 **Environmental influences on faunal assemblages**

Environmental variables and turf morphology explained little variation in faunal abundance and richness, as the only correlation r > |0.5| between these was the one occurring between abundance and fetch (r = -0.59). Faunal taxa that were correlated with certain sites and coralline species clustered into three main groups, and these were associated with particular environmental/turf morphological variables (Fig. 2.6c,d). *Mesoginella koma*, *Fictonoba carnosa*, Ostracoda, *Philanisus plebeius*, *Pagurapseudes* sp., *Eunice* sp. and Phoxocephalidae were all positively correlated with percentage fine sediment, total sediment and depth, and negatively correlated with percentage coarse sediment, fetch and frond height. *Pisinna semiplicata*, *Seila* sp., Apseudidae, *Lepidonotus polychromus*, Phyllodocidae, Syllidae and *Seba typica* were positively correlated with percentage medium sediment, algal biomass and thallus width. *Caprellina longicollis*, *Caprella equilibra*, *Podocerus wanganui*, *Elasmopus* sp., *Raumahara rongo*, *Parapherusa crassipes*, *Gitanopsis* sp., Ischyroceridae and Nematoda were positively correlated with fetch, percentage coarse sediment and frond height, and negatively correlated with depth, percentage fine sediment and total sediment. DistLM found significant correlations of faunal assemblage composition with fetch (13.9%), depth (11.7%), thallus width (6.3%), frond height (3.9%), percent fine sediment (3.0%), and total sediment (2.7%), with these six variables explaining 31.5% (adjusted r^2) of total variation (Table 2.2).

Table 2.2 **DistLM (stepwise, adjusted r^2) sequential test based on replicate (n = 3) proportional abundance of faunal assemblages (fourth-root, Bray-Curtis resemblance) associated with five coralline turf species and associated physical/turf structural variables (normalised).**

	Pseudo-F	P	% variation	% cumulative variation
Fetch	6.4	0.001	13.9	13.9
Depth	6.2	0.001	11.7	25.6
Thallus width	3.5	0.001	6.3	31.9
Frond height	2.3	0.006	3.9	35.8
% Fine sediment	1.7	0.032	3.0	38.8
Total sediment	1.6	0.046	2.7	41.6
Adjusted r^2 = 31.5%				

2.4. Discussion

To my knowledge, this study is the first to compare the faunal assemblages of different subtidal coralline turf species. In my study system, the total abundance and richness of turf-associated fauna varied much more in space than with host species identity, justifying the lumping of turf species for the study of these assemblage properties, which in the case of total abundance may be a reasonable indicator of the value of a habitat as a foraging ground for fish (e.g., Choat & Kingett 1982, Wellenreuther & Connell 2002). However, the taxonomic compostion of the fauna differed significantly across both host turf species and sites, reflecting potentiallyimportant differences in the functioning of theassemblages (e.g., Thrush et al. 2011) that would be obscured by lumping.

Although the taxonomic composition of faunal assemblages varied across host turf species, differences were mostly due to changes in the relative abundances of taxa rather than the presence/absence of particular taxa, and there was little evidence of host-specificity. All common taxa occurred on at least two host species, and most were found on all five host species. The unpalatable calcareous nature of coralline turf (Taylor & Steinberg 2005) may have contributed to this, as host specificity, although relatively rare amongst algal-dwelling fauna (Hay et al. 1990), is usually due to consumption of host tissues (Poore et al. 2000). Herbivorous coralline turf fauna likely eat mostly epiphytic algae (Edgar 1993) and/or detritus (Thrush et al. 2011), so will be largely unaffected by intrinsic properties of their host. Although not quantified during this study, it is possible that the composition and/or abundance of algal epiphytes and detritus influence the taxonomic composition of turf-associated faunal assemblages. The close taxonomic relatedness of the turf species (all belonging to the family Corallinaceae) may also have contributed to the lack of host-specificity in the fauna.

The absence of clear patterns in assemblage composition across sites was surprising, given the significant influence of site on faunal assemblages. Relationships between algal properties and environmental variables are complex (Prathep et al. 2003), and the significant interaction detected between turf species and site in this study likely contributed to the lack of predictable patterns in assemblage composition across both species and sites. The overall generalist nature of the fauna (relative to site and coralline turf species), which was dominated by amphipods, gastropods and polychaetes, suggested they occupy broad niches (as in Thrush et al. 2011), and the very high frequency of occurrence of some taxa (*Podocerus karu*, *Gammaropsis* sp., *Nereis falcaria*, Syllidae) indicated their resilience to habitat variability. The variation in total abundance and richness (but not dominance) across sites, but not coralline species, indicated that differences in the morphology of coralline species did not significantly influence these assemblage properties.

However, despite high variability, subtle patterns in assemblage composition associated with coralline species and sites were apparent. High correlations between physical factors, and the propensity of some coralline species to inhabit different physical habitats/sites, e.g., short-fronded corallines were not present at wave-exposed sites, made it difficult to isolate the influence of individual variables on assemblages. Also, correlations with turf structure may have been confounded with other turf properties (Kelaher et al. 2001), e.g., bacterial biofilms on turf fronds can induce invertebrate settlement (Huggett et al. 2008) and chemicals within algal tissue can deter fauna (Poore & Steinberg 1999). Assemblages at wave-exposed sites (which were also shallower and contained longer-fronded corallines) were distinguished by a number of amphipod taxa, whose ability to cling to algal fronds and/or build tubes can reduce the risk of dislodgment from waves (Tararam & Wakabara 1981). Many were suspension feeders (*Podocerus wanganui*, Ischyroceridae, *Caprellina longicollis* and *Caprella equilibra*), or were commensal on sessile suspension-feeding organisms (*Raukumara rongo*), and likely benefitted from a greater supply of food in the water column brought by wave action (Fenwick 1976), and the reduced levels of fine sediment (negatively correlated with fetch), which can clog feeding apparati (Airoldi 2003). Herbivorous amphipods, e.g., *Elasmopus* sp. and *Parapherusa crassipes* (F. Melitidae) (J. Thomas pers. comm.), at these sites were likely advantaged by conditions conducive to algal growth, such as the increased light in shallower depths (Gambi et al. 1992) and the potential of longer fronds to provide more area for epiphyte attachment (Taylor & Cole 1994).

Many of the fauna characterising assemblages at wave-sheltered sites with high sediment loads in this study are adapted to live in sediment (e.g., the polychaete *Eunice* sp., the amphipod family Phoxocephalidae, and the gastropod *Fictonoba carnosa carnosa*), and can use sediment as both a habitat (Kelaher et al. 2001) and a source of food (Olabarria & Chapman 2001).

The majority of fauna that distinguished assemblages at sites associated with higher proportions of medium sediment (also higher algal biomass and wider thalli) belonged to higher trophic levels, e.g., the polychaetes *Lepidonotus polychromus* and Phyllodocidae, are carnivores and/or scavengers, while the gastropod *Seila* sp. is thought to eat sponges. Infaunal assemblages inhabiting medium/coarse sediment often contain high numbers of carnivores, which may feed on the animals living amongst the interstitial spaces within the sediment (Muniz & Pires 1999). The variables appearing to influence faunal assemblages in subtidal coralline turfs in this study also do so in intertidal turfs, e.g., fetch (Dommasnes 1968), depth within tidepools (Bussell et al. 2007), sediment (Kelaher & Castilla 2005) and frond morphology (Grahame & Hanna 1989).

Site-related factors strongly influenced faunal abundance and richness in this study. The most abundant and rich assemblages were from Kempts Bay, the most wave-sheltered site, which was also shallow and contained a high proportion of fine sediment. The extra habitat (Kelaher et al. 2001) and food provided by the sediment (Olabarria & Chapman 2001) may have supported these abundant and rich assemblages. The lack of influence of site-related variables on dominance contrasts with other studies on algal-dwelling fauna that found a negative association between evenness and sediment (Kelaher & Castilla 2005) and wave exposure (Fenwick 1976).

Overall, my results indicate that faunal assemblages within subtidal coralline turfs are more strongly structured by site-related physical factors than by turf-related properties (e.g., as in Kelaher et al. 2003 for intertidal turfs), suggesting that turf species may be safely lumped for sampling for certain monitoring purposes and for investigating particular ecological questions (assuming my results are generalisable to other regions). However, the influence of turf species identity on faunal composition mandates a species-specific approach for a fuller understanding of turf fauna interactions. In this study host identity and spatial variation did not explain all variation detected in the taxonomic composition of faunal assemblages, suggesting the influence of other unquantified factors. These merit further research, and are likely to include biotic processes such as predation (Coull & Wells 1983, Worthington & Fairweather 1989, Hayakawa et al. 2012) and competition (Matias et al. 2012).

Chapter 3. The Structure and Function of Coralline Turf-Dwelling Fauna Along an Environmental Gradient

3.1. Introduction

The functioning of ecosystems is dependent on the organisms that inhabit them (Diaz & Cabido 2001).This is because the biological traits, i.e., aspects of behaviour, life history and morphology, of these organisms have the ability to either directly or indirectly influence ecological functioning (Frid et al. 2008). As the biological traits exhibited by organisms can not necessarily be predicted by taxonomic relatedness, they have the potential to provide greater insight into community functioning than can be inferred from the taxonomic composition of the community (Bremner et al. 2003, Frid et al. 2008). Originally developed for freshwater (e.g., Townsend & Hildrew 1994, Doledec et al. 1999) and terrestrial (e.g., Olff et al. 1994, McIntyre et al. 1995) ecosystems, biological traits analysis (BTA) is increasingly being applied to marine habitats (Bolam & Eggleton 2014), where it is often used to determine the response of communities to natural and anthropogenic variation in environmental factors (e.g., Bremner et al. 2006b, Bremner 2008, Paganelli et al. 2012). In the sea, BTA has largely been used on soft-sediment faunal assemblages (e.g., Bremner et al. 2003, Hewitt et al. 2008, Oug et al. 2012), mostly to investigate functional responses to human impacts such as fishing (e.g., Tillin et al. 2006) and dredging (e.g., Bolam 2014). Comparatively little attention has been paid to animals inhabiting marine hard substrates (but see Munari 2013,) including the fauna living amongst seaweeds attached to these substrates (but see Thrush et al. 2011, Törnroos et al. 2013). Algal turfs occur on shallow rocky substrates worldwide and in many areas are increasing in abundance, likely due to environmental changes induced by anthropogenic impacts such as eutrophication (Connell et al. 2014). They host an abundant and diverse assemblage of small (<10 mm) mobile invertebrates (Taylor 1998, Kelaher & Castilla 2005, Cowles et al. 2009) that contribute strongly to the flux of materials through reef ecosystems (Taylor 1998), and are an important food for higher trophic levels such as many fish species (Choat & Kingett 1982). Due to the ecological significance of turf-associated animals, and the global prevalence of turfs, it is important to determine whether changes in the physical environment influence the functioning of these animal assemblages. Previous studies have highlighted the strong influence of environmental variables on the structure of turf-dwelling animal assemblages (Dommasnes 1968, Kelaher & Castilla 2005). I aimed to determine the relative sensitivities of biological traits and taxonomic composition, and overall animal abundance, to an environmental gradient driven by variation in physical factors and host morphology, for small mobile invertebrates inhabiting subtidal coralline turf.

3.2. Methods

3.2.1 Field

I sampled seven sites spanning ~8.5 km along the southern coast of the Tawharanui Peninsula in warm temperate northeastern New Zealand (36°S, 174°E; Fig. 3.1). Reefs at the eastern end of the peninsula were wave-exposed, deep, and relatively free of fine sediment, while reefs at the western end were wave-sheltered, shallow, and subject to sedimentation. The reefs were dominated by coralline turf (*Corallina officinalis*) and brown macroalgae (mostly the laminarian *Ecklonia radiata* and fucaleans of the genus *Carpophyllum*).

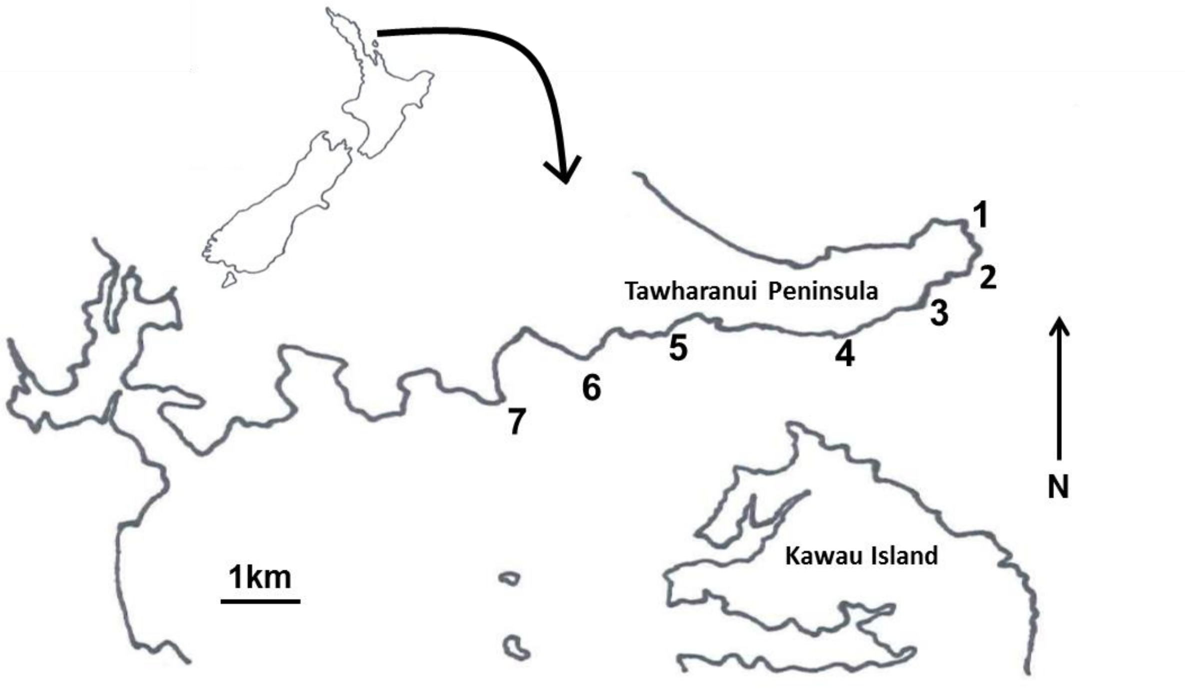

Figure 3.1 Study sites along the southern side of the Tawharanui Peninsula in northeastern New Zealand: (1) Takatu Point, (2) Elephant Point, (3) Bluebell Point, (4) Unnamed Point, (5) Matatuahu Point, (6) Motutara Point, and (7) Karangatuoro Point.

During autumn 2012, samples were taken from patches of *Corallina officinalis* (the only coralline turf species present) between the depths of 0-10 m (below mean low tide). At each of the seven sites, coralline turf and associated fauna were scraped and vacuumed from a haphazardly-selected 50.3 cm^2 area (n = 5) into a 0.2-mm mesh bag, using the suction sampler of Taylor et al. (1995). In association, sediment samples (n = 5) were collected by sliding a knife under a 13.9-cm^2 container pushed through the turf down to the underlying rock, collecting any remaining sediment with a syringe, and placing the overall sample in a ziploc bag. Lengths of five fronds from each turf patch were also measured *in situ*. The relative wave exposure of each site was estimated by summing fetch values (to a maximum of 300 km) at 10° intervals. The depth-averaged maximum tidal current speed for each site at a 1 km by 1 km grid was available from www.mfe.govt.nz/publications/ser/marine-environment-classification-jun05/.

3.2.2 **Laboratory**

Faunal samples were washed through an 8-mm mesh sieve to establish an upper size limit for the individuals studied. The few individuals retained on the 8-mm sieve, usually consisting of hermit crabs, nereid polychaetes and ophiuroids, were not considered further. Animals < 8mm were washed over a 1-mm mesh sieve, and all mobile invertebrates retained were identified as far as possible (see Gordon 2009, 2010 for taxonomic authorities) and counted. These were also washed over a 2.8-mm mesh sieve to split them into size classes for traits analysis. Fauna < 1mm were excluded from this study due to the difficulty of identifying small individuals. Turf fronds were removed from sediment samples and oven-dried at 60°C for 48 hours to determine dry weight. The remaining sediment from each sample, from which large fauna were also removed, was wet-sieved into three size fractions: coarse (> 1 mm), medium (0.125-1 mm) and fine (0.063-0.125 mm), each of which was oven-dried at 60°C to determine dry weight. Turf frond widths were measured for ten thalli haphazardly chosen from one frond per faunal sample, and the resulting values pooled to obtain an overall mean value per frond (as in Taylor & Cole 1994).

3.2.3 **Biological Traits**

Faunal assemblages were defined using eight biological trait categories (encompassing 23 traits) based on morphology, size, life history and behaviour (Table 3.2).

All trait categories were chosen for their ability to influence ecological functioning (as recommended by Frid et al. 2008), although choice of these was limited by information availability. The definitions of traits within each trait category were carefully considered in order for these to be relevant to all fauna found associated with the turf during this study. Trait information was derived from the literature (Appendix 3.1), with the exception of size and body form, which were determined during the study. If information on a taxon was unavailable I used the most closely related taxon for which data existed. If no information was available (this occurred for < 1% of traits) equal values were given across all traits. If taxa exhibited a number of traits within a category, fuzzy coding (Chevenet et al. 1994) was applied, where values were assigned to multiple traits within each category such that they summed to 1 (as in Hewitt et al. 2008). Each trait score for each taxon was then multiplied by the abundance of that taxon, and these abundance-weighted values summed across all taxa within each replicate to gain a frequency value for each trait. These values were expressed as a proportion of the total number of individuals in the replicate to prevent variation in total abundance from obscuring trends in composition.

3.2.4 **Statistical Analyses**

I used one-way analysis of variance (ANOVA) to test for differences in faunal abundance and richness (defined as the total number of taxa) between sites, and Holm-Sidak pairwise comparisons to investigate any significant differences. Data were tested for normality and homogeneity of variance, and log-transformed to meet these assumptions if necessary. Correlations between aspects of faunal assemblages (abundance, richness, proportional abundance of taxonomic groups and proportional abundance-weighted trait frequencies) and the environmental gradient (distance of each site from the easternmost site, Takatu Point) were determined using Pearson correlations based on site means. The strengths of relationships between frequencies of proportional abundance-weighted traits and individual environmental/turf morphology variables were also determined using Pearson correlations on replicate-level data. To examine patterns in taxonomic composition, the abundances of taxa (at the replicate level) were converted to the proportion of total individuals that they comprised in their sample. These data were fourth-root transformed then subjected to a principal coordinate's analysis (PCO) run on a Bray-Curtis dissimilarity matrix (Anderson et al. 2008). Fourth-root transformation was used to down-weight the importance of abundant fauna (Clarke & Gorley 2006) as the main purpose of multivariate analyses were to determine patterns in the taxonomic composition, rather than in the abundance (which was analysed separately as a univariate statistic), of faunal assemblages. Vectors were used to display correlated taxa (vector length ≥ 0.6) and traits (vector length ≥ 0.7), and all environmental variables, to the above assemblage patterns. Vector lengths (= √(PC12 + PC22) (Anderson et al. 2008) were based on Pearson correlations of proportional faunal abundance (data fourth- root transformed) and environmental variables (data normalised).The same analysis was performed on the abundance-weighted biological traits data (also scaled by total abundance). The ability of environmental variables to explain patterns in taxonomic and traits composition was determined using a distance-based linear model (DistLM). The variable ‘percent medium sediment’ was excluded from this due to its strong ($r = - 0.88$) Pearson correlation with ‘percent coarse sediment’ (Clarke & Gorley 2006). The DistLM model used a stepwise selection procedure and adjusted r^2 selection criterion and was based on the same biological data, transformations and similarity measures used in the PCO analyses and environmental/turf morphology data (normalised). All multivariate analyses were run using the software package PRIMER v.6 (Clarke & Gorley 2006) and its associated add-on PERMANOVA+ (Anderson et al. 2008).

3.3. Results

3.3.1 Environmental Gradient

Environmental factors and turf structure changed to varying degrees along the Tawharanui Peninsula (Fig. 3.2a-h). Fetch ($r^2 = 0.69$), depth ($r^2 = 0.65$), and thallus width ($r^2 = 0.43$) had a strong negative relationship with distance from Takatu Point (the wave-exposed easternmost site), while algal biomass ($r^2 = 0.70$), percentage fine sediment ($r^2 = 0.58$) and frond height ($r^2 = 0.35$) had a positive relationship with distance from Takatu Point. Relationships with distance from Takatu Point were weak ($r^2 < 0.2$) for percentage medium sediment, current speed, total sediment, and percentage coarse sediment.

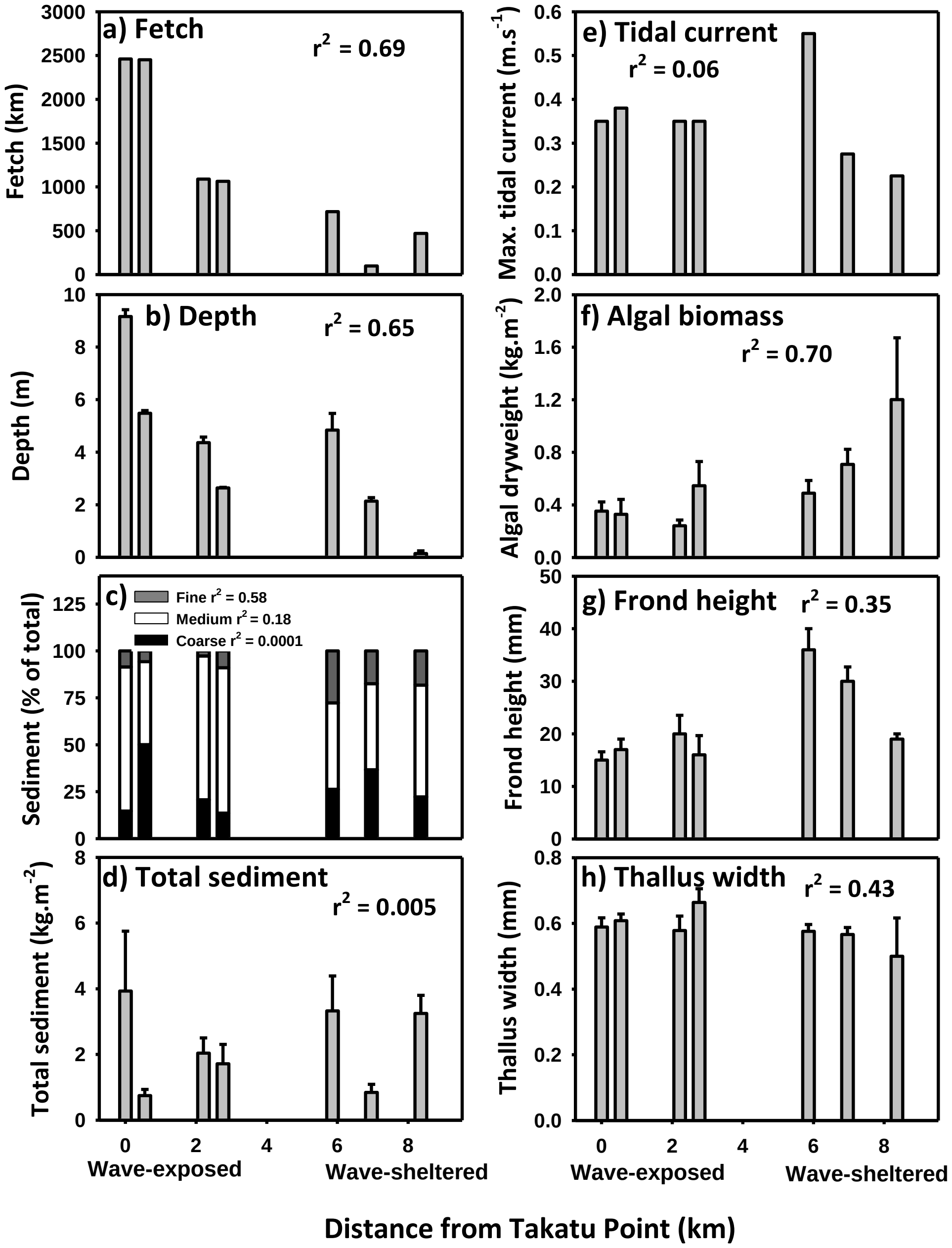

Figure 3.2 Environmental variables and features of algal morphology associated with subtidal *Corallina officinalis* turf at sites located along the southern side of Tawharanui Peninsula in northeastern New Zealand. Bars represent mean + SE, n = 5. Sediment size fractions are defined as; coarse sediment (1 mm), medium (0.125 - 1 mm) and fine (0.125 - 0.63 mm).

3.3.2 Abundance and Taxonomic Richness

A total of 118 mobile taxa (size 1-8 mm) were recorded from subtidal *C. officinalis* (Appendix 3.1). These included arthropods (56 taxa), molluscs (44 gastropods and 2 bivalves), polychaetes (11 taxa), echinoderms (4 taxa) and nematodes (1 taxon). Total abundance had a strong negative relationship with distance from Takatu Point ($r^2 = 0.57$), with site means ranging from 12,225 ± 1,355 SE ind.m^{-2} at the wave-sheltered end to 53,643 ± 4,203 SE ind.m^{-2} at the wave-exposed end, and significant differences existing amongst the sites (one-way ANOVA: $F_6 = 11.83$, $p < 0.001$) (Fig. 3.3a). Richness also had a negative relationship with distance from Takatu Point ($r^2 = 0.38$), with site means ranging from 20.2 ± 2.2 to 33.2 ± 1.5 SE total taxa (Fig. 3.3b). Richness only differed significantly between sites 3 and 6 (One-way ANOVA: $F_6 = 3.49$, $p = 0.01$, pairwise comparisons not shown). Arthropods and molluscs (mostly gastropods) were numerically dominant at all sites, and relationships between each of the broad taxonomic groups and the environmental gradient were relatively weak ($r^2 < 0.4$) (Fig. 3.3c).

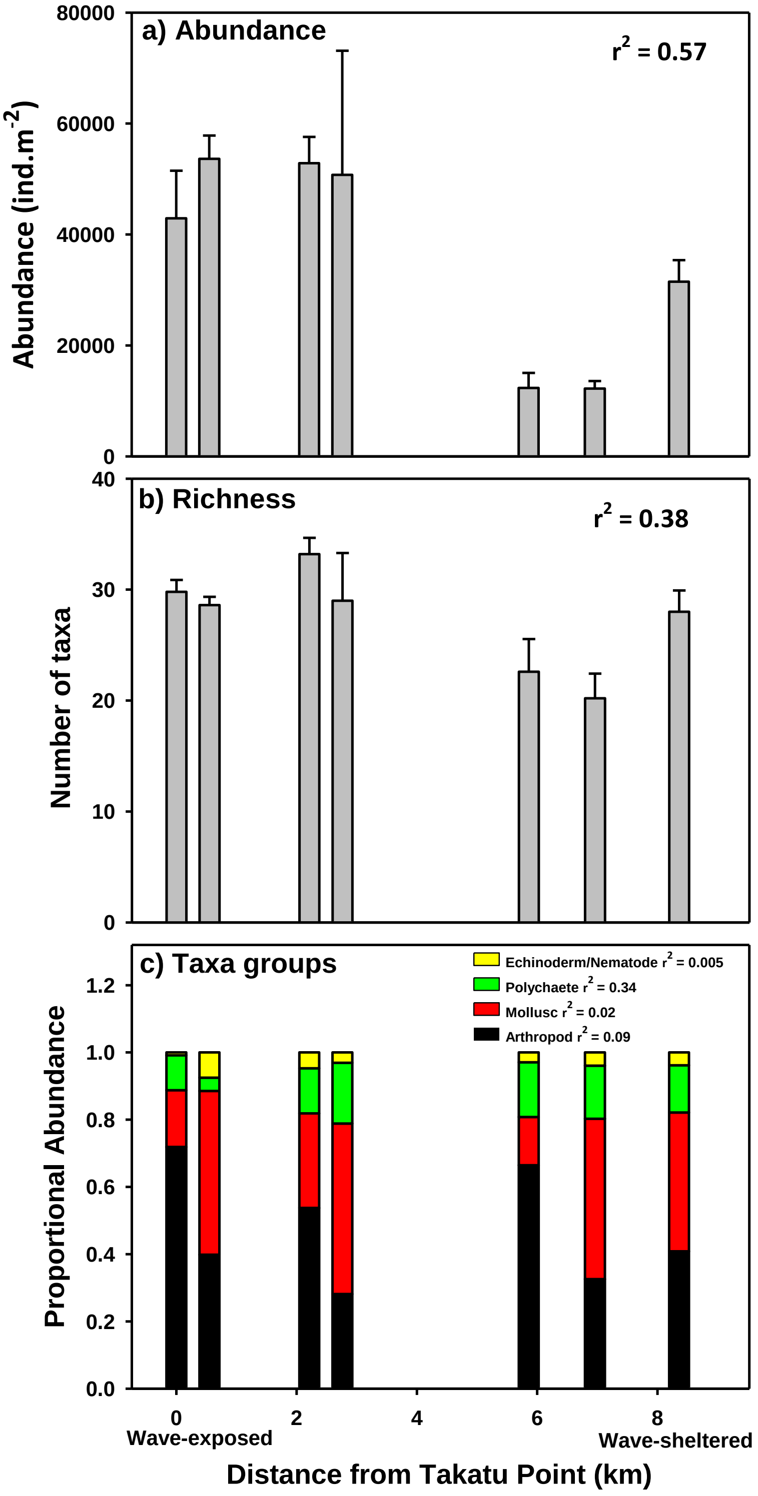

Figure 3.3 Abundance (a), taxonomic richness (b), and proportional abundance of broad taxonomic groups (c) of small mobile invertebrates inhabiting subtidal *Corallina officinalis* turf at sites along an environmental gradient on Tawharanui Peninsula in northeastern New Zealand. Bars represent mean + SE, n = 5.

3.3.3 **Taxonomic Composition**

The PCO run on relative abundances of taxa showed moderately tight clustering of replicates by site, with wave-sheltered sites grouping on the left end of the X-axis (i.e., more negative values of principal coordinate (PC 1) and wave-exposed sites on the right (Fig. 3.4a). Within each of those groupings the sites were ordered along PC 2 according to their distance from Takatu Point (i.e., 5-7 for the wave sheltered sites and 1-4 for the wave-exposed sites). A combination of environmental variables (physical factors and turf morphology) explained 39% of variation in taxonomic composition (DistLM adjusted r^2 = 0.39), and of these fetch (19% of variation) and current speed (10% of variation) were the most powerful (Table 3.1a). Vectors representing taxa whose abundances were highly correlated (vector length > 0.6) with PC 1 and/or PC 2 clustered into five main groups in multivariate space. Relative abundances of *Podocerus karu*, *Gammaropsis* sp., *Protohyale* sp., *Cyclaspis* sp. and *Fictonoba rufolactea* were positively correlated with depth, fetch and total sediment. Ostracoda, *Eatoniella limbata*, *Neolepton antipodum*, *Eatoniella olivacea*, *Fictonoba carnosa*, *Pisinna zosterophila*, Syllidae and *Merelina taupoensis* were positively correlated with % medium sediment and thallus width. Nuculidae and *Rissoina* sp. were positively correlated with algal biomass and negatively correlated with fetch, depth and total sediment. *Pisinna semiplicata*, *Paradexamine houtete* and Paguridae were positively correlated with frond height, percentage fine sediment and percentage coarse sediment and negatively correlated with thallus width and percentage medium sediment while Corophiidae was positively correlated with current speed (Fig. 3.4b,c).

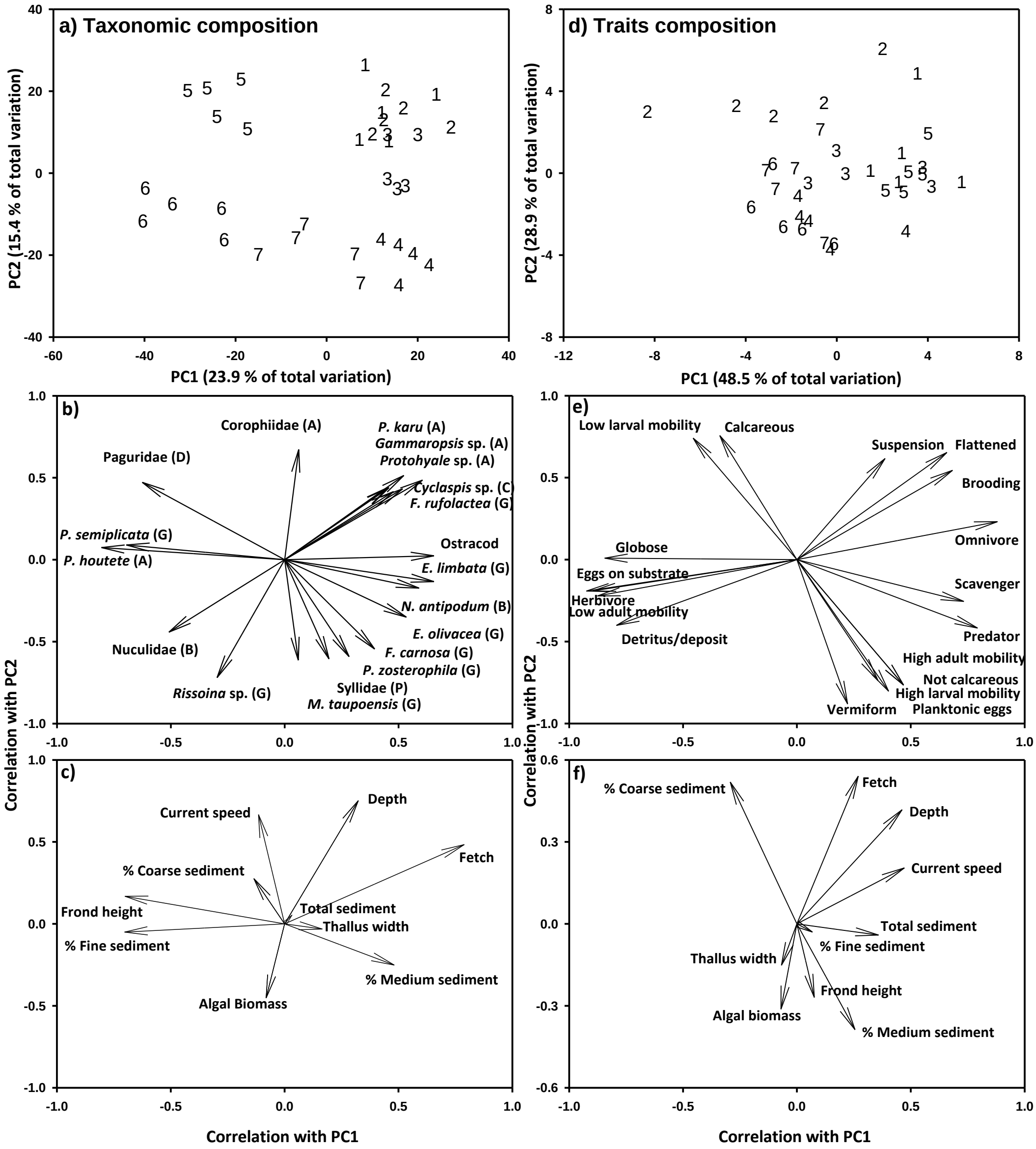

Figure 3.4 Principal coordinates analysis (fourth-root, Bray Curtis similarity) of faunal assemblages with associated vectors based on Pearson correlations with PC1 and PC2. Faunal assemblages are based on; a-b) taxonomic composition and d-e) traits composition. All environmental variables are also included as vectors (c) for taxonomic composition and (f) for traits composition - see methods for details regarding the calculation of vector lengths. Full names of abbreviated species are *Eatoniella limbata*, *Eatoniella olivacea*, *Pisinna zosterophila*, *Merelina taupoensis*, *Paradexamine houtete*, *Pisinna semiplicata*. Broad taxonomic groups are indicated by letters; A = amphipod, B = bivalve, C = cumacean, D = decapod, G = gastropod.

Table 3.1 DistLM sequential test describing the association between environmental variables and patterns in (a) taxonomic composition (proportional abundance) and (b) traits composition (proportional abundance-weighted traits frequencies) of faunal assemblages occupying subtidal coralline turf along an environmental gradient.

a) Taxa - Sequential test (DistLM - stepwise, adjusted r^2)

	Pseudo-*F*	*p*	Prop. Var.	Prop. cum. var.
Fetch	7.6	0.001	0.19	0.19
Current	4.7	0.001	0.10	0.29
Depth	3.2	0.001	0.07	0.36
% Coarse sediment	2.7	0.003	0.05	0.41
Frond height	2.1	0.01	0.04	0.45
% Fine sediment	1.7	0.05	0.03	0.48
Thallus width	1.3	0.20	0.02	0.51
Algal biomass	1.3	0.20	0.02	0.53
Total sediment	1.3	0.20	0.03	0.55
Adjusted r^2 = 0.39				

b) Traits - Sequential test (DistLM - stepwise, adjusted r^2)

	Pseudo-*F*	*p*	Prop. var.	Prop. cum. var.
Depth	6.1	0.001	0.16	0.16
% Coarse sediment	5.4	0.002	0.12	0.28
Frond height	3.6	0.02	0.07	0.35
Fetch	2.7	0.04	0.05	0.41
Algal biomass	2.2	0.09	0.04	0.45
Current speed	2.7	0.06	0.05	0.50
% Fine sediment	1.9	0.10	0.03	0.53
Thallus width	1.4	0.20	0.02	0.56
Adjusted r^2 = 0.42				

3.3.4 **Biological traits**

The PCO run on biological traits (Fig. 3.4d) yielded weaker patterns than were seen for the taxonomic data. Replicates clustered more weakly by site, and there was only a weak trend for sites to group according to their position along the environmental gradient. All 23 biological traits occurred in at least one individual animal at every site (Fig. 3.5a-h). Traits that were more commonly exhibited across all sites, relative to other traits in their category, were small size, globose shape, calcareous exterior, detritus/deposit feeding mode, and low larval mobility. Traits that were uncommonly exhibited across all sites, compared to others in their category, included carnivorous diet, large size, non-calcareous exterior and moderate adult mobility. Environmental variables accounted for 42% of variation in biological traits composition (DistLM adjusted $r^2 = 0.42$), and of these depth (16% of variation) and percentage coarse sediment (12% of variation) explained the most (Table 3.1b). Most correlations between traits and individual environmental/turf morphology variables were relatively weak ($r < |0.5|$), although 21 (from a total of 230) were moderately strong ($r = |0.5| - |0.62|$) (Table 3.2). Vectors representing traits that were highly correlated (vector length > 0.7) with PCO assemblage patterns clustered into four main groups. In one group, suspension feeding, omnivorous diet, brooding of eggs and flattened body form had a positive relationship with fetch, depth and current speed. Scavenger and predator had a positive relationship with total sediment. High adult mobility, non-calcareous exterior, high larval mobility, planktonic eggs and vermiform had a positive relationship with percent medium sediment and frond height and a negative relationship with percent coarse sediment. Detritus/deposit feeding, low adult mobility, herbivorous diet, eggs on substrate and globose had a negative relationship with depth, fetch and current speed while low larval mobility and calcareous exterior had a positive relationship with percent coarse sediment and a negative relationship with percent medium sediment and frond height (Fig. 3.4e,f). Most traits had a weak relationship with the overall gradient, as represented by distance from the tip of the peninsula, with only three traits, suspension feeding ($r^2 = 0.52$) (negative relationship) and detritus/deposit feeding ($r^2 = 0.4$) and vermiform shape ($r^2 = 0.39$) (positive relationships), displaying an r^2 value > 0.3 with the gradient (Fig. 3.5a-h).

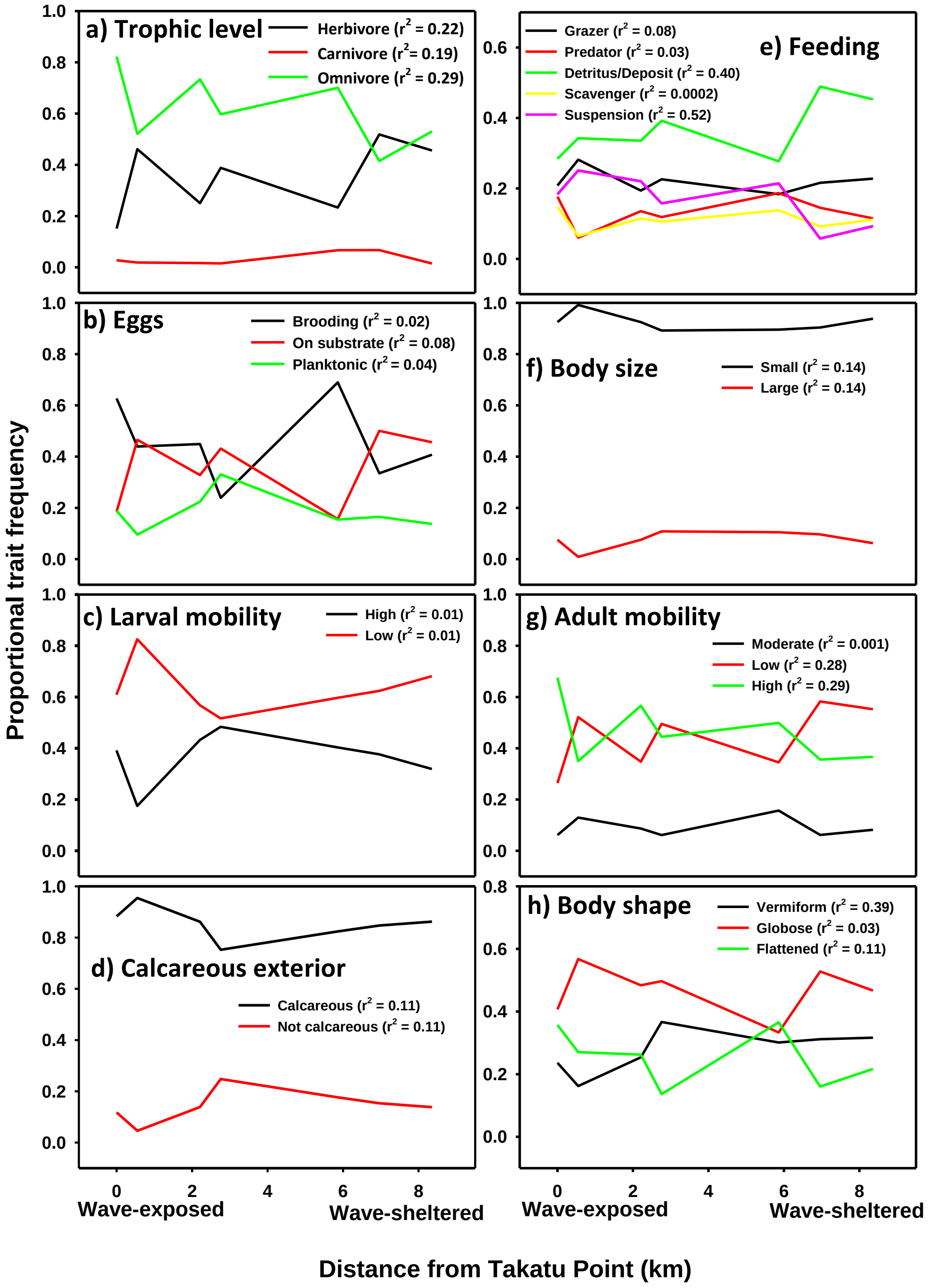

Figure 3.5 Proportions of abundance-weighted trait frequencies of small mobile invertebrate assemblages in *Corallina officinalis* turfs along a gradient of wave exposure and other variables (southern side of Tawharanui Peninsula) in northeastern New Zealand.

Table 3.2 Pearson correlations (r) between proportional abundance-weighted trait frequencies of coralline turf-dwelling fauna and environmental variables. All correlations were based on replicate data except for fetch and current speed, as the values for these were determined per site. Bold numbers indicate correlations > |0.5|.

	Fetch	Depth	Current	Total sediment	% Coarse sediment	% Medium sediment	% Fine sediment	Algal biomass	Frond height	Thallus width
Feeding Method										
Grazer	0.16	-0.03	-0.24	-0.30	0.02	0.06	-0.15	-0.13	-0.36	0.27
Predator	-0.16	0.26	0.36	0.29	-0.40	0.23	0.34	0.10	0.13	-0.19
Detritus/deposit feeder	**-0.58**	**-0.58**	**-0.58**	-0.20	0.07	-0.09	0.04	0.28	0.03	0.03
Scavenger	0.11	0.32	0.33	0.42	-0.44	0.35	0.18	0.04	0.00	-0.02
Suspension feeder	**0.56**	0.37	0.42	0.07	0.28	-0.18	-0.20	-0.29	0.09	-0.06
Trophic level										
Herbivore	-0.43	**-0.54**	-0.45	-0.39	0.23	-0.26	0.07	0.15	0.05	0.10
Carnivore	-0.41	0.00	0.30	-0.09	-0.01	-0.22	0.47	0.16	0.41	-0.13
Omnivore	**0.51**	**0.54**	0.39	0.40	-0.22	0.31	-0.16	-0.18	-0.13	-0.08
Treatment of Eggs										
Brooding	0.29	**0.52**	**0.54**	0.31	0.12	-0.21	0.19	-0.21	0.31	-0.23
Substrate attached	-0.33	**-0.53**	**-0.59**	-0.37	0.18	-0.12	-0.13	0.14	-0.12	0.07
Planktonic eggs	0.04	-0.05	0.02	0.07	**-0.52**	**0.58**	-0.12	0.15	-0.36	0.29
Body Size										
Small (< 2.8 mm)	0.32	0.15	-0.20	-0.04	0.41	-0.17	-0.49	0.01	-0.40	-0.07
Large size (> 2.8 mm)	-0.32	-0.15	0.20	0.04	-0.41	0.17	0.49	-0.01	0.40	0.07
Adult Mobility										
High (free-living/can swim)	0.35	**0.52**	0.25	0.20	-0.26	0.36	-0.21	-0.11	-0.20	-0.03
Moderate (tube/burrow, can swim)	0.17	0.03	**0.51**	0.09	0.24	-0.35	0.22	-0.01	0.41	-0.01
Low (doesn't swim)	-0.40	**-0.54**	-0.41	-0.23	0.19	-0.27	0.15	0.12	0.08	0.03
Larval Mobility										
High (planktonic)	-0.16	-0.04	0.16	0.25	**-0.62**	**0.54**	0.15	0.11	-0.01	0.05
Low (brooded/direct development)	0.16	0.04	-0.16	-0.25	**0.62**	**-0.54**	-0.15	-0.11	0.01	-0.05
Body Shape										
Vermiform	-0.42	-0.42	-0.05	0.14	**-0.52**	0.37	0.30	0.45	-0.03	0.16
Globose	-0.07	-0.22	-0.47	-0.34	0.23	-0.09	-0.30	-0.10	-0.17	0.08
Flattened	0.40	**0.55**	0.49	0.22	0.19	-0.21	0.05	-0.26	0.19	-0.21
Calcareous Exterior										
Calcareous	0.20	0.20	-0.11	-0.12	0.46	-0.40	-0.14	-0.33	0.16	-0.23
Not calcareous	-0.20	-0.20	0.11	0.12	-0.46	0.40	0.14	0.33	-0.16	0.23

3.4. Discussion

I found that the proportional taxonomic composition of faunal assemblages inhabiting subtidal coralline turf exhibited a higher level of variation along an environmental gradient than did the proportional biological traits composition as a whole. This result supports the idea that substantial species turnover can occur within the environmental constraints imposed upon biological traits (Usseglio-Polatera et al. 2000, Bremner et al. 2006b). Other studies have also found biological traits to be a less sensitive indicator of changing habitat conditions than taxonomic composition (e.g., Bremner et al. 2006b), suggesting that functioning persisted regardless of changes in taxa (e.g., Hewitt et al. 2008, Verissimo et al. 2012, Munari 2013). The ability of assemblages differing in taxonomic composition to function in a similar manner allows BTA to be used across different taxonomic groups of organisms (Bremner et al. 2006b), and also across large geographical scales where different species contribute to the overall make-up of assemblages (Bremner et al. 2003, Hewitt et al. 2008). In my study, although a small number of individual traits were responsive to the gradient, the ability of BTA as a whole (in its multivariate form) to detect changes in conditions along the environmental gradient was limited due to the unresponsive nature of the majority of traits. In contrast, other studies have demonstrated that BTA can detect environmental changes, possibly due to the larger magnitude/scale of environmental variation in these studies, e.g., those occurring along a pollution gradient of heavy metals (Oug et al. 2012) and a large-scale river system (e.g., Usseglio-Polatera et al. 2000).

I also found that the subtidal coralline turfs examined in this study hosted an abundant (12,225-53,643 ind.m^{-2}) and diverse (118 taxa) assemblage of small (1-8mm) mobile animals dominated by amphipods and gastropods, and that total animal abundances were much higher at the wave exposed sites. The ability of the turf to ameliorate wave stress by providing recesses to hide in and fine structures to cling to (Dommasnes 1968) may have facilitated the high animal abundances at wave exposed sites.This likely allowed animals to benefit from factors associated with strong water movement, e.g., replenishment of organic particles in the water column for suspension feeders (Fenwick 1976) and a reduction in harmful fine sediment (Airoldi 2003, Prathep et al. 2003).

The proportional taxonomic composition of the animal assemblages was strongly correlated with the environmental gradient. The influence of environmental/turf structural variables on faunal assemblage composition is well documented for subtidal (e.g., Dommasnes 1968, Cowles 2010) and intertidal (e.g., Grahame & Hanna 1989, Kelaher et al. 2001, Kelaher & Castilla 2005) coralline turfs. The two variables that best explained overall patterns in proportional taxonomic composition were fetch (a proxy for wave action) and current speed. Most of the taxa that were positively correlated with fetch and current speed were amphipods and ophiuroids. Amphipods can adapt to high water movement by clinging to algal fronds and/or building tubes to avoid dislodgment (Tararam & Wakabara 1981), while ophiuroids likely inhabited the base of the turf (Pentreath 1970) where they would be relatively protected from water motion. A number of suspension-feeders (e.g., the amphipod *Podocerus karu* and the ophiuroid *Ophiactis resiliens*) were also positively correlated with fetch and likely benefited from an increased supply of particulate food in the water column (Fenwick 1976). Taxa that were negatively correlated with high water movement included a number of gastropods and the polychaete family Syllidae. These taxa likely benefited from the habitat and food supplied by the higher percentage of fine sediment associated with more sheltered conditions (Prathep et al. 2003), e.g., the gastropods *Rissoina* spp. and *Pisinna zosterophila* are detritus/deposit feeders.

The strong influence of overall abundances on biological trait frequencies along the gradient highlights the ability of changes in animal density to drive ecological function (Hewitt et al. 2008, Paganelli et al. 2012). However, when expressed as a proportion of total abundance, assemblage-level patterns in traits composition did not appear to be strongly influenced by the gradient, and only a few traits exhibited moderately strong positive (vermiform and detritus/deposit-feeding) and negative (suspension-feeding) correlations with distance from the wave-exposed end of the gradient. As in this study, biological traits relating to feeding methods are often responsible for distinguishing assemblages (Oug et al. 2012). Suspension-feeding, usually associated with high water movement (Fenwick 1976), is important in ecosystem functioning as it transfers energy and materials from the water column to the benthos (Bremner 2008), while detritus/deposit feeding, often associated with organically-rich fine sediment (Olabarria & Chapman 2001, Prathep et al. 2003), is functionally important as it incorporates uneaten primary production into the food web (Bremner 2008). Vermiform shape, also responsive along the gradient, may be advantageous for moving within fine sediment and this trait was also positively correlated with percent fine sediment in the BTA of benthic assemblages in Italy (Paganelli et al. 2012). As environmental conditions at the sheltered end of the gradient are generally more representative of coastal habitats subject to anthropogenic impact, e.g., they contain higher loads of fine sediment (Airoldi 2003, Thrush et al. 2003), the results of this study indicate that future human impacts on turf habitats may lead to subsequent reductions in the overall function, and relative changes in the type of functions mentioned above, of animal assemblages.

The two variables that best explained overall patterns in biological traits composition were depth (correlated most positively with omnivory, flattened shape, egg brooding and high adult mobility, and most negatively with detritus/deposit feeding, herbivory, eggs deposited on substrate and low adult mobility), and the percentage of coarse sediment (correlated most positively with low larval mobility, calcareous exterior and small size, and most negatively with a vermiform shape, planktonic eggs and high larval mobility). However, most individual traits were only weakly correlated with individual environmental variables, indicating their relative stability in the face of changing environmental conditions (e.g., Bremner et al. 2006b).

Despite the environmental gradient, a number of biological traits distinguished turf-associated faunal assemblages by being consistently more common than others within the same trait category across all sites. The general small size of fauna and the high occurrence of detritus/deposit feeding is likely explained by the complex structure of *Corallina officinalis* turf, which offers only small spaces for fauna to dwell (Dommasnes 1968), and which can trap detritus/fine sediment within its branches (Cowles et al. 2009). The high level of omnivory exhibited by turf fauna reflects an ability to utilize a variety of food sources, and could suggest they occupy relatively wide niches (Thrush et al. 2011). Low, as opposed to high, larval mobility was also frequently exhibited by fauna, which is in contrast to the findings of Thrush et al. (2011), but similar to those of Hagermann (1966) for algal-dwelling fauna and Boström et al. (2010) for seagrass fauna. In my turfs, this was driven by the high number of brooding peracarid crustaceans and egg-laying gastropods with direct larval development e.g., eatoniellids. Low dispersal suggests that the persistence of populations of turf-dwelling animals relies on the immigration of adults from nearby turfs and/or the recruitment of juveniles from within the turf. As high larval mobility can indicate an unstable habitat (Paganelli et al. 2012), the frequent occurrence of low larval mobility suggests that the habitat provided by the turf is relatively stable, possibly due to the perennial nature of the turf and its ability to ameliorate environmental stresses such as wave action (Dommasnes 1968). Traits may strongly map onto taxonomic relationships (Munari 2013), and the frequent occurrence of the traits calcareous exterior and globose shape in this study reflects the numerical dominance of molluscs (calcareous and often globose) and arthropods (calcified, albeit lightly) within the turf.

Biological traits analysis has the potential to shed light on the functioning of communities in marine habitats (Bremner et al. 2006a, Van der Linden et al. 2012). This includes the ability to compare ecological functioning across assemblages that are not taxonomically equivalent (Bremner et al. 2006b) and quantify functional redundancy within them (Hewitt et al. 2008). A shortcoming of BTA is that it is relatively time consuming as taxonomic identification must still be conducted as well as literature searches to gather trait information. I also suggest caution be exercised if using BTA as a management tool as there are a number of methological decisions that need to be carefully considered. One of these is that BTA results are heavily dependent on the choice of trait categories and the definition of traits within them. The choice of many trait categories, and the overall effectiveness of BTA, relies on the availability of detailed and accurate data (Usseglio-Polatera et al. 2000), which is currently lacking for many marine communities (e.g., Paganelli et al. 2012, Munari 2013). For example, in my study, many biological traits with strong links to ecosystem function, e.g., life span, growth rate, fecundity (Bremner et al. 2006a), were omitted due to a lack of information. Due to this, important patterns in ecosystem functioning were likely to have been missed as the inclusion of as many biological traits as possible will provide the most information regarding overall ecological functioning (Bremner et al. 2006a, Marchini et al. 2008). Limited information can also hamper the interpretation of BTA results in regards to ecological functioning, as links between biological traits and their ecosystem function are often unknown (Munari 2013). In regards to the definition of traits, differences in function (e.g., Duffy et al. 2001) can exist within broadly defined traits, possibly obscuring fine-scale patterns and misleading predictions of functional redundancy. For example, ‘grazer’ is a feeding-related trait commonly used in marine BTA studies including ours, even though in our study system arthropods and gastropods are not functionally redundant in terms of their grazing impacts on epiphytes (Berthelsen & Taylor 2014).

In light of this discussion I suggest quantifying a larger number of faunal traits and understanding the links between these and functioning, followed by careful consideration of the definition of these traits during BTA, be undertaken if this technique is to be utilized to its full potential in this and other similar habitats.

Chapter 4. The Impacts of Small Mobile Invertebrates on Subtidal Coralline Turf

4.1. Introduction

Small herbivorous invertebrates (mesograzers) are often highly abundant on seaweeds and seagrasses (Brawley 1992), where they exert strong grazing pressure (Poore et al. 2012). Feeding directly on host tissue can have serious negative consequences for the host macrophyte (e.g., Tegner & Dayton 1987, Reynolds et al. 2012, Poore et al. 2014), but mesograzers more commonly eat epiphytic algae (Bell 1991, Edgar 1991). This should benefit their host, as epiphytes compete with hosts for light and nutrients (van Montfrans et al. 1984) and increase the risk of frond breakage due to drag (D'Antonio 1985). Thus the potential for mutualism exists between mesograzers and their host macrophytes (Aumack et al. 2011), where the mesograzers derive food in the form of algal epiphytes, along with shelter from predators (Coull & Wells 1983) and wave action (Dommasnes 1968), while the host is kept free of fouling organisms (Duffy 1990, Hay et al. 2004). Mesograzers may even help macrophytes resist vigorous overgrowth by epiphytes responding to anthropogenic eutrophication, an increasingly common stressor in coastal waters (Myers & Heck 2013).

Impacts of small mobile arthropods have generally been examined using mesocosms or cages (e.g., Brawley & Adey 1981, Duffy & Hay 2000), but these methods suffer from various artefacts such as shading (Lotze et al. 2001) and altered water flow (Kamermans et al. 2002). In response, Poore et al. (2009) developed a cageless poison-based method of reducing densities of amphipods, and potentially other arthropods, in the field. They applied it in a temperate seaweed bed, where they found no impacts of mesograzers on either host or epiphytes. However, the method has since been used in 4 seagrass habitats, with strong impacts of mesograzers on algal epiphytes found in each case (Cook et al. 2011, Myers & Heck 2013, Whalen et al. 2013, Reynolds et al. 2014). The variation in results arising from these studies indicates that similar experiments need to be run in a wide range of coastal benthic habitats before I can generalise about the impact of mesograzers on host macrophytes and their epiphytes, and how this is influenced by properties of the local environment (e.g., depth, wave exposure and sedimentation), the mesograzer assemblage (abundance, taxonomic composition and size structure) and the host macrophytes and their epiphytes (productivity, taxonomic composition and relative susceptibilities to grazing).

Coralline algal turfs occur on shallow hard-bottom habitats worldwide (Nelson 2009, Connell et al. 2014) and host a diverse and highly abundant assemblage of small mobile invertebrates (Taylor 1998, Kelaher & Castilla 2005, Cowles et al. 2009). Coralline algal fronds are calcareous and unpalatable to most mesograzers (e.g., Taylor & Steinberg 2005, Taylor & Brown 2006). It is likely, therefore, that mesograzers instead feed on algal epiphytes growing on the turf (e.g., Kelaher et al. 2001) and that a mutualistic relationship may exist between mesograzers and the turf.

Many temperate reefs are subject to episodic strong wave action, which can overwhelm the effects of herbivores by detaching large numbers of individual macrophytes and/or epiphytes (Anderson & Martone 2014). On the other hand, heavy wave action can benefit algae by reducing the grazing impacts of herbivores through limiting their access or foraging ability (Duggins et al. 2001, Taylor & Schiel 2010).

In my study I tested whether arthropod mesograzers reduce epiphytic overgrowth of subtidal coralline turf in the field using the cageless method of Poore et al. (2009). During the experiment I also quantified wave action in order to determine the relative impacts of large waves and mesograzers on epiphytes.

4.2. Materials and Methods

4.2.1 **Study site**

The study site was Kempts Bay (36° 15’ S, 174° 45’ E), a moderately wave-exposed shallow subtidal rocky reef adjacent to the Cape Rodney-Okakari Point Marine Reserve, in warm temperate northeastern New Zealand. My experiment was run in patches of coralline turf (almost exclusively *Corallina officinalis*) surrounded by stands of large brown macroalgae (mostly the kelp *Ecklonia radiata*).

4.2.2 **Experimental reduction of arthropod densities**

The method of Poore et al. (2009) entails impregnating plaster blocks with the insecticide carbaryl (1-naphthyl-N-methylcarbamate). In the field the carbaryl is released as the plaster dissolves. Carbaryl contains carbamates, which inhibit the enzyme cholinesterase found in arthropod nervous systems and are particularly toxic to amphipods (Duffy & Hay 2000). Carbaryl does not affect algal growth (Carpenter 1986, Poore et al. 2009) and is often used in marine herbivory experiments to reduce densities of amphipod grazers (e.g., Duffy & Hay 2000, Newcombe & Taylor 2010).

I prepared cylindrical plaster blocks of volume 350 ml in a similar fashion to Poore et al. (2009) using superfine casting plaster and plastic moulds made from 80-mm diameter uPVC pipe with a plastic base. Two types of block were produced: “plaster” blocks contained a mixture of 429 g plaster and 250 ml water, while “carbaryl” blocks also contained 45 g of carbaryl (80% wettable powder). Blocks were air-dried for ~four days before use. To ensure that the plaster blocks lasted at least a week at my wave-exposed study site, I protected the majority of each block from dissolution within a housing, which consisted of a 107-mm length of 80-mm internal diameter uPVC pipe on a plastic base (Fig. 4.1). Twenty-six 16-mm diameter holes were drilled near the base of the housing to enable the slow release of carbaryl as the bottom end of the plaster block dissolved. Each housing (containing a block) was bolted to a metal rod cemented into the seafloor. A removable cap allowed for the replacement of blocks in the field.

Figure 4.1 Housing containing a plaster block impregnated with the insecticide carbaryl, which was secured in wave-exposed subtidal coralline turf to reduce arthropod densities.

4.2.3 Experimental design

My experiment had three treatments: (1) carbaryl (carbaryl-impregnated plaster block in a housing) to reduce arthropod density, (2) plaster control (plaster block in a housing) to control for any effects of the plaster and/or housing on algae, and (3) unmanipulated control (no block or housing) to provide a natural baseline (n = 5 replicates per treatment). Replicates were situated in individual turf patches that were 0.7 - 2.4 m deep at mean low tide, larger than 0.25 m^2, and separated by at least 2 m. This distance was found by us (pilot study data not shown), and Reynolds et al. (2014), to be beyond the limit of carbaryl effectiveness and is in accordance with other cageless studies in which plots were placed at least 1 - 2 m apart (Poore et al. 2009, Cook et al. 2011, Myers & Heck 2013, Whalen et al. 2013). The experiment began on 1 November 2012 (spring) and continued for 111 days until 19 February 2013 (summer). Blocks were replaced ~weekly and on two occasions (day 59 and 96), when wave action prevented access for 14 and 18 days respectively, blocks had completely dissolved. Water temperatures ranged from 15.2 - 21.7°C during the study.

4.2.4 **Wave action**

Mean significant wave height (average height of the highest third of all waves counted) per day, used to quantify wave action, was determined from forecast outputs (based on the position 36°0’ S and 175°5’ E) obtained from the “Pacific Integrated Ocean Observing System” (www.ioos.noaa.gov/regions/pacioos.html, accessed on 5 December 2013) and generated by the model package used in Arinaga & Cheung (2012) using Wavewatch III of Tolman et al. (2002).

4.2.5 **Faunal composition**

To check the effectiveness of the carbaryl treatment, on day 106 I collected a circular sample (area of 50.3 cm^2) of coralline turf and fauna from each replicate using the suction sampler of Taylor et al. (1995). The sample was collected in a 0.2-mm mesh bag and preserved in Glyo-Fixx (Titford & Horenstein 2005). Fauna retained on a 0.5-mm sieve were identified to the lowest practical taxonomic level (usually Order or Family) and enumerated. Blotted weight of coralline turf (mean per sample), used to standardise amphipod densities for comparison with other studies, was determined from three of the unmanipulated control samples after washing algae through a 2-mm sieve (to remove sediment) and blotting it dry.

4.2.6 **Algal composition**

To quantify algal composition, each replicate was photographed from above, every 1-3 weeks using a Canon G12 camera with inbuilt flash. Additional closeup photographs were taken to help with algal identifications. The brightness and contrast of photographs was standardised by eye using Adobe Photoshop CS5.1, and an inner circle representing the housing was drawn on unmanipulated controls using ImageJ software. A circle covering 622 cm^2 of seafloor was then digitally drawn around the housings in each photo replicate. These circles extended 98 mm from the housing edges, a range over which I (pilot data not shown) and all other cageless studies (Poore et al. 2009, Myers & Heck 2013, Whalen et al. 2013, Reynolds et al. 2014) found carbaryl to strongly reduce amphipod densities. Due to blurred/incomplete photos, quadrat size on days 11, 33, 45 had to be reduced slightly, and several replicates on days 33 and 85 were not quantified.

Percent coverage of taxa was estimated visually (Dethier et al. 1993) by myself following a training and validation exercise. Visual estimates were compared to measurements obtained using the software ImageJ (a much more time-consuming process) until an acceptable level of accuracy was reached ($r^2 \geq 0.7$ with no bias). Taxa in the photo quadrats were classified as follows: (1) filamentous and microscopic algae (identity unknown but included F. Ectocarpaceae and *Ostreopsis siamensis*), (2) the brown alga *Colpomenia* spp. (*C. sinuosa* and/or *C. claytoniae*), (3) the green alga *Ulva* spp., (4) the green alga *Codium fragile*, (5) red foliose algae (including the genera *Hymenena*, *Aphanocladia* and *Gigartina*), (6) coralline turfing algae (mostly *Corallina officinalis*), and (7) sessile invertebrates. Items excluded prior to calculating percentage covers were: sand (transient; averaged 1.4% and never more than 10%), overhanging algae (i.e., holdfast outside the quadrat or growing on housing), marker tape in the unmanipulated control, overhanging housings (occurring if photos were not taken directly from above), mobile fauna (fish and molluscs), and areas from which turf had previously been removed to sample fauna.

4.2.7 Identification of grazers

Arthropod grazers likely to consume the algal taxa that increased in the carbaryl treatment were identified from the literature (see Results). One of the two taxa identified was available in sufficient numbers for a feeding assay. In July 2013 I measured the rate at which hyalid amphipods consumed *Colpomenia* spp. and *Ulva* spp. in a no-choice assay. Hyalids consisted of a mix of *Protohyale rubra* and *Protohyale grenfelli* as these species could not be separated due to the difficulty of identifying females and juveniles. Amphipods and algae were collected from the study site, and an assay started on the same day. Two large amphipods were added to a plastic bowl containing a pre-weighed piece of algae of 27 - 32 mg blotted weight in 300 ml of seawater. As a control for autogenic weight change, a matching container with tissue from the same algal individual was set up without amphipods (n = 10 for each algal taxon and grazing treatment). The feeding assay took place indoors, with a 12:12 light:dark regime, and water temperature kept close to ambient (14°C) using a water bath. The assay ran for approximately three days but individual grazed replicates and their paired controls were stopped earlier if most of the algae had been eaten. Only one amphipod died during the assays and this was replaced. Algal pieces were then again blotted dry and weighed. Amphipod feeding rates were calculated by scaling for autogenic change as in Taylor & Brown (2006).

4.2.8 Statistical analyses

One-way analysis of variance (ANOVA) in SigmaPlot 11.0 was used to test for differences in densities between faunal groups. Data were tested for normality and homogeneity of variance, and were log-transformed to meet these assumptions if necessary. Pairwise multiple comparisons using the Holm-Sidak method were used to investigate significant differences detected by ANOVA. To display temporal changes in algal community composition, a non-metric multidimensional scaling (nmMDS) analysis was run on the mean percentage cover of algae and sessile invertebrates, using a Bray-Curtis dissimilarity matrix based on square root-transformed data. One-way analysis of similarity (ANOSIM) and post hoc pairwise comparisons were used to test for significant differences in mean algal community composition. Multivariate analyses (Clarke 1993) were conducted with the software package PRIMER v6 (Clarke & Gorley 2006).

4.3. Results

4.3.1 Faunal composition

The average density of total arthropods was significantly (F_2,12 = 7.65, $p < 0.01$) reduced in the carbaryl treatment compared to unmanipulated and plaster controls by 87% and 85% (pairwise comparisons: $p < 0.01$ and $p = 0.01$), respectively (Fig. 4.2). Relative to unmanipulated controls, carbaryl reduced amphipod densities by 96%, ostracods by 81%, isopods by 89% and decapods by 71%. In unmanipulated controls, amphipods comprised 57% of total arthropods, with a mean density of 22874 ± 6452 (SE) ind.m^{-2} (28 ± 7.9 ind.g coralline wet weight^{-1}). The average total density of non-arthropods (mostly gastropod molluscs, polychaetes and ophiuroids) did not differ significantly between the three treatments (F_2,12 = 1.60, $p > 0.1$). In unmanipulated controls, gastropod molluscs were the most abundant non-arthropod taxon (108401 ± 10262 (SE) ind.m^{-2}).

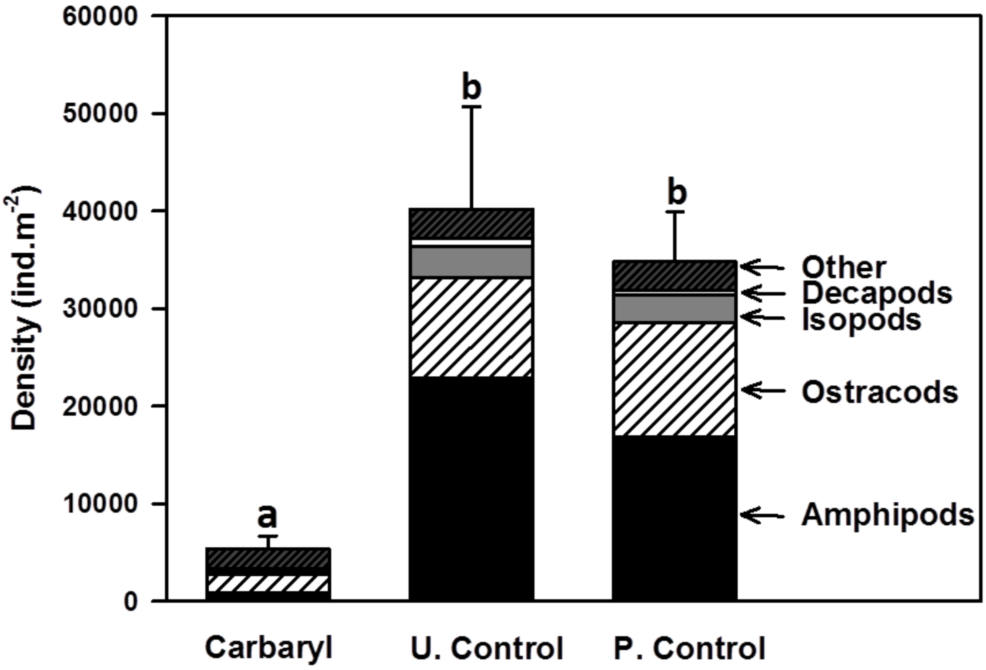

Figure 4.2 Mean (+ 1SE) densities of arthropod taxa (> 0.5 mm) in coralline turf on day 106 of study. The three treatments are carbaryl, unmanipulated control (u. control) and plaster control (p. control) (n = 5). 'Other' includes tanaids, cumaceans, marine mites, trichopterans, pycnogonids and copepods. Bars labelled with the same lower case letter do not differ significantly (*p* > 0.05) according to Holm-Sidak pairwise comparison.

4.3.2 **Algal composition**

Algal composition was similar in all treatments at the beginning of the study (ANOSIM: R = -0.07, p > 0.5) (Fig. 4.3). By day 45, algal composition differed significantly between the treatments (ANOSIM: R = 0.42, p < 0.01), with the carbaryl treatment different to both the unmanipulated and plaster controls (pairwise comparison: R = 0.62, p < 0.01 and R = 0.63, p < 0.01), which were not different from each other (R = 0.08, p > 0.1). Similar differences in algal composition were present at the study end (day 111), with the carbaryl treatment significantly different (ANOSIM: R = 0.72, p < 0.01) from both the unmanipulated and plaster controls (pairwise comparisons: R = 0.97, p < 0.01 and R = 1, p < 0.01), and no significant difference detected between the controls (R = 0.26, p > 0.05). On day 111 the total mean cover of epiphytes was 88% in the carbaryl treatment compared to 38% in unmanipulated controls, a 2.3-fold difference (Fig. 4.4A). All green and brown algal taxa were more abundant in the carbaryl treatment by day 111. Mean cover of filamentous and microscopic algae was 63% in the carbaryl treatment vs 11% in unmanipulated controls (Fig. 4.4B), with the corresponding values being 18.7% vs 2.6% for *Colpomenia* spp. (Fig. 4.4C) and 2.5% vs 0.3% for *Ulva* spp. (Fig. 4.4D). Conversely, the cover of red foliose algal epiphytes was lower in the carbaryl treatment than in unmanipulated controls (4% vs 24%; Fig. 4.4E). The similarity of the plaster control to the unmanipulated control showed that the main effect of the carbaryl treatment was due to the carbaryl rather than to the associated plaster and/or housing. Cover of sessile invertebrates was never greater than 2% in any replicate. Photographs of a typical replicate of all treatments at days 45 and 111 are shown in Fig. 4.5.

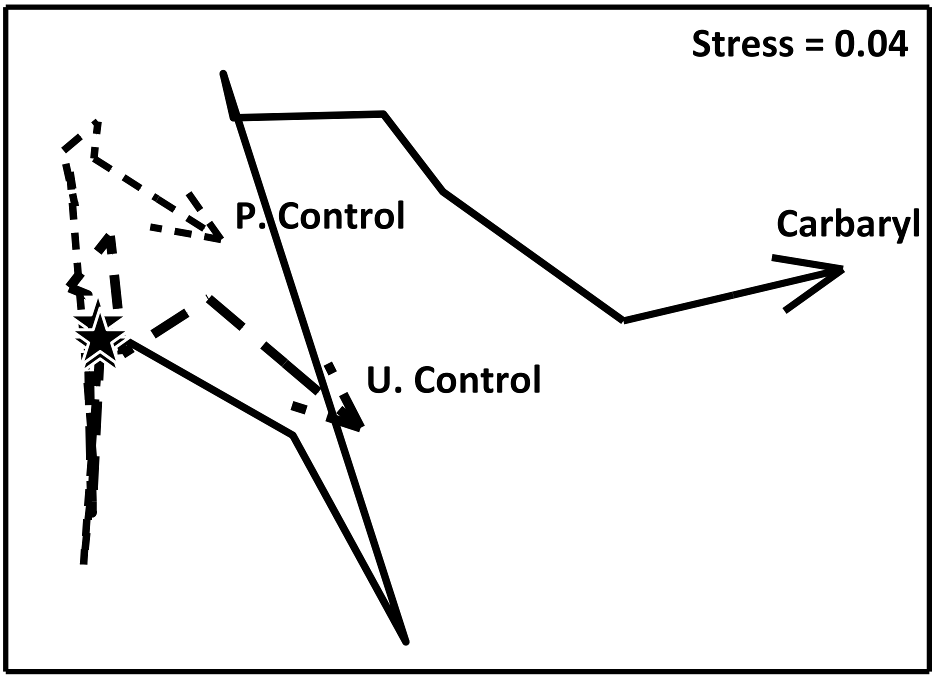

Figure 4.3 Non-metric MDS plot showing the relative changes in mean algal community composition in a coralline turf habitat over time (star symbols represent day 11 and arrows represent day 111). The three treatments are carbaryl (solid line), unmanipulated control (u. control) (long dashed line) and plaster control (p. control) (short dashed line).

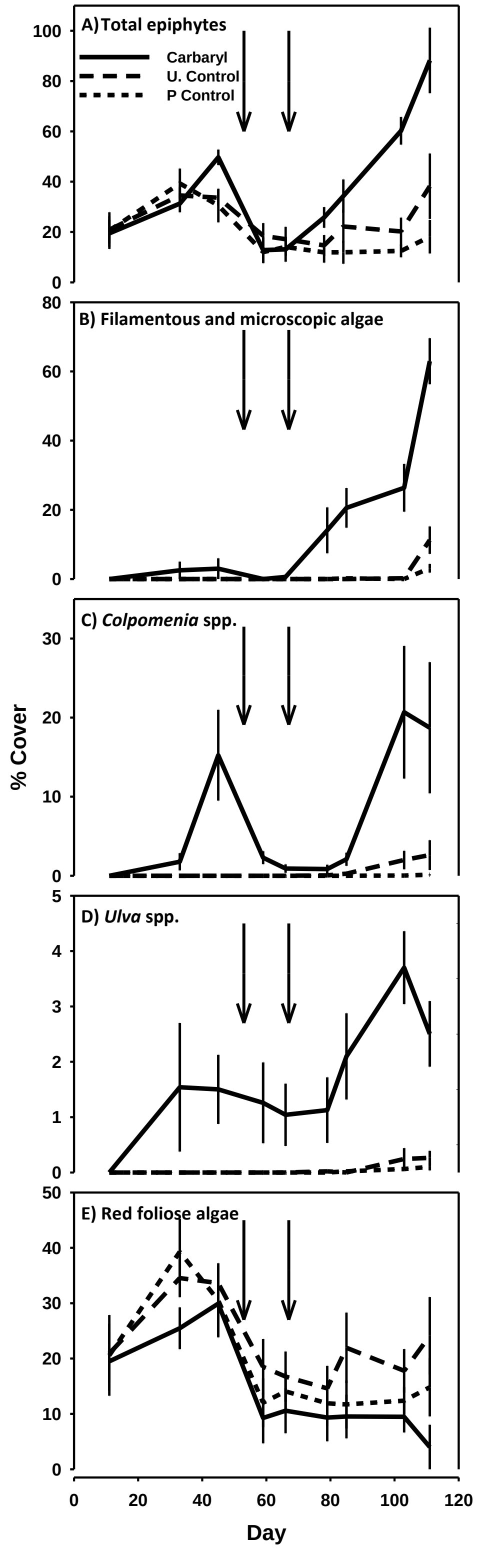

Figure 4.4 Mean (± 1SE) changes in the covers of epiphyte taxa on coralline turf in response to arthropod exclusion (carbaryl) and two controls (unmanipulated and plaster). A) all epiphytes combined, B-E) individual/grouped epiphyte taxa. The arrows denote the two strongest storms to occur during the experiment.

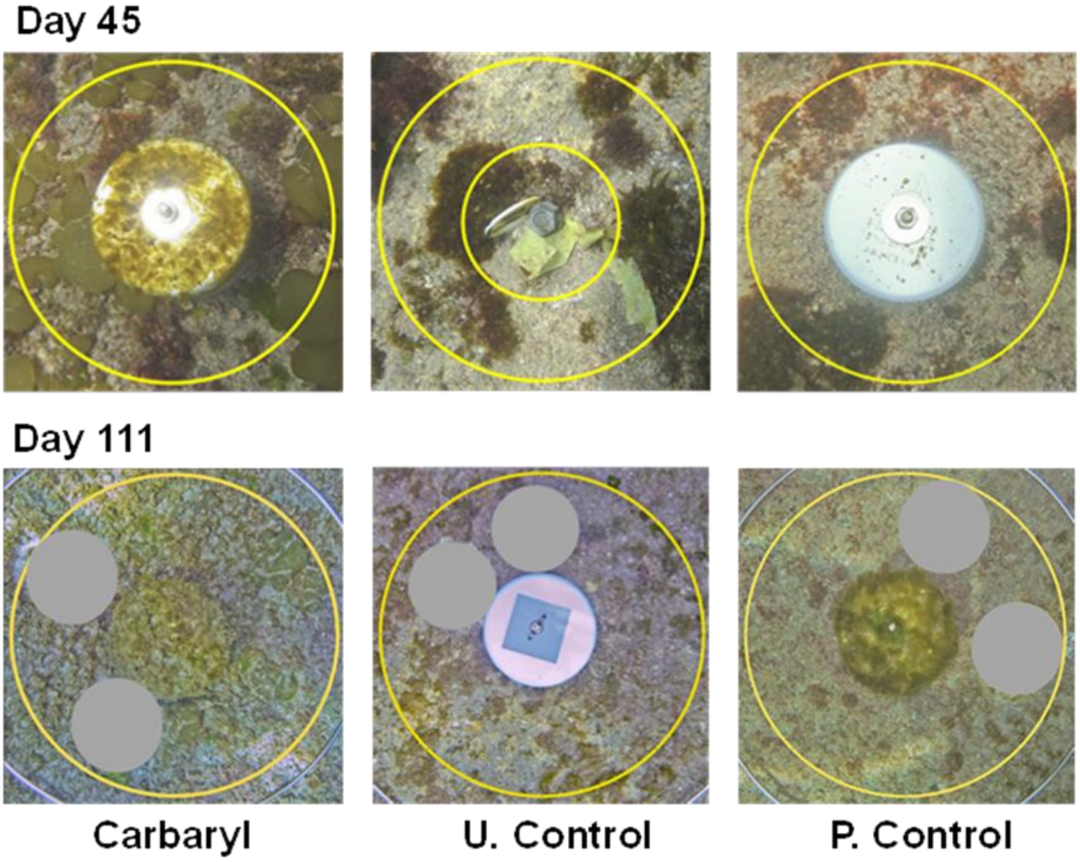

Figure 4.5 Representative photos of coralline turf on days 45 (reduced quadrat area) and 111. Arthropod densities were reduced in the carbaryl treatment; the other two treatments are controls (unmanipulated and plaster). In the unmanipulated control on day 111 a new housing cap was temporarily placed in the center of the site for the photograph (hence its lack of algal growth). The grey circles mark places from where faunal samples were previously taken.

4.3.3 **Storms**

Two large (mean wave height > 3 m) storms with maximum wave heights of 3.7 m (day 53) and 3.3 m (day 67) occurred during the study. In comparison, the mean wave height during the experiment, excluding the days of increased wave height caused by the two large storms, was 1.3 ± 0.05 (SE) m. The first storm coincided with large decreases in the covers of *Colpomenia* spp., *Ulva* spp., ‘filamentous and microscopic’ algae and red foliose algae in the carbaryl treatment, and decreases in red foliose algae in both of the control treatments (Fig. 4.4 A-E). During the second storm the algal taxa mentioned above remained relatively low in cover.

4.3.4 **Grazers responsible**

A literature search indicated that of the fifteen amphipod families identified from my samples, the Hyalidae (Brawley 1992) and Aoridae (Taylor & Brown 2006) were likely to be mesograzers. At least two species of hyalids (*Protohyale grenfelli* and *Protohyale rubra*) and two species of aorids (*Aora* sp. and *Microdeutopus apopo*) were present. Mesograzing amphipods (of which 72% were *Protohyale* spp. and 28% aorids) were present at densities of 6007 ± 2209 (SE) ind.m^{-2} (equivalent to 7.4 ± 2.7 ind.g^{-1} coralline blotted wet weight) unmanipulated controls. In a no-choice feeding assay, hyalid amphipods (combination of *P. rubra* and *P. grenfelli*) consumed *Colpomenia* spp. and *Ulva* spp. at average rates of 1.68 ± 0.45 and 0.26 ± 0.13 (SE) mg seaweed blotted weight ind^{-1} d^{-1}, respectively. The family Eatoniellidae was the numerically dominant gastropod grazer, with densities of 43599 ± 5882 (SE) ind. m^{-2} in the carbaryl treatment.

4.4. Discussion

This is the first cageless study to detect strong impacts of arthropod mesograzers in a subtidal temperate reef habitat. I found that small coralline turf-dwelling arthropods can significantly reduce the overall abundance of algal epiphytes on their host and alter the epiphyte assemblage’s taxonomic composition. Amphipod densities were reduced by a similar proportion (> 85%) to those reported in other cageless studies (Poore et al. 2009, Cook et al. 2011, Myers & Heck 2013). However, my finding of a large (2.3-fold, or 131%) increase in epiphytic cover following mesograzer exclusion is in contrast with the results of Poore et al. (2009), who found no such impacts in another temperate reef habitat. Although varying in magnitude (with increases in epiphyte cover of 25%, 70%, 447% and 590% following amphipod exclusion), the results from cageless seagrass studies (Cook et al. 2011, Myers & Heck 2013, Whalen et al. 2013, Reynolds et al. 2014) correspond with mine, suggesting that amphipods play a strong role in controlling epiphyte overgrowth in these two 2 habitats, and likely others. Mesograzer exclusion caused an increase in cover of green and brown, but not red, epiphytic algal taxa. Mesograzer impacts on algal composition are often taxon -specific for both the herbivore and primary producer, and thus not easily generalized, although global trends from exclusion experiments are consistent with my result for these broad algal categories (Poore et al. 2012). Results from the cageless experiments, together with those from previous studies using other methods such as field observations (e.g., Tegner & Dayton 1987), mesocosms (e.g., Duffy & Hay 2000, Newcombe & Taylor 2010) and field experiments (e.g., Brawley & Fei 1987, Davenport & Anderson 2007, Poore et al. 2014), clearly show that mesograzers can have a major impact on seaweeds.

It is unclear why arthropod mesograzers had a strong impact on epiphytes in my coralline turf within 45 days, but little effect on epiphytes of the brown seaweed *Sargassum linearifolium* in a similar shallow temperate habitat after 70 days (Poore et al. 2009). It is difficult to meaningfully compare grazing pressure between the studies, due to differences in sampling methods (e.g., sieve mesh size) and potential differences in the taxonomic composition and size-structure of mesograzer communities. However, natural densities of mesograzing amphipods were similar in both studies (7.4 ind. [>0.5 mm] .g^{-1} coralline turf $^{-1}$ versus vs. 12 ind. [>0.3 mm] .g^{-1} *Sargassum*$^{-1}$). I note that these densities were measured only once during each study, and it is likely they varied over time as has previously been shown for amphipods in subtidal coralline turfs (e.g., Choat & Kingett 1982) and on *Sargassum linearifolium* (e.g., Poore & Steinberg 1999). A possible explanation for the greater response to arthropod exclusion in my study is that my experiment was conducted in spring/summer, seasons associated with rapid algal growth (King & Schramm 1976, Nelson 2013) and high epiphyte abundance (Dromgoole 1973, Edgar 1983), compared to winter (although see Jennings & Steinberg 1997), when the study by Poore et al. (2009) was conducted. Another factor may have been the greater difference in palatability between host seaweed and epiphytes in my system; coralline algae are much less edible to mesograzers than *Sargassum* (e.g., Taylor & Steinberg 2005).

Gammarid amphipods of the genus *Protohyale* (F.family Hyalidae) were naturally abundant in subtidal coralline turf and consumed *Colpomenia* spp. and *Ulva* spp. in a feeding assay, strongly suggesting they were responsible for reducing abundances of these epiphytes in nature. Hyalid amphipods are predominantly herbivorous (Brawley 1992) and often eat their algal hosts as well as the epiphytes they support. For example *Protohyale* (=*Hyale*) *rubra* consumed both epiphytic and host macroalgal taxa in a feeding assay (Poore 1994), and greater field abundances of *Protohyale* (=*Hyale*) *nigra* occurred on epiphytised, as opposed to clean, brown seaweeds (Poore et al. 2000). Hyalids, which display species-specific diet preferences, feed on a variety of green, brown, and red algal taxa under laboratory conditions (Tararam et al. 1985, Buschmann 1990). *P. rubra*, present in my field/laboratory studies, was similarly found by Poore (1994) to consume epiphytes from the genera *Ulva* and *Colpomenia* in the laboratory. *Protohyale grenfelli*, also present in my field/laboratory studies, is endemic to New Zealand, and no previous studies could be found regarding its diet. *Colpomenia* spp. was consumed at a faster rate than Ulva spp. by hyalid amphipods in my feeding assays. Poore & Steinberg (1999) also found high amphipod feeding rates on *Colpomenia. peregrina*, attributing this to compensatory feeding on this nutritionally poor algal species. However, although feeding assays were carried out on larger algal individuals, I note that the very low densities of *Ulva* spp. and *Colpomenia* spp. in the unmanipulated plots would suggest that much of the mesograzer control is due to consumption of early life- history stages (e.g., Worm & Chapman 1998, Lotze et al. 2001).

Amphipods belonging to the genera *Aora* and *Microdeutopus* (F.family Aoridae) may also have reduced epiphyte abundances in my field controls. Aorids can be herbivorous: for example, *Aora typica*, common in my study region, consumes various algal taxa, including *Ulva* sp., under laboratory conditions (Taylor & Brown 2006), while *Microdeutopus* sp. also eat algae including *Ulva* spp. (Borowsky 1980, Heckscher et al. 1996). Although isopods, ostracods and decapods were less abundant than amphipods, and taxa within these groups were considered unlikely to be significant grazers of macroalgal epiphytes, they were also negatively impacted by carbaryl, and therefore possibly contributed to grazing impacts in my field controls.

Functional redundancy occurs when multiple taxa perform the same ecosystem function. Redundancy has been demonstrated for epiphyte consumption by various arthropod mesograzers (Duffy et al. 2001). In my experiment, extremely abundant herbivorous gastropods of the family Eatoniellidae did not control epiphytes in the absence of amphipods. As eatoniellids have a diet of microalgae and microdetritus (Ponder 1965), rather than larger algal epiphytes, my results may be due to a lack of dietary overlap with amphipods rather than low eatoniellid feeding rates. The inability of other mesograzers to control algal epiphytes when amphipods were absent was also reported by cageless seagrass experiments (e.g., Cook et al. 2011, Myers & Heck 2013, Whalen et al. 2013). This highlights the critical role played by grazing amphipods in the functioning of benthic ecosystems.

Mutualistic interactions, important determinants of ecosystem processes (Hay et al. 2004), are thought to exist between epiphyte-grazing amphipods and host macroalgae

(Amsler et al. 2014). Coralline turf fronds are compact and can protect arthropod mesograzers from water motion (Dommasnes 1968) and predation (Coull & Wells 1983), and also provide them with a food source in the form of algal epiphytes. In turn, the mesograzers potentially benefit the coralline by removing epiphytes (present study), which could reduce the growth and reproductive output of the underlying coralline (Konar 1993). It is therefore likely that, by reducing fouling epiphytes, mesograzers maintain the health of coralline turf and could potentially play a role in buffering turfs from the indirect negative impacts of coastal eutrophication (e.g., Myers & Heck 2013).

As in other subtidal habitats (e.g., Dayton & Tegner 1984, Duggins et al. 2003), storm-driven disturbance had strong impacts on algal composition. Covers of red foliose algae, *Ulva* spp., and *Colpomenia* spp. decreased greatly following storms. The rapidity of the loss, and the presence of *Colpomenia* spp. on nearby beaches after storms (my observation), indicates that the reduction in epiphyte cover was likely caused by wave action. An alternative explanation is that mesograzers reinvaded carbaryl replicates when wave action prevented replacement of the plaster blocks. However, although reinvasion probably occurred (Pavia et al. 1999), the rapid consumption of large amounts of epiphytes does not seem likely as blocks also dissolved completely during a weaker storm (Day 96) without similar results. Decreases in epiphyte cover were most apparent in at the mesograzer exclusion sites where epiphyte communities were effectively ‘reset’ (i.e., became more similar to controls), showing that storm disturbance and grazing had similar effects on epiphyte composition and abundance. The mesograzers thus prevented the overgrowth of coralline turf by epiphytes during calm periods.

Chapter 5. General Discussion

This thesis investigated interactions between small mobile invertebrates and subtidal coralline turf. Coralline turf-dwelling fauna were abundant and diverse, with assemblages dominated by arthropods, gastropods and polychaetes (Chapters 2, 3, 4). The most common traits exhibited by these animals were small size, globose shape, calcareous exterior, detritus/deposit feeding, omnivorous diet and low larval mobility (Chapter 3). Faunal assemblages differed among coralline turf species and sites, with a significant interaction between host species and site, presumably because the relationship between fauna and their host alga was modified by local environmental conditions. Faunal assemblages described by taxonomic, as opposed to biological, traits were more sensitive to changes along an environmental gradient (Chapter 3). Experimental reductions of arthropod densities within subtidal coralline turfs for ~3.5 months revealed that amphipods exerted strong top-down control of epiphytes of the turf during calm periods, by preventing their overgrowth.

5.1. Interactions between turf and small mobile invertebrates - beneficial for both?

In line with previous studies on subtidal turfs (e.g., Taylor 1998, Cowles et al. 2009, Milne & Griffiths 2014), I found high densities of animals amongst coralline turfs (Chapters 2, 3, 4). The suitability of subtidal coralline turf as a habitat for fauna was influenced by spatial variation in environmental variables and, to a lesser extent, by turf morphology (or other species-related properties) (Chapters 2, 3). The influence of environmental factors and algal morphology on faunal assemblages was complex, with interactions between these two factors appearing to modify habitat suitability for fauna. However, the overall high diversity and abundances of fauna indicate that these turfs are generally good hosts for small mobile invertebrates. It is assumed that, along with a number of other benefits, fauna within coralline turfs gain protection from environmental stresses (Dommasnes 1968) and predation (Coull & Wells 1983). My research showed that important food sources provided to fauna by turf include detritus trapped amongst its matrix (as most fauna are detritus/deposit feeders) (Chapter 3) and algal epiphytes (Chapter 4).

My research showed for the first time that it is not only the small mobile invertebrates that benefit from this turf/fauna interaction, but also possibly the turf, as mesograzing arthropods reduced epiphyte loads (Chapter 4). These epiphytes may have detrimental impacts on the turf by competing with turf for resources such as light and nutrients (van Montfrans et al. 1984), and also increasing the risk of frond breakage (D’Antonio 1985). It is also possible that mesograzers promote the persistence of turf patches by feeding on the propagules of larger macroalgal species that could eventually overgrow and shade the turf (Connell 2005). Overall, my research shows that interactions between coralline turfs and small mobile invertebrates are important for supporting diverse and abundant small mobile invertebrates (Chapters 2, 3), and also probably the health of the turf (Chapter 4), in shallow temperate reefs.

5.2. Ecosystem-wide consequences of turf/invertebrate interactions

The results of interactions between turfs and their fauna may have ecosystem-wide implications. The high variability in the structure (abundance and composition) of faunal assemblages may have a number of impacts on the surrounding ecosystem. One of these is that variation in faunal abundance and composition may reflect differing food quality for benthic carnivorous fish, which can detect differences in the density (Wellenreuther & Connell 2002) and the identity (Choat & Kingett 1982) of turf-dwelling prey. The variation in assemblage structure may also determine the ability of fauna to control epiphytic algae, as grazing by some guilds (e.g., hyalid amphipods) has more of an impact on epiphytes than others (e.g., gastropods) (Chapter 4). The ability of mesograzers to structure the composition and abundance of primary producers can have a profound influence on the ecosystem, as primary producers, among other things, provide food for a range of other reef-dwelling animals. In my study, mesograzing amphipods reduced the abundance of green (*Ulva* sp.) and brown (*Colpomenia* sp.) algal epiphytes and this could be detrimental for other herbivores, e.g., fish of the genera *Girella* and *Aplodactylus* (Clements & Zemke-White 2008), that feed on these seaweeds.

The relative inedibility of coralline turf (due to its calcareous nature) means that most turf fauna feed on food sources other than their host. The majority of turf fauna are detritus/deposit feeders, although many are also suspension feeders (Chapter 3) or grazers feeding on epiphytes (Chapter 4). These feeding modes incorporate organic matter from both within the benthos (e.g., epiphytes and detritus) and the water column (e.g., suspended organic matter) into small mobile invertebrates. These food sources fuel the high productivity of these fauna (Taylor 1998, Cowles et al. 2009), which is in turn available for higher trophic levels. On rocky reefs most small fishes feed mainly on small mobile invertebrates (Jones 1988, Holbrook & Schmitt 1988).

5.3. The future of interactions between turfs and small mobile invertebrates

Coralline turfs are tolerant of a range of environmental conditions (Chapter 3). Shallow coastal habitats are becoming increasingly subject to human impacts, including higher levels of sediment and nutrients (Gorgula & Connell 2004, Thrush et al. 2003). These conditions may be detrimental to large canopy-forming macroalgae but beneficial to turfs, including coralline turfs (Connell 2005), which are becoming more prevalent worldwide (Connell et al. 2014). However, coralline algae contain magnesium calcite, which is highly susceptible to dissolution under low pH conditions, making them vulnerable to the impacts of ocean acidification (Orr et al. 2005, Hall-Spencer et al. 2008). The effects of ocean acidification on coralline algae may be further exacerbated by damage caused by solar UV radiation (Gao & Zheng 2010). The long-term persistence of coralline turf is therefore in jeopardy, and this will have major consequences not only for the small invertebrates inhabiting them but also for the invertebrates that use them as a settlement cue (Williams et al. 2008, Nelson 2009).

Like coralline turfs, the fauna inhabiting them (both epifauna and infauna) can survive a range of environmental conditions including high levels of fine sediment (Chapters 2, 3), indicating that turfs occupying human-impacted coastlines may still host a range of faunal taxa. My research also found that total animal abundance in turf was negatively correlated with fine sediment along a gradient. This finding is supported by Cowles (2010) who used a mesocosm experiment to show that suspended fine sediment (i.e., turbidity) reduced abundances of small mobile invertebrates. A reduction in overall invertebrate abundance may negatively affect animals that feed on these invertebrates.

As environmental conditions change, so may the functioning of faunal assemblages within coralline turfs (Chapter 3). My research shows that as levels of fine sediment increase so do the proportions of detritus/deposit feeding fauna, and also the number of vermiform-shaped fauna. However, some turf-dwelling fauna may be sensitive to environmental impacts (de-la-Ossa-Carretero et al. 2012, Myers & Heck 2013), e.g., in my study abundances of mesograzing amphipods in turf were negatively correlated with the fine sediment load (Chapter 3). In impacted ecosystems, a reduction in the density of mesograzing amphipods, in combination with elevated nutrient levels, is likely to cause an increase in fouling epiphytes, which may ultimately threaten the health of marine macrophytes, e.g., seagrasses (Myers & Heck 2013) and coralline turfs (Chapter 4).

Overall, due to the likely mutualistic relationship between turfs and small mobile invertebrates, any future threats to either coralline turfs or their fauna are likely to be detrimental to the other.

5.4. Conclusions

Subtidal turf-dwelling fauna were abundant and diverse (Chapters 2, 3, 4). My research highlighted the moderate to strong associations of fauna with a number of environmental variables (Chapters 2, 3), and the surprisingly relatively weak associations between fauna and features of turf morphology (Chapters 2, 3). It also stressed the influence of other unknown variables in structuring these assemblages. These probably include biotic interactions that are likely to be numerous and complex, due to the diverse and abundant nature of these fauna. Faunal assemblages described by their biological traits were less sensitive to an environmental gradient than when described by their taxonomic composition (Chapter 3), suggesting that the traits of turf-dwelling fauna were more stable than their taxonomic composition in the face of environmental variability. Small mesograzing arthropods (e.g., hyalid amphipods) exerted strong top-down control on the abundance and composition of algal epiphytes growing on subtidal coralline turfs, suggesting that the relationship between turfs and arthropod mesograzers is also beneficial for the turf (i.e., mutualistic) (Chapter 4).

5.5. Future Research

Several questions are worthy of further investigation:

(1) When fauna are associated with a particular host coralline species, is this due to the host's morphology or some other unmeasured species-specific property? Artificial turfs could be used to separate the effects of host morphology from other species-specific properties of the host (e.g., Kelaher 2003).

(2) What are the impacts of individual environmental variables on turf assemblages? This could be investigated by transplanting patches of turf (with faunal assemblages intact) to mesocosms, where the impacts of different individual environmental variables on faunal assemblages could be experimentally manipulated. For example, Cowles (2010) used mesocosms to investigate the influence of suspended sediment on small invertebrates inhabiting artificial seaweed units.

(3) Was the unexplained variation in faunal assemblage patterns amongst coralline turfs of different species driven by biotic interactions occurring within these assemblages? Biotic interactions between animals inhabiting coralline turfs could be investigated in laboratory experiments (e.g., Mathias et al. 2012, Hayakawa et al. 2012). These could be used to determine the impacts of biotic interactions such as predation and competition on the growth and survival of turf-dwelling faunal taxa. Field experiments in general are likely to be difficult due to the small size and high mobility of many of the turf fauna (Edgar & Aoki 1993).

(4) Besides arthropods, do other mesograzing groups, e.g., gastropods, affect the abundance and composition of epiphytic algae on subtidal coralline turfs? This could be investigated using similar cageless methods to those used in Chapter 4. However to do this, carbaryl (used to kill arthropods) would need to be replaced with a gastropod-specific poison, e.g., copper (Sousa 1979, Johnson 1992). Although less realistic than field-based studies, the impacts of gastropod herbivory on turf could also be investigated using mesocosm experiments (e.g., Atalah et al. 2007).

(5) Does the magnitude of mesograzer impacts on epiphyte abundance and composition in subtidal coralline turf change with season? In my study, abundances of arthropod mesograzers were experimentally reduced during spring and summer (Chapter 4). It would be interesting to use the same methods to determine whether their ability to control algal epiphyte abundance changes with season. As ephemeral algal epiphytes bloom during spring and summer, it is possible that the impacts of mesograzers in other seasons may be smaller, as conditions in these seasons are often less favourable for algal growth (e.g., cooler water temperatures and fewer daylight hours).

(6) Do mesograzers feed on the propagules of larger macroalgal species, e.g., *Ecklonia radiata*, and prevent these from overgrowing the turf? The presence of turf may prevent the establishment of larger macroalgae, thus maintaining turf patches within seaweed forests. This could be due to the presence of sediment within the turf, as this is detrimental to the settlement of macroalgal propagules (Airoldi 1998, Schiel et al. 2006). However, grazing of the early life stages of macroalgae by mesograzers (e.g., Lotze et al. 2001, Chapter 4) may also stop the establishment of macroalgae in turf patches. To determine whether mesograzers play a role in maintaining turf patches in kelp forests, field experiments, using the same methods of arthropod reduction applied in Chapter 4, could be implemented in turf patches. However, the timing of these experiments would need to coincide with the recruitment periods for larger macroalgal species, e.g., *Ecklonia radiata* has fertile sori from may to november (Schiel 1988). For the most conclusive results, all mesograzing guilds (not just arthropods) would need to be excluded from the turf e.g., herbivorous gastropods can also feed on the early life stages of macroalgae (Parker & Chapman 1994).

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Appendix

Appendix 2.1 Mean (n = 4) abundance (ind.m^{-2}) of all taxa found in association with five coralline turf species from seven sites on shallow rocky reefs in northeastern New Zealand. See Fig. 2.1 for full site names.

		Amphiroa anceps			***Corallina officinalis***			***Jania rosea***		***Jania sagittata***			***Corallina* sp. 1**		
Class/Order	**Taxa**	**GW**	**GE**	**WR**	**KB**	**GE**	**OP**	**OP**	**GN2**	**GN2**	**GN1**	**OP**	**GE**	**WR**	**GW**
Gastropod	***Cominella quoyana***	0	0	32	0	0	0	0	0	0	0	0	0	0	0
Gastropod	***Seila* sp.**	0	0	32	0	0	0	0	0	0	0	0	32	32	32
Gastropod	***Zemitrella pseudomarginata***	0	0	0	0	0	0	32	0	0	0	32	0	0	64
Gastropod	***Zemitrella choava***	159	191	95	223	64	0	637	64	64	32	159	0	32	159
Gastropod	***Austromitra rubiginosa***	32	0	0	95	0	0	32	0	0	32	32	0	0	32
Gastropod	***Eatoniella limbata***	32	764	1496	2769	127	9834	6365	446	859	255	6110	159	223	350
Gastropod	***Pisinna semiplicata***	95	891	2769	0	32	0	0	0	32	0	32	1750	159	255
Gastropod	***Eatoniella roseola***	0	64	0	0	0	0	0	0	0	0	0	0	0	0
Gastropod	***Eatoniella globosa***	0	0	0	0	0	0	0	0	0	0	0	127	0	64
Gastropod	***Eatoniella olivacea***	0	0	637	2832	0	255	95	0	0	0	95	0	0	0
Gastropod	***Eatoniella albocolumella***	0	95	32	7543	64	732	2896	64	0	0	1337	0	2482	0
Gastropod	***Pisinna zosterophila***	318	255	382	2641	477	223	446	0	0	0	605	64	2100	1273
Gastropod	***Epitonium jukesianum***	0	64	0	0	0	0	0	0	0	0	0	0	0	32
Gastropod	***Eulima perspicua***	0	0	32	0	0	0	0	0	0	0	0	0	0	0
Gastropod	***Lamellaria ophione***	0	0	64	0	0	0	0	0	32	32	0	0	0	0
Gastropod	***Mesoginella koma***	0	382	255	0	191	32	0	0	0	0	0	127	64	0
Gastropod	***Dentimargo cairoma***	0	0	32	0	32	0	0	0	0	0	0	0	0	0
Gastropod	***Dicathais orbita***	0	0	0	0	0	0	32	0	0	64	0	0	0	32
Gastropod	***Muricopsis octogonus***	0	0	0	32	0	0	0	0	0	0	0	0	0	32
Gastropod	***Murexsul* sp.**	0	0	0	0	0	0	0	0	0	0	0	0	32	0
Gastropod	***Xymene traversi***	32	0	0	32	0	32	159	64	64	64	0	64	64	255

Appendix 2.1 continued

		Amphiroa anceps			***Corallina officinalis***			***Jania rosea***		***Jania sagittata***			***Corallina* sp. 1**		
Class/Order	**Taxa**	**GW**	**GE**	**WR**	**KB**	**GE**	**OP**	**OP**	**GN2**	**GN2**	**GN1**	**OP**	**GE**	**WR**	**GW**
Gastropod	***Doto* sp.**	0	0	0	0	0	0	0	0	95	127	0	0	0	0
Gastropod	***Chemnitzia* sp.**	32	32	64	159	0	32	95	0	0	0	0	32	64	64
Gastropod	***Eatonina subflavescens***	32	0	0	0	0	0	0	0	32	0	0	32	0	0
Gastropod	***Pisinna olivacea impressa***	0	0	1400	64	0	0	0	0	0	0	32	0	64	0
Gastropod	***Fictonoba carnosa carnosa***	95	827	1368	796	1050	286	668	0	0	0	191	95	509	64
Gastropod	***Fictonoba rufolactea***	2164	350	255	987	223	2514	3883	95	32	64	2228	255	2355	2323
Gastropod	***Merelina taupoensis***	286	127	700	764	95	32	1400	95	32	127	255	64	700	223
Gastropod	***Merelina lyalliana***	0	0	32	0	0	0	0	0	0	0	0	0	0	0
Gastropod	***Onoba candidissima***	0	64	0	0	32	0	32	0	0	0	0	0	0	0
Gastropod	**Triphoridae**	0	127	95	159	95	95	32	191	159	95	64	223	0	255
Gastropod	***Astraea heliotropium***	0	32	0	32	0	32	0	0	0	0	32	0	0	64
Gastropod	**Polyplacophora**	0	0	32	0	0	32	0	0	0	0	0	64	64	0
Gastropod	**Rissoidae**	0	64	764	32	64	32	127	0	0	0	0	32	605	0
Gastropod	***Rissoina chathamensis***	0	0	64	32	0	0	64	0	0	0	0	0	32	0
Gastropod	***Rissoina achatinoides***	0	0	0	0	0	0	0	0	0	0	0	0	64	0
Gastropod	***Sigapatella novaezelandiae***	32	0	0	0	0	0	0	0	0	0	0	0	0	0
Gastropod	***Pusillina semireticulata***	32	0	0	0	0	0	0	0	0	32	0	0	0	0
Gastropod	***Herpetopoma* sp.**	32	0	0	0	0	0	0	0	0	0	0	0	32	0
Gastropod	***Zaclys* sp.**	0	0	0	0	0	0	0	0	32	0	0	0	0	0
Gastropod	***Cantharidella tesselata***	32	0	0	0	0	0	0	0	0	0	0	0	64	0
Gastropod	***Trochus viridus***	0	0	32	0	0	0	0	0	0	0	0	0	0	0

Appendix 2.1 continued

		Amphiroa anceps			***Corallina officinalis***			***Jania rosea***		***Jania sagittata***			***Corallina* sp. 1**		
Class/Order	**Taxa**	**GW**	**GE**	**WR**	**KB**	**GE**	**OP**	**OP**	**GN2**	**GN2**	**GN1**	**OP**	**GE**	**WR**	**GW**
Gastropod	***Risellopsis varia***	32	0	0	0	0	0	0	0	0	0	0	0	0	0
Gastropod	***Zemitrella fallax***	0	0	0	0	0	0	0	0	0	0	0	0	0	32
Gastropod	***Tugali* sp.**	0	0	0	0	0	0	0	0	0	0	0	0	32	0
Gastropod	***Runnica katipoides***	32	0	0	0	0	0	0	0	0	0	0	0	0	0
Gastropod	***Calliostoma punctulata***	0	0	0	0	0	0	0	0	0	0	0	0	0	32
Gastropod	***Rissoina achatina***	0	0	64	0	0	0	0	0	0	0	0	0	0	0
Echinoderm	***Evechinus chloroticus***	0	159	223	127	0	64	32	0	32	0	64	95	32	64
Echinoderm	***Cosinasterias muricata***	0	0	0	0	0	95	0	0	0	0	0	0	0	0
Echinoderm	**Ophiuroidea**	446	891	1082	350	95	191	637	191	223	446	286	318	127	255
Echinoderm	***Amphiura* sp.**	64	0	0	0	0	64	32	0	0	0	0	0	0	0
Echinoderm	***Amphipholis squamata***	318	477	1528	286	127	987	127	64	64	0	95	286	509	127
Echinoderm	***Ophiactis* sp.**	191	95	95	0	0	32	32	0	159	95	0	64	159	127
Polychaete	**Nemertea**	0	0	0	0	0	0	0	0	0	0	0	0	0	32
Polychaete	**Nematoda**	318	159	127	1400	32	382	318	668	382	318	350	95	414	414
Polychaete	***Eunice* sp.**	0	95	382	0	573	0	0	0	0	0	0	95	127	0
Polychaete	**Lumbrineridae**	32	0	32	414	0	127	32	0	0	95	64	0	32	0
Polychaete	***Nothria* sp.**	318	223	0	0	541	382	64	0	0	0	255	0	255	605
Polychaete	***Brevibrachium maculatum***	0	32	0	0	0	0	64	0	0	0	0	0	0	0
Polychaete	***Ophiodromus* sp.**	32	0	32	32	64	32	0	0	0	64	0	0	64	32
Polychaete	***Nereis falcaria***	923	859	1050	12825	286	2100	3533	1273	1655	1878	3373	1655	1719	1782
Polychaete	***Perinereis* sp.**	64	0	0	382	0	0	0	0	0	0	0	64	127	0

Appendix 2.1 continued

		Amphiroa anceps			***Corallina officinalis***			***Jania rosea***		***Jania sagittata***			***Corallina* sp. 1**		
Class/Order	**Taxa**	**GW**	**GE**	**WR**	**KB**	**GE**	**OP**	**OP**	**GN2**	**GN2**	**GN1**	**OP**	**GE**	**WR**	**GW**
Polychaete	***Neanthes* sp.**	0	0	0	0	0	0	0	0	0	0	0	0	0	32
Polychaete	***Platynereis* sp.**	191	191	127	95	0	95	286	191	64	127	95	64	159	64
Polychaete	**Phyllodocidae**	64	0	0	0	0	0	0	0	64	95	32	32	64	64
Polychaete	***Lepidonotus polychromus***	477	64	159	95	0	95	0	95	95	95	0	64	127	64
Polychaete	***Odontosyllis polycera***	127	64	0	64	32	127	0	0	0	0	0	95	0	32
Polychaete	**Syllidae**	1559	1846	2196	6588	382	1178	1209	923	1337	1464	1878	891	1687	1178
Decapod	***Eurynolambrus australis***	32	0	0	0	0	0	0	0	0	32	0	0	0	0
Decapod	***Notomithrax minor***	32	0	0	0	0	0	0	0	0	0	0	0	0	0
Decapod	***Halicarcinus* spp.**	286	64	32	95	32	605	223	446	191	286	159	64	0	64
Decapod	**Paguridae**	159	1878	1050	223	637	732	923	127	95	127	414	159	127	1368
Decapod	***Petrolisthes novaezelandiae***	64	64	0	0	0	64	0	0	159	95	0	0	0	32
Decapod	***Liocarcinus corrugatus***	0	0	32	0	0	0	0	0	0	0	0	32	0	0
Decapod	***Alpheus* sp.**	159	32	32	159	0	0	0	0	0	286	32	32	127	127
Decapod	***Hippolyte* sp.**	32	0	0	0	0	0	0	0	0	0	0	0	0	0
Isopod	***Plakarthrium typicum***	32	32	0	0	0	0	0	0	0	32	0	0	0	0
Isopod	***Batedotea elongata***	0	0	32	0	0	0	0	0	0	0	0	0	0	0
Isopod	**Gnathiidae**	0	0	0	0	0	0	95	0	0	32	0	64	32	32
Isopod	**Anthuridae**	0	0	0	0	0	32	32	0	0	0	0	0	32	0
Isopod	***Cassidinopsis admirabilis***	891	382	668	1241	127	32	668	318	32	32	923	987	446	286
Isopod	***Neastacilla* sp.**	95	1114	350	0	0	350	64	32	32	127	0	0	0	64
Isopod	***Cymodocella capra***	0	0	32	0	0	0	0	0	0	64	0	64	64	0

Appendix 2.1 continued

		Amphiroa anceps			***Corallina officinalis***			***Jania rosea***		***Jania sagittata***			***Corallina* sp. 1**		
Class/Order	**Taxa**	**GW**	**GE**	**WR**	**KB**	**GE**	**OP**	**OP**	**GN2**	**GN2**	**GN1**	**OP**	**GE**	**WR**	**GW**
Isopod	***Joeropsis* sp.**	127	0	0	414	0	32	32	0	95	95	32	0	95	32
Isopod	**Holognathidae**	0	32	0	0	64	0	0	0	0	0	0	0	0	0
Isopod	**Munnidae**	0	0	0	0	0	0	0	0	0	32	0	0	0	0
Isopod	***Dynamenoides decima***	0	0	32	0	0	0	0	0	0	0	0	0	0	0
Isopod	***Cilicaea dolorosa***	32	0	64	32	32	159	95	223	127	32	95	64	32	127
Isopod	***Ischyromene* sp.**	64	0	0	0	0	0	0	0	0	0	0	0	0	0
Isopod	***Dynamenopsis varicolor***	0	0	0	32	0	0	0	32	0	64	0	0	0	0
Arachnida	**Arachnida**	0	0	0	0	0	32	0	0	0	0	0	0	0	0
Trichoptera	***Philanisus plebeius***	64	509	414	350	350	223	318	0	0	0	95	159	32	95
Ostracoda	**Ostracoda**	1082	2514	1528	1273	1273	1018	1432	0	0	0	1146	1464	923	1114
Cumacea	**Cumacea**	0	446	159	64	414	0	0	32	0	0	0	95	32	191
Arachnida	**Halacaridae**	0	0	0	32	0	0	0	0	0	0	0	0	0	0
Pycnogonida	**Pycnogonida**	32	32	32	32	0	350	127	255	318	191	159	0	255	159
Tanaid	***Pagurapseudes* sp.**	95	5792	1591	191	8784	509	1591	0	0	0	191	414	64	3214
Tanaid	**Apseudidae**	1973	477	1623	95	0	32	318	159	127	255	223	477	827	286
Tanaid	**Tanaidacea**	64	95	0	159	0	127	446	64	95	0	159	0	64	64
Amphipod	***Gitanopsis* sp.**	223	0	0	32	0	32	382	350	605	127	32	0	127	159
Amphipod	***Aora typica***	127	64	732	64	95	382	223	286	127	0	127	605	477	159
Amphipod	**Aoridae**	32	0	127	1241	0	0	64	286	64	286	32	127	32	0
Amphipod	***Caprellina longicollis***	0	0	0	127	64	95	3851	1178	64	1018	1050	0	32	95
Amphipod	***Caprella equilibra***	0	0	0	0	0	0	0	605	255	95	0	0	0	0

Appendix 2.1 continued

		Amphiroa anceps			*Corallina officinalis*			*Jania rosea*		*Jania sagittata*			*Corallina* sp. 1		
Class/Order	**Taxa**	**GW**	**GE**	**WR**	**KB**	**GE**	**OP**	**OP**	**GN2**	**GN2**	**GN1**	**OP**	**GE**	**WR**	**GW**
Amphipod	***Ceina egregia***	286	0	127	95	32	127	191	95	32	0	255	64	0	64
Amphipod	***Taihape karori***	0	0	0	859	127	64	0	32	0	0	0	159	159	127
Amphipod	***Paradexamine houtete***	95	64	64	127	668	95	318	0	95	64	127	32	0	0
Amphipod	**Eusiridae**	0	0	0	0	0	0	64	0	64	0	0	0	0	64
Amphipod	***Protohyale* spp.**	668	446	286	1910	350	382	2005	764	64	95	350	732	159	159
Amphipod	***Notopoma* sp.**	127	414	0	0	0	0	32	0	0	0	64	446	318	159
Amphipod	***Ericthonius pugnax***	64	1050	95	0	0	0	0	32	32	0	32	0	0	0
Amphipod	**Ischyroceridae**	541	0	0	637	32	700	509	1591	1750	2260	1878	286	318	477
Amphipod	**Lysianassidae**	95	255	64	509	0	2514	1146	32	32	127	700	64	32	95
Amphipod	***Elasmopus* spp.**	223	64	0	0	0	95	859	286	605	923	223	0	32	382
Amphipod	***Maera* sp.**	1114	0	64	127	0	0	0	32	32	1082	32	191	64	0
Amphipod	***Nihotunga noa***	0	0	0	0	0	0	0	64	0	0	0	0	0	0
Amphipod	***Gammaropsis* sp.**	1528	1814	4296	7638	223	4010	2069	2355	1082	2832	3914	541	1114	1400
Amphipod	**Phoxocephalidae**	0	318	255	382	95	0	32	0	0	0	32	64	0	0
Amphipod	***Podocerus karu***	3278	4583	5410	17536	318	5442	3119	4615	1018	1368	7956	923	2260	2705
Amphipod	***Podocerus wanganui***	0	0	0	0	0	0	541	414	127	32	0	0	0	0
Amphipod	***Tetradeion crassum***	223	2992	95	0	4360	796	2864	64	318	0	605	2355	64	127
Amphipod	***Raumahara rongo***	32	32	0	95	0	0	0	796	350	382	127	0	32	32
Amphipod	***Seba typica***	95	64	32	0	0	0	0	0	32	0	0	32	127	32
Amphipod	***Hornellia whakatane***	573	350	541	1082	191	573	891	32	95	32	637	573	509	318
Amphipod	***Podocerus manawatu***	0	32	32	0	0	0	541	0	0	0	0	0	0	0
Amphipod	**Ampithoidae**	0	0	0	0	32	0	0	0	0	0	0	0	0	0
Amphipod	***Bircenna* sp.**	0	32	0	0	0	0	0	0	0	0	0	0	95	0
Amphipod	***Parapherusa crassipes***	255	32	0	1178	0	159	446	1591	2514	2196	1018	0	668	1082

Appendix 3.1 Fuzzy coded trait values for each faunal taxa used in Biological Traits Analysis.

		Feeding Traits					Trophic Level			Method of Egg Deposition			Mean Body Size		Adult Mobility			Larval Mobility		Body Form			Calcareous Exterior	
Class	Taxa	Grazer	Predator	Detritus/Deposit	Scavenger	Suspension	Herbivore	Carnivore	Omnivore	Brooded	On substrate	Planktonic	Small	Large	High	Moderate	Low	High	Low	Vermiform	Globose	Flattened	Yes	No
Gastropoda	*Zemitrella* spp.	0.17	0.5	0.17	0.17	0	0	0	1	0	1	0	1	0	0	0	1	0.5	0.5	0.2	0.8	0	1	0
Gastropoda	*Austromitra* sp.	0	1	0	0	0	0	1	0	0	1	0	1	0	0	0	1	0.5	0.5	0.2	0.8	0	1	0
Gastropoda	*Pusillina semireticulata*	0.5	0	0.5	0	0	1	0	0	0	1	0	1	0	0	0	1	0.5	0.5	0.1	0.9	0	1	0
Gastropoda	*Eatoniella limbata*	0.5	0	0.5	0	0	1	0	0	0	1	0	1	0	0	0	1	0	1	0.1	0.9	0	1	0
Gastropoda	*Pisinna semiplicata*	0	0	1	0	0	1	0	0	0	1	0	1	0	0	0	1	0	1	0.1	0.9	0	1	0
Gastropoda	*Eatonina subflavescens*	0.5	0	0.5	0	0	1	0	0	0	1	0	1	0	0	0	1	0	1	0	1	0	1	0
Gastropoda	*Pisinna zosterophila*	0	0	1	0	0	1	0	0	0	1	0	1	0	0	0	1	0	1	0.2	0.8	0	1	0
Gastropoda	*Epitonium jukesianum*	0	1	0	0	0	0	1	0	0	1	0	1	0	0	0	1	1	0	0.3	0.7	0	1	0
Gastropoda	*Mesoginella koma*	0	0.5	0	0.5	0	0	1	0	0	1	0	0	1	0	0	1	0	1	0.1	0.9	0	1	0
Gastropoda	*Dentimargo cairoma*	0	0.5	0	0.5	0	0	1	0	0	1	0	1	0	0	0	1	0	1	0.3	0.7	0	1	0
Gastropoda	*Xymene traversi*	0	1	0	0	0	0	1	0	0	1	0	0	1	0	0	1	0.5	0.5	0.2	0.8	0	1	0
Gastropoda	*Chemnitzia* sp.	0	1	0	0	0	0	1	0	0	1	0	1	0	0	0	1	1	0	0.5	0.5	0	1	0
Gastropoda	*Pisinna olivacea impressa*	0	0	1	0	0	1	0	0	0	1	0	1	0	0	0	1	0	1	0.2	0.8	0	1	0
Gastropoda	*Fictonoba carnosa carnosa*	0	0	1	0	0	1	0	0	0	1	0	1	0	0	0	1	0.5	0.5	0.3	0.7	0	1	0
Gastropoda	*Fictonoba rufolactea*	0	0	1	0	0	1	0	0	0	1	0	1	0	0	0	1	0.5	0.5	0.3	0.7	0	1	0
Gastropoda	*Merelina taupoensis*	0.5	0	0.5	0	0	1	0	0	0	1	0	1	0	0	0	1	0.5	0.5	0.4	0.6	0	1	0
Gastropoda	*Merelina* sp.	0.5	0	0.5	0	0	1	0	0	0	1	0	1	0	0	0	1	0.5	0.5	0.4	0.6	0	1	0
Gastropoda	*Onoba fumata*	0.5	0	0.5	0	0	1	0	0	0	1	0	1	0	0	0	1	0	1	0	1	0	1	0
Gastropoda	*Onoba candidissima*	0.5	0	0.5	0	0	1	0	0	0	1	0	1	0	0	0	1	0	1	0.3	0.7	0	1	0
Gastropoda	*Merelina lacunosa*	0.5	0	0.5	0	0	1	0	0	0	1	0	1	0	0	0	1	0.5	0.5	0.4	0.6	0	1	0
Gastropoda	*Herpetopoma* sp.	1	0	0	0	0	1	0	0	0	1	0	1	0	0	0	1	0.5	0.5	0	1	0	1	0
Gastropoda	*Bouchetriphora* sp.	0	1	0	0	0	0	1	0	0	1	0	1	0	0	0	1	0.5	0.5	0.6	0.4	0	1	0
Gastropoda	*Astraea heliotropium*	1	0	0	0	0	1	0	0	0	0.5	0.5	0	1	0	0	1	1	0	0	0.8	0.2	1	0
Gastropoda	*Eatoniella albocolumella*	0.5	0	0.5	0	0	1	0	0	0	1	0	1	0	0	0	1	0	1	0.1	0.9	0	1	0
Gastropoda	*Eatoniella olivacea*	0.5	0	0.5	0	0	1	0	0	0	1	0	1	0	0	0	1	0	1	0.1	0.9	0	1	0
Gastropoda	*Eatoniella globosa*	0.5	0	0.5	0	0	1	0	0	0	1	0	1	0	0	0	1	0	1	0.1	0.9	0	1	0
Gastropoda	*Rissoina fucosa*	0.5	0	0.5	0	0	1	0	0	0	1	0	1	0	0	0	1	0.5	0.5	0.3	0.7	0	1	0
Gastropoda	*Rissoina* sp.	0.5	0	0.5	0	0	1	0	0	0	1	0	1	0	0	0	1	0.5	0.5	0.3	0.7	0	1	0
Gastropoda	*Taron* sp.	0	0.5	0	0.5	0	0	1	0	0	1	0	1	0	0	0	1	0.5	0.5	0.1	0.9	0	1	0
Gastropoda	*Sigapatella* spp.	0	0	0	0	1	0	0	1	1	0	0	0	1	0	0	1	0	1	0	0.5	0.5	1	0
Gastropoda	Cantharidus sp.	1	0	0	0	0	1	0	0	0	0.5	0.5	1	0	0	0	1	0.5	0.5	0.2	0.8	0	1	0
Gastropoda	*Maoricolpus roseus*	0	0	0.5	0	0.5	0	0	1	0	1	0	0	1	0	0	1	1	0	0.7	0.3	0	1	0
Gastropoda	*Rissoina fictor*	0.5	0	0.5	0	0	1	0	0	0	1	0	0	1	0	0	1	0.5	0.5	0.3	0.7	0	1	0
Gastropoda	*Neoguraleus sinclairi*	0	1	0	0	0	0	1	0	0	1	0	0	1	0	0	1	1	0	0.2	0.8	0	1	0
Gastropoda	*Trochus viridis*	1	0	0	0	0	1	0	0	0	0.5	0.5	0	1	0	0	1	1	0	0.1	0.9	0	1	0
Gastropoda	*Bulla quoyii*	0.5	0	0.5	0	0	1	0	0	0	1	0	1	0	0	0	1	1	0	0.1	0.9	0	1	0
Gastropoda	*Zaclys* sp.	0	1	0	0	0	0	1	0	0	1	0	1	0	0	0	1	1	0	0.6	0.4	0	1	0
Gastropoda	*Runnica katipoides*	0.5	0	0.5	0	0	1	0	0	0	1	0	1	0	0	0	1	0	1	0.33	0.33	0.33	1	0
Polyplacophora	*Notoplax violacea*	0	0.5	0	0.5	0	0	1	0	0	0	1	0	1	0	0	1	0.95	0.05	0.1	0.4	0.5	1	0
Polyplacophora	*Leptochiton inquinatus*	1	0	0	0	0	1	0	0	0	0	1	0	1	0	0	1	0.95	0.05	0.1	0.4	0.5	1	0
Polyplacophora	Polyplacophora	1	0	0	0	0	1	0	0	0	0	1	0	1	0	0	1	0.95	0.05	0.1	0.4	0.5	1	0
Polyplacophora	Acanthochitonidae	1	0	0	0	0	1	0	0	0	0	1	0	1	0	0	1	0.95	0.05	0.1	0.4	0.5	1	0
Polyplacophora	*Sypharochiton pelliserpentis*	1	0	0	0	0	1	0	0	0	0	1	0	1	0	0	1	0.95	0.05	0.1	0.4	0.5	1	0
Polyplacophora	*Onithochiton* sp.	1	0	0	0	0	1	0	0	0.8	0	0.2	0	1	0	0	1	0.2	0.8	0.1	0.4	0.5	1	0
Bivalvia	*Neolepton antipodum*	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	1	1	0	0	0.8	0.2	1	0
Bivalvia	Nuculidae	0	0	1	0	0	1	0	0	0	0	1	0	1	0	0	1	1	0	0	0.7	0.3	1	0
Ophiuroidea	Ophiuroidea	0	0	0.33	0.33	0.33	0	0	1	0.5	0	0.5	1	0	0	0	1	0.5	0.5	0	0.5	0.5	1	0
Ophiuroidea	*Ophiactis resiliens*	0	0	0.33	0.33	0.33	0	0	1	0.5	0	0.5	0	1	0	0	1	0.5	0.5	0	0.5	0.5	1	0
Ophiuroidea	Amphiura sp.	0	0	0.33	0.33	0.33	0	0	1	0.5	0	0.5	0	1	0	0	1	0.5	0.5	0	0.5	0.5	1	0
Ophiuroidea	*Amphipholis squamata*	0	0	0.33	0.33	0.33	0	0	1	1	0	0	0	1	0	0	1	0	1	0	0.5	0.5	1	0
Polychaeta	Dorvilleidae	0.25	0.25	0.25	0.25	0	0	0	1	0.45	0.1	0.45	1	0	1	0	0	0.55	0.45	1	0	0	0	1
Polychaeta	*Eunice* spp.	0.1	0.35	0.2	0.35	0	0	0	1	0.1	0.45	0.45	1	0	0	0	1	0.8	0.2	1	0	0	0	1
Polychaeta	*Nothria* sp.	0.1	0.35	0.2	0.35	0	0	0	1	0.1	0.1	0.8	1	0	0	0	1	0.8	0.2	1	0	0	0	1
Polychaeta	*Ophiodromus* sp.	0	1	0	0	0	0	1	0	0.1	0.1	0.8	1	0	1	0	0	0.8	0.2	1	0	0	0	1
Polychaeta	*Perinereis* sp.	0.25	0.25	0.25	0.25	0	0	0	1	0	0	1	0	1	1	0	0	1	0	1	0	0	0	1
Polychaeta	*Platynereis* sp.	0.25	0.25	0.25	0.25	0	0	0	1	0	0	1	0	1	1	0	0	1	0	1	0	0	0	1
Polychaeta	*Nereis falcaria*	0.25	0.25	0.25	0.25	0	0	0	1	0	0	1	1	0	1	0	0	1	0	1	0	0	0	1
Polychaeta	Phyllodocidae	0	0.5	0	0.5	0	0	1	0	0.1	0.1	0.8	1	0	1	0	0	0.8	0.2	1	0	0	0	1

Appendix 3.1 Continued

		Feeding Traits					Trophic Level			Method of Egg Deposition			Mean Body Size		Adult Mobility			Larval Mobility		Body Form			Calcareous Exterior	
Class	**Taxa**	**Grazer**	**Predator**	**Detritus/Deposit**	**Scavenger**	**Suspension**	**Herbivore**	**Carnivore**	**Omnivore**	**Brooded**	**On substrate**	**Planktonic**	**Small**	**Large**	**High**	**Moderate**	**Low**	**High**	**Low**	**Vermiform**	**Globose**	**Flattened**	**Yes**	**No**
Polychaeta	*Lepidonotus polychromus*	0	0.5	0	0.5	0	0	1	0	0	0	1	0	1	1	0	0	1	0	0.8	0	0.2	0	1
Polychaeta	Syllidae	0.25	0.25	0.25	0.25	0	0	0	1	0.3	0	0.7	1	0	1	0	0	0.7	0.3	1	0	0	0	1
Polychaeta	Onuphidae	0.25	0.25	0.25	0.25	0	0	0	1	0.3	0	0.7	1	0	0	0	1	0.7	0.3	1	0	0	0	1
Nematoda	Nematoda	0.25	0.25	0.25	0.25	0	0	0	1	0.33	0.33	0.33	1	0	0	0	1	0.5	0.5	1	0	0	0	1
Decapoda	*Pilumnus lumpinus*	0	0	0	1	0	0	1	0	1	0	0	0	1	1	0	0	1	0	0	0.5	0.5	1	0
Maxillopoda	Harpacticoida	0.25	0.25	0.25	0.25	0	0	0	1	1	0	0	1	0	1	0	0	1	0	0.2	0.8	0	1	0
Pycnogonida	Pycnogonida	0	1	0	0	0	0	1	0	1	0	0	1	0	0	0	1	0	1	0	0.3	0.7	1	0
Arachnida	Arachnida	0	1	0	0	0	0	1	0	0	1	0	1	0	0	1	0	0	1	0	0.8	0.2	1	0
Ostracoda	Ostracoda	0.2	0.2	0.2	0.2	0.2	0	0	1	0.33	0.33	0.33	1	0	1	0	0	1	0	0	0.9	0.1	1	0
Insecta	*Philanisus plebeius*	0.8	0.2	0	0	0	0	0	1	0	1	0	1	0	0	1	0	0	1	1	0	0	1	0
Malacostraca	*Notomithrax minor*	0.5	0.5	0	0	0	0	0	1	1	0	0	0	1	1	0	0	1	0	0	0.6	0.4	1	0
Malacostraca	*Halicarcinus cookii*	0.25	0.25	0.25	0.25	0	0	0	1	1	0	0	1	0	1	0	0	1	0	0	0.5	0.5	1	0
Malacostraca	Paguridae	0	0.333	0.333	0.333	0	0	0	1	1	0	0	1	0	0	0	1	1	0	0.4	0.6	0	1	0
Malacostraca	*Petrolisthes novaezelandiae*	0	0	0	0.5	0.5	0	0	1	1	0	0	1	0	1	0	0	1	0	0	0.4	0.6	1	0
Malacostraca	*Liocarcinus corrugatus*	0.25	0.25	0.25	0.25	0	0	0	1	1	0	0	0	1	1	0	0	1	0	0	0.5	0.5	1	0
Malacostraca	*Alpheus* sp.	0	0	0	1	0	0	1	0	1	0	0	0	1	0	1	0	1	0	0.6	0.4	0	1	0
Malacostraca	*Hippolyte* sp.	0.25	0.25	0.25	0.25	0	0	0	1	1	0	0	0	1	1	0	0	1	0	0.8	0.2	0	1	0
Malacostraca	Mysidae	0	0	0.5	0	0.5	0	0	1	1	0	0	1	0	1	0	0	0	1	0.6	0.4	0	1	0
Malacostraca	*Amphoroidea media*	1	0	0	0	0	1	0	0	1	0	0	0	1	1	0	0	0	1	0.1	0.4	0.5	1	0
Malacostraca	Paranthuridae	0.25	0.5	0.25	0	0	0	0	1	1	0	0	1	0	0	1	0	0	1	1	0	0	1	0
Malacostraca	*Cassidinopsis admirabilis*	0.5	0	0.5	0	0	1	0	0	1	0	0	1	0	1	0	0	0	1	0	0.8	0.2	1	0
Malacostraca	*Neastacilla* sp.	0	0	0	0	1	0	0	1	1	0	0	1	0	1	0	0	0	1	1	0	0	1	0
Malacostraca	*Cymodocella capra*	0.5	0	0.5	0	0	1	0	0	1	0	0	1	0	1	0	0	0	1	0	0.8	0.2	1	0
Malacostraca	*Joeropsis* sp.	0.2	0.2	0.2	0.2	0.2	0	0	1	1	0	0	1	0	1	0	0	0	1	0.3	0	0.7	1	0
Malacostraca	Munnidae	0	0	0	1	0	0	1	0	1	0	0	0	1	1	0	0	0	1	0	0.5	0.5	1	0
Malacostraca	Holognathidae	0.2	0.2	0.2	0.2	0.2	0	0	1	1	0	0	1	0	0	1	0	0	1	0.8	0	0.2	1	0
Malacostraca	*Dynamenopsis varicolor*	0.5	0	0.5	0	0	1	0	0	1	0	0	1	0	1	0	0	0	1	0	0.5	0.5	1	0
Malacostraca	*Cilicaea dolorosa*	0.5	0	0.5	0	0	1	0	0	1	0	0	1	0	1	0	0	0	1	0	0.7	0.3	1	0
Malacostraca	*Scutuloidea* sp.	0.8	0	0.2	0	0	1	0	0	1	0	0	1	0	1	0	0	0	1	0	0.6	0.4	1	0
Malacostraca	*Cyclaspis* sp.	0.25	0.25	0.25	0.25	0	0	0	1	1	0	0	1	0	1	0	0	0	1	0.5	0.5	0	1	0
Malacostraca	Diastylidae	0.25	0.25	0.25	0.25	0	0	0	1	1	0	0	1	0	1	0	0	0	1	0.5	0.5	0	1	0
Malacostraca	*Pagurapseudes* sp.	0.2	0.2	0.2	0.2	0.2	0	0	1	1	0	0	1	0	0	0	1	0	1	0.4	0.6	0	1	0
Malacostraca	Apseudidae	0.2	0.2	0.2	0.2	0.2	0	0	1	1	0	0	1	0	0	1	0	0	1	0.1	0.8	0.1	1	0
Malacostraca	*Tanaopsis* sp.	0.2	0.2	0.2	0.2	0.2	0	0	1	1	0	0	1	0	0	1	0	0	1	1	0	0	1	0
Malacostraca	*Parakonarus kopure*	0.2	0.2	0.2	0.2	0.2	0	0	1	1	0	0	1	0	0	1	0	0	1	1	0	0	1	0
Malacostraca	*Gitanopsis* sp.	0	0.25	0.25	0.25	0.25	0	0	1	1	0	0	1	0	1	0	0	0	1	0	0.2	0.8	1	0
Malacostraca	*Aora* sp.	0.33	0	0.33	0	0.33	0	0	1	1	0	0	1	0	0	1	0	0	1	0.1	0.1	0.8	1	0
Malacostraca	*Caprellina longicollis*	0.2	0.2	0.2	0.2	0.2	0	0	1	1	0	0	1	0	1	0	0	0	1	1	0	0	1	0
Malacostraca	*Ceina egregia*	0.7	0	0.3	0	0	1	0	0	1	0	0	1	0	1	0	0	0	1	0	0.2	0.8	1	0
Malacostraca	*Taihape karori*	0.7	0	0.3	0	0	1	0	0	1	0	0	1	0	1	0	0	0	1	0	0.2	0.8	1	0
Malacostraca	*Paradexamine houtete*	0.5	0	0.5	0	0	1	0	0	1	0	0	1	0	1	0	0	0	1	0	0.3	0.7	1	0
Malacostraca	*Protohyale* sp.	0.6	0.1	0.2	0.1	0	0	0	1	1	0	0	1	0	1	0	0	0	1	0.1	0.1	0.8	1	0
Malacostraca	*Ericthonius pugnax*	0	0.25	0	0	0.75	0	0	1	1	0	0	1	0	0	1	0	0	1	0.4	0.2	0.4	1	0
Malacostraca	Ischyroceridae	0.2	0.1	0	0	0.7	0	0	1	1	0	0	1	0	0	1	0	0	1	0.1	0.2	0.7	1	0
Malacostraca	Lysianassidae	0.25	0.25	0.25	0.25	0	0	0	1	1	0	0	1	0	1	0	0	0	1	0.1	0.2	0.7	1	0
Malacostraca	*Elasmopus* spp.	1	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	0	1	0.1	0.2	0.7	1	0
Malacostraca	*Maera* sp.	0.5	0	0.5	0	0	1	0	0	1	0	0	0	1	1	0	0	0	1	0.1	0.2	0.7	1	0
Malacostraca	Cyproideidae	0	0.5	0.5	0	0	0	0	1	1	0	0	1	0	1	0	0	0	1	0	0.3	0.7	1	0
Malacostraca	*Gammaropsis* sp.	0	0	0.25	0	0.75	0	0	1	1	0	0	1	0	0	1	0	0	1	0.1	0.2	0.7	1	0
Malacostraca	Phoxocephalidae	0	0.75	0.25	0	0	0	0	1	1	0	0	1	0	1	0	0	0	1	0.1	0.2	0.7	1	0
Malacostraca	*Podocerus karu*	0	0	0	0	1	0	0	1	1	0	0	1	0	1	0	0	0	1	0.15	0.25	0.6	1	0
Malacostraca	*Tetradeion crassum*	0.2	0.2	0.2	0.2	0.2	0	0	1	1	0	0	1	0	1	0	0	0	1	0	0.2	0.8	1	0
Malacostraca	*Raumahara rongo*	0	1	0	0	0	0	1	0	1	0	0	1	0	1	0	0	0	1	0	0.2	0.8	1	0
Malacostraca	*Seba typica*	0	1	0	0	0	0	1	0	1	0	0	1	0	1	0	0	0	1	0.2	0.1	0.7	1	0
Malacostraca	*Hornellia whakatane*	0	0	0	0	1	0	0	1	1	0	0	1	0	1	0	0	0	1	0.1	0.1	0.8	1	0
Malacostraca	*Parapherusa crassipes*	1	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	0	1	0.2	0.1	0.7	1	0
Malacostraca	Eusiridae	0.2	0.2	0.2	0.2	0.2	0	0	1	1	0	0	1	0	1	0	0	0	1	0.2	0.1	0.7	1	0
Malacostraca	Corophiidae	0	0	0.25	0	0.75	0	0	1	1	0	0	1	0	0	1	0	0	1	0.1	0.2	0.7	1	0
Malacostraca	Amphipoda	0.2	0.2	0.2	0.2	0.2	0	0	1	1	0	0	1	0	0.5	0.5	0	0	1	0.33	0.33	0.33	1	0
Malacostraca	Dexaminidae	0.5	0	0.5	0	0	1	0	0	1	0	0	1	0	1	0	0	0	1	0	0.3	0.7	1	0