MACROALGAE AS MICROHABITAT:

SEAWEED TRAITS AND WAVE ACTION AS PREDICTORS

OF INVERTEBRATE EPIFAUNAL DIVERSITY

by

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ABSTRACT

In many coastal environments, anthropogenic stressors yield changes in seaweed biodiversity. Here, I describe three studies addressing how such floristic changes might affect provision of habitat by seaweeds for small mobile invertebrate epifauna. In chapter 2, I used observational and manipulative (transplant) experiments to test how changes in seaweed biodiversity influenced biodiversity of associated invertebrates. I found that invertebrate epifaunal richness and abundance were not affected by changes in seaweed biodiversity. Invertebrate assemblage structure was, in most cases, not influenced by changes in seaweed composition; only when algal assemblages were composed of monocultures of species with 'foliose' morphologies did I observe a change in invertebrate assemblage structure. Correlations between algal functional composition and invertebrate assemblage structure were observed, but not between algal species composition and invertebrate assemblage structure. These results suggest that changes in seaweed biodiversity will have implications for invertebrate epifauna only under specific scenarios of algal change. In Chapter 3, I tested the performance of host taxonomic relatedness and functional (i.e. morphological) group affiliation as predictors of associated invertebrate epifauna. Neither general framework performed well; invertebrate assemblages found on congeneric host species were as similar as those found on hosts classified in different kingdoms, and taxon richness and abundance of invertebrates varied substantially within seaweed functional groups. Species identity was identified as a key predictor of the performance of seaweeds as hosts for invertebrate epifauna. In chapter 4, I examined the context dependence of these host identity effects by testing how host morphological complexity and maximum wave velocity interacted to determine local invertebrate diversity. Three types of host species were identified: a) morphologically 'simple' thalli that were minimally utilized as habitat under any of the tested wave regimes, b) thalli that were coarsely branched and were utilized by invertebrates under relatively benign wave conditions but became less utilized under higher wave action, and C) 'complex' algal hosts that supported diverse invertebrate assemblages under all tested wave conditions. Together, these studies support the view that invertebrates that use seaweeds as habitat are host-generalists,

and therefore consequences for invertebrates of changes in seaweed biodiversity are likely to be minimal.

Keywords: biodiversity, British Columbia, community ecology, epifauna, facilitation, functional group, habitat-provision, intertidal, invertebrate, marine, morphology, seaweed, taxonomy, wave exposure

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CO-AUTHORSHIP STATEMENT

Chapter 2: Do changes in seaweed biodiversity influence associated invertebrate epifauna? I had the idea for this study, and I set up, sampled, and analyzed the data. I acknowledge the contributions of Robert DeWreede to the conceptual development and methods used for this experiment. I wrote the first draft of the manuscript, and comments by Rob DeWreede and two anonymous reviewers contributed to the readability and rigor of the final report. A version of this chapter is published: Bates, C.R. and R.E. DeWreede (2007) *Journal of Experimental Marine Biology and Ecology* **344**: 206-214.

Chapter 1: General Introduction

1.1 Conceptual framework

1.1.1 Changing world, changing biodiversity

As global human populations increase, our collective influence on the earth's biota becomes more profound. In the majority of populated regions, human actions are responsible for both extirpating and introducing species and for causing changes in biological composition (Hooper *et al.* 2005). Such changes are happening at levels of organization from genes to communities (Grosberg and Cunningham 2001), and invasive species are problematic in many ecosystem types (Kaiser 1999). Awareness of these changes has led to concerns about the consequences of altered biodiversity for community and ecosystem processes (Naeem *et al.* 1994).

In the marine environment, coastal zones are particularly threatened (Gray 1997) because an estimated 67% of the world's human population lives within 60 km of the coast (Hammond 1992). Examples of anthropogenic stressors on coastal biodiversity include climate change, resource over-harvesting, toxic pollutants, eutrophication, coastal habitat alteration, tourism, introduced species, and marine litter (Suchanek 1994, Gray 1997, Crowe *et al.* 2000, Bax *et al.* 2003). The greatest threat to marine biodiversity is habitat loss (Gray 1997).

1.1.2 Changes in seaweed biodiversity

Seaweeds, the benthic marine algae, are susceptible to impacts by human activities (Schramm and Nienhuis 1996, Scott and Tittley 1998, Ducrotoy 1999). The work described in this thesis was motivated in part by my previous studies of the dynamics of marine algae in the Bay of Fundy (Bates 2002, Bates *et al.* 2005, 2007). My observations there of degraded seaweed assemblages, in conjunction with my perception that seaweeds are typically overlooked in coastal conservation and management plans, prompted an interest in understanding the consequences of anthropogenic changes in biodiversity of marine algae. Of the many functions that benthic marine algae perform, I chose to study their role as "habitat modifying

organisms" (HMOs) (Bruno and Bertness 2000) in intertidal environments. Seaweeds provide habitat to a wide array of organisms, the bulk of which are small mobile invertebrate epifauna (Taylor 1998).

1.1.3 Habitat modification

The ramifications of changes in biodiversity are compounded when the affected species are providers of biogenic habitat for other species. Although such positive interactions have long been known to influence community structure, recent years have seen increased interest in understanding the biological and physical factors that regulate biogenic habitat provision (Bertness and Leonard 1997, Stachowicz 2001, Bruno *et al.* 2003). Habitat modification is thought to be important in circumstances where a HMO can ameliorate abiotic or biotic stressors that would otherwise prevent the coexistence of associated species or assemblages (Crain and Bertness 2006). Habitat modifying species have been variously referred to as 'foundation species' (Dayton 1972), 'ecosystem engineers' (Jones *et al.* 1997), and 'keystone facilitators' (Hacker and Gaines 1997). Habitat modification can be active, mediated by the actions of an HMO, for example when beavers fall trees to create dams (Wright *et al.* 2002), or habitat modification can occur passively, where the simple presence of the habitat modifier acts to ameliorate stressors. This latter process is of interest here.

1.2 Community ecology as a predictive science

Ecologists are increasingly asked to predict the consequences of changes in biodiversity (Hawkins 1999, Benedetti-Cecchi et al. 2001). Predicting the consequences of biotic changes is not a simple task; such predictions are hindered by several conceptual and practical limitations. Biological assemblages can be highly variable in space and time (Benedetti-Cecchi 2001), so the scale of investigation can influence results and conclusions. As well, "standard" ecological procedures may not be sufficient to address the scientific and predictive needs of managers and policy makers (Lawton 1999). In practice, most ecologists have studied pairwise comparisons of species

interactions, and the conclusions of these studies are often specific to the sites, dates, and organisms examined (McGill *et al.* 2006). Several reviews have lamented the "failures" and lack of generalities of community ecology (Lawton 1999, Simberloff 2004), drawing the possibility that community ecology may not be able to provide answers about the consequences of changes in biodiversity that are consistent across different spatial and temporal scales, different species or ecosystems.

However, there are several recently proposed approaches that hold promise for community ecology as a predictive science (McGill *et al.* 2006). In the following sections, I briefly outline several concepts that allow investigators to look past species identity towards more general predictive frameworks: biodiversity-ecosystem function relationships, functional diversity, phylogenetic / taxonomic perspectives in community ecology, and the study of functional trait performance along environmental gradients.

1.2.1 Biodiversity-ecosystem function relationships

To understand the consequences of changes in biodiversity on ecosystem processes, investigators have created or manipulated assemblages along a gradient of biodiversity (variously incorporating species richness, functional richness, and composition of taxonomic and functional groups) and measured subsequent changes in ecosystem properties (Loreau *et al.* 2001, Naeem and Wright 2003). Despite early debates about problems of experimental designs and mechanisms underpinning observed patterns, biodiversity-ecosystem function research has offered several general insights about the relationship between diversity and ecosystem properties (Hooper *et al.* 2005). However, investigations about the relationships between biodiversity and function in marine environments were relatively scarce (Duarte 2000) until recently (Bolam *et al.* 2002, Stachowicz *et al.* 2002, Solan *et al.* 2004, Bruno *et al.* 2005).

1.2.2 Functional group diversity

Recognition that species can play similar roles within assemblages has given rise to the idea that taxa can be grouped together into functional groups (Gitay and Noble 1997). Inherent in the idea of functional groups is that species can be functionally equivalent or redundant: loss of a particular species can be compensated for by the presence of functionally similar species. Evidence exists to suggest that functional group diversity is important to ecosystem processes (Tilman *et al.* 1997, Diaz and Cabido 2001, Petchey and Gaston 2002, Diaz *et al.* 2003). However, there is considerable debate about the best way to delineate functional groups (Gitay and Noble 1997), and to whether or not species can really be considered redundant (Rosenfeld 2002, Loreau 2004). As with biodiversity-ecosystem function research, most of the data available on functional diversity are not from marine environments (Gray 1997). The idea of functional groupings remains an intriguing approach to assessing changes in biodiversity, and for understanding the consequences of these changes for ecosystem and community-level properties.

1.2.3 Phylogenetic / taxonomic perspectives in community ecology

Phenotypes are, to a large extent, driven by genotypes. In an ecological context, it makes sense that closely related species, through shared genotypes, will exhibit similar phenotypes, and therefore function similarly (Webb *et al.* 2002). As taxonomic relationships are increasingly resolved, relatedness can be used to generate hypotheses about ecological performance based on relative taxonomic or genetic distances. This approach is still quite new, however interest is growing. Recently developed metrics of taxonomic similarity (Clarke *et al.* 2006) make it possible to calculate taxonomic distances based on a Linnaean classification scheme, so advanced knowledge about phylogenetic tree reconstruction is not necessary to test hypothesis based on taxonomic relatedness.

1.2.4 Functional trait performance along environmental gradients.

Part of the lack of generality of community ecology stems from the use of nomenclaturally linked (i.e. species identity-based) statements that could be more effective if they focused on the functional traits of the organisms under study (McGill *et al.* 2006). Functional traits are measurable properties of organisms that strongly influence performance (McGill *et al.* 2006), and trait diversity can underpin the relationship between biodiversity and ecosystem function (Walker *et al.* 1999).

The environments in which organisms live are rarely constant, yet more often than not, community ecology research does not acknowledge environmental gradients (McGill *et al.* 2006, but see Belcher *et al.* 1995, Peltzer *et al.* 1998, Helmuth *et al.* 2002, Puijalon and Bornette 2004). Examples of environmental gradients include temperature, nutrients, moisture, and hydrodynamic regime. Gray (1997) suggests, rightly so, that "no ecological system... ...can be studied in isolation from the environment in which it exists". The recognition of gradients is an important element to increasing the realism of ecological studies, and to understanding how spatial variation influences ecological processes.

McGill *et al.* (2006) suggest that, in part, studying functional traits across environmental gradients could help to transform community ecology into a more quantitative and predictive science. This would improve our ability to provide information relevant to understanding the ramifications of stressors of anthropogenic origin, such as global climate change.

These developments in community ecology are interesting and progressive. However, there is also current research suggesting that species identity is important to ecosystem processes (Bruno *et al.* 2005, O'Connor and Crowe 2005). Despite criticisms of community ecology (Lawton 1999), it is difficult to avoid studying communities of organisms; in order to study community ecology, we must study specific communities (Simberloff 2004).

1.3 Objectives of this thesis

I have attempted to acknowledge these developments in community ecology when defining my research questions. The studies described in this thesis are unified not only by a common study system, but also by an interest in gaining a broader understanding about the value of studying species versus generalizing across taxa. In doing so, I can develop insight not only into the role of seaweeds as habitat for invertebrate epifauna and the consequences of changes in seaweed assemblages, but also about several new paradigms for community ecology.

1.3.1 Questions

Three general questions are addressed in this thesis; I look here at how changes in seaweed biodiversity, seaweed species identity and an environmental gradient (i.e. wave velocity) influence invertebrate biodiversity. Specifically, I ask:

1) How do changes in biodiversity of habitat-forming seaweeds influence the biodiversity of invertebrate epifauna using this biogenic habitat? (Chapter 2)

2) How do seaweed taxonomic relatedness and functional group affiliation perform as predictors of habitat associations between seaweeds and mobile invertebrate epifauna? (Chapter 3)

3) How does seaweed architectural complexity interact with a gradient of wave force to determine patterns of invertebrate diversity? (Chapter 4)

1.4 The study system

These questions were addressed using an intertidal seaweed-epifauna system. The intertidal is an excellent study environment in which to address my research questions; diverse assemblages of seaweeds and invertebrates persist across several

environment gradients of (e.g. temperature, desiccation, wave force) that occur across short distances (Hawkins 1999).

1.4.1 Seaweeds

Seaweeds, the macroscopic marine algae, are a morphologically and phylogenetically diverse group of organisms. They range from small, undifferentiated filaments and simple blades to large and complex, highly differentiated thalli with specialized structures for attachment, reproduction, photosynthesis, and flotation (Graham and Wilcox 2000). Seaweeds are a polyphyletic group, encompassing a vast array of genetic diversity and spanning two kingdoms of life. There are three major taxon groups of seaweeds, the reds (Phylum Rhodophyta), greens (Phylum Chlorophyta), and browns (Class Phaeophyceae). Seaweeds comprise the dominant biomass in many temperate rocky nearshore ecosystems (Figure 1.1), and they are ecologically important components of a milieu regulated by complex species interactions and a constantly fluctuating environment.

1.4.2 Invertebrate epifauna

Small mobile invertebrate epifauna are a subset of invertebrates defined by their vagility, habitat and size range (0.2 mm to 30.0 mm) rather than their taxonomic affinity. Mobile epifauna are free to move between hosts, unlike sessile epifauna such as bryozoans or barnacles. Throughout this thesis, small mobile invertebrate epifauna will be referred to as 'associated invertebrate epifauna', or simply 'epifauna'. Epifauna are a highly diverse group, representing a wide array of invertebrate taxa. Commonly encountered phyla include: Arthropoda, Mollusca, Annelida, Echinodermata, and Nematoda (Figure 1.2). Epifauna found on seaweeds may or may not use their hosts as a food source (Arrontes 1999).

1.4.3 Study sites

These studies were undertaken in southern Barkley Sound, British Columbia, Canada (Figure 1.3). Collections were taken at six sites; two sites were located at each of Nudibranch Point (48°48'53" N, 125°10'20" W; 48°48'53" N, 125°10'19" W), Scott's Bay (48°50'05" N, 125°05'39"W; 48°50'04"N, 125°05'38"W) and Dixon Island (48°51'07"N, 125°05'25"W; 48°51'12"N, 125°05'20"W). These sites are "typical" shores for the area, subjected to a gradient of wave exposure, and are located within two kilometres of the Bamfield Marine Sciences Centre. Four of the sites were selected based on pre-existing measurements of wave exposure (Bates *et al.*, unpublished data), with two additional sites added to broaden the geographic range and to fill in the spectrum of possible water motion measurements.

Figure 1.1: The lower intertidal zone of Nudibranch Point, Barkley Sound, British Columbia is dominated by a wide diversity of seaweed forms. This lush cover is typical of lower intertidal shores in the region.

Figure 1.2: A selection of the diverse array of small mobile invertebrate epifauna found on seaweeds in southern Barkley Sound, British Columbia.

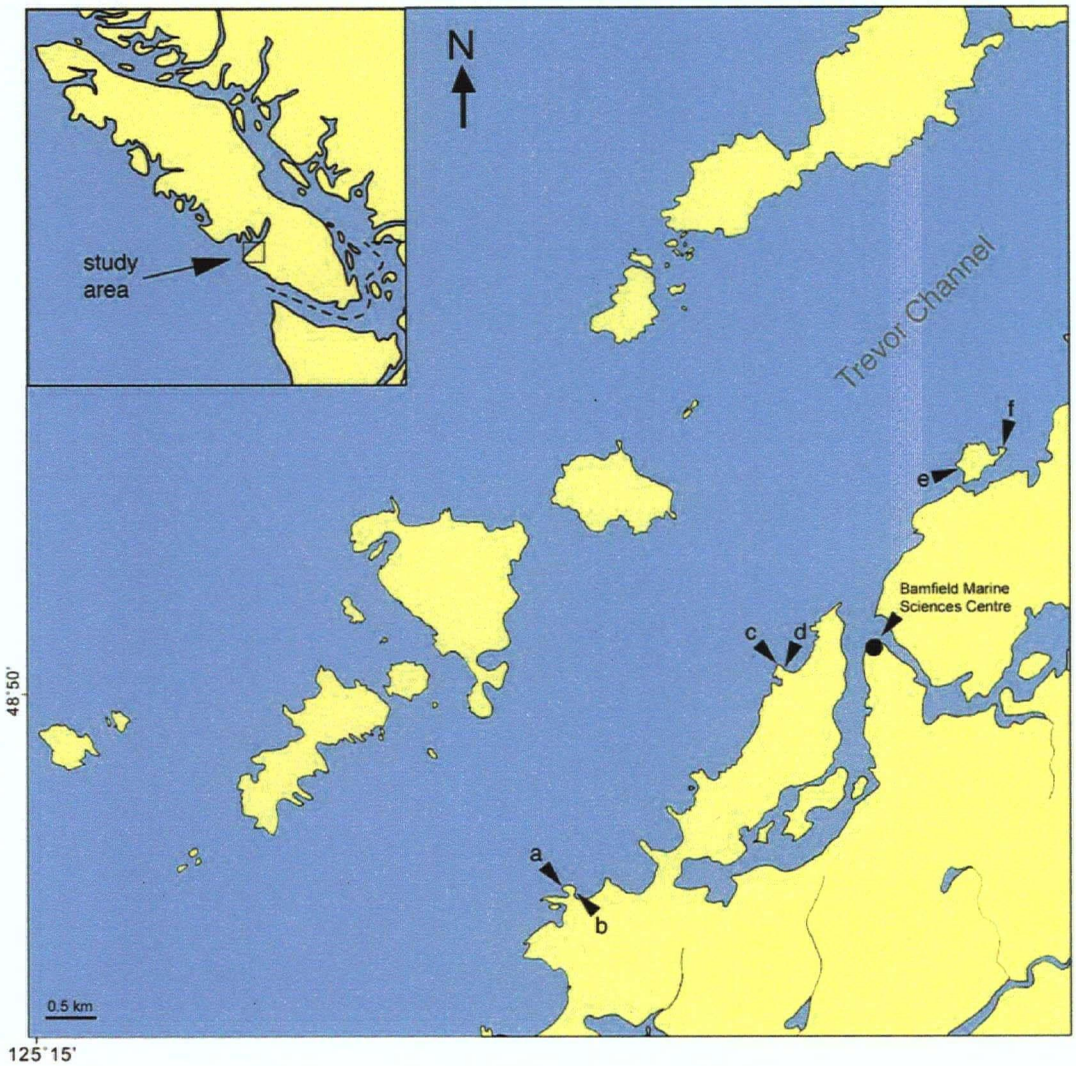

Figure 1.3: Map of study area in southern Barkley Sound, British Columbia, indicating six study sites: Nudibranch Point (a: exposed; b: sheltered), Scott's Bay (c: exposed; d: sheltered), and Dixon Island (e: exposed; f: sheltered). Inset box shows Vancouver Island, British Columbia, Canada.

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Chapter 2: Do changes in seaweed biodiversity influence associated invertebrate epifauna?

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2.1 Introduction

Local biodiversity is often positively influenced by the presence of habitat-forming or habitat modifying organisms (Thompson *et al.* 1996, Stachowicz 2001). The importance of biogenic habitat provision and of positive interactions in general is increasingly acknowledged, particularly in marine systems (Bertness *et al.* 1999, Bruno and Bertness 2000, Stachowicz 2001, Bruno *et al.* 2003). Biogenic habitat provision is most often investigated as the creation or modification of habitat by one species for a group of other species (Castilla *et al.* 2004, Wonham *et al.* 2005). However, many situations exist where habitat-forming species are components of assemblages of taxa that can collectively act as habitat (Bruno and Bertness 2000, Stachowicz 2001, Bruno *et al.* 2003). Investigations into assemblage-level influence on biogenic habitat provision are much less frequent and, where available, have yielded mixed results, showing positive, negative, and neutral relationships between facilitator diversity and diversity of associated organisms (Bruno and Bertness 2000).

These mixed results concerning habitat provision by multi-species communities may stem from problems of defining facilitator diversity, because various components of diversity (e.g., richness, composition) can affect processes differentially (Diaz and Cabido 2001, Naeem 2002) and it can be difficult to separate the effects of different components of diversity (Naeem and Wright 2003). Biodiversity, as it relates to ecosystem functioning, can be defined in a variety of different ways, incorporating the number of species (Magurran 1988, Petchey 2000), the functional roles of the species (Tilman *et al.* 1997, Diaz and Cabido 2001, Petchey and Gaston 2002), and the identity of the species or the functional groups that compose the assemblage.

While much work in biodiversity research has focused on species richness as the independent variable, there is debate about the relative importance of species richness, functional richness and species or functional group identity (Tilman *et al.* 1997, Bruno *et al.* 2005). Here, I describe my efforts to address these concepts in an intertidal study system, where I test how variation in four seaweed assemblage-level parameters (i.e. seaweed species richness, functional group richness, species composition, and functional group composition) influences associated small mobile epifauna. Understanding the relative influence of these different components of biodiversity on biogenic habitat provision is becoming increasingly important as human activities

continue to alter composition of biological communities and reduce diversity (Coleman and Williams 2002). Habitat loss has been pinpointed as the major cause of declining biodiversity (Tilman *et al.* 1994), and the implications are compounded if habitat-forming species are lost.

Anthropogenic changes in seaweed diversity have been observed in nearshore marine environments from many regions throughout the world, most notably in Europe (Schramm and Nienhuis 1996) and in eastern Canada (Lotze and Milewski 2004, Bates *et al.* 2005). Anthropogenic stressors that result in changes in seaweed assemblages include eutrophication, silt deposition, trampling, habitat alteration, and harvest of predators or herbivores. These stressors act by compromising the basic requirements of marine algae, which include substrate to attach to, light and nutrients for photosynthesis, and potential for successful dispersal and recruitment. As a result, stressed algal assemblages often shift from mosaics of longer-lived, perennial algae to assemblages dominated by ephemeral, fast growing, nutrient scavenging annuals (Lotze *et al.* 1999), often referred to as 'green-tides'. These observed changes involve different components of biodiversity, including the number and identity of seaweed species and functional groups. Because seaweeds are vital biogenic habitat providers for small mobile invertebrates, an understanding of the relationships between different components of seaweed diversity and invertebrate diversity is important for predicting the implications of marine floristic change.

Here, I ask (1) Is seaweed species richness positively correlated with invertebrate species richness and abundance? (2) Is seaweed functional richness positively correlated with invertebrate species richness and abundance? (3) Does species composition of host seaweed assemblages correlate with invertebrate assemblage structure? and (4) Does functional composition of host seaweed assemblages correlate with invertebrate assemblage structure?

2.2 Materials and methods

I initiated this study with observational collections to determine natural levels of seaweed diversity and structure of associated mobile epifauna. I then performed manipulative experiments over two years to determine the implications of varied combinations of seaweed species richness, functional richness, and species and functional composition on the structure of associated mobile epifaunal assemblages. This study was done in June to August over two years (2003-2004) at Nudibranch Pt. (Figure 1.3). Nudibranch Pt. is a relatively pristine site with gently sloping, semi wave-exposed rocky reefs, and a rich assemblage of seaweeds (Table 2.1). Site preparation took place in April and May 2003 and observational and manipulative quadrats measured 16 x 47 cm, oriented perpendicular to the water line. This quadrat size was chosen as a manageable area to sample, and made efficient use of transplant materials. Current taxonomic authorities can be found by consulting Gabrielson *et al.* (2006).

2.2.1 Defining seaweed functional groups

To assign seaweed species into functional groups (Table 2.1), I used functional form groupings following Steneck and Dethier (1994). Owing to the limitations of the transplant method (described below), I used only four of a possible seven seaweed functional groups (Table 2.1): foliose, corticated foliose, leathery, and corticated terete (i.e. rounded in cross section). As asserted by Farina *et al.* (2003), the functional/morphological approach in marine algae has had variable support for a *gradient* of functional performance across groups, but the *endpoints* are well established, ranging from fast growing opportunistic 'simple' forms (i.e. the foliose group) at one end, to the slower-growing, typically later successional species with 'complex' thalli (i.e. corticated terete) at the other end. My discussion of seaweed functional composition concentrates on the differences between these endpoints.

2.2.2 Observational study

The purpose of the observational study was two-fold: to determine natural levels of seaweed species richness, functional richness, and total seaweed biomass to aid in the creation of realistic 'controls' for transplanted seaweed communities; and to obtain baseline descriptions of the relationships between seaweed community parameters and invertebrate diversity. Ten observational quadrats were sampled in May 2003 by harvesting a patch located 50 cm to the right of ten randomly selected manipulative quadrats (described below). Within each observational quadrat, each seaweed species present, along with associated invertebrates, was collected and immediately placed into separate zippered collection bags. Samples were then frozen for a minimum of 24 hours to euthanize epifauna before processing.

2.2.3 Manipulative experiment

To separate the influence of seaweed species richness, functional richness, and functional composition on associated invertebrate epifauna, I created seaweed communities that varied each of these parameters while holding the other variables constant. I use the approach of 'synthetic removal experiments' as described by Schmid *et al.* (2002), where the experimental design includes intact communities and then omits certain species or groups of species to determine their effects. Prior to each transplant experiment, quadrats were scraped clear of existing biota. I then established six treatments.

2.2.4 Experimental treatments

Three variables were considered when determining composition of seaweed treatment quadrats: Seaweed species richness (S), seaweed functional richness, (F), and seaweed functional composition (FC). A fourth parameter, seaweed species composition, was incorporated by randomly selecting species within functional groups

according to the guidelines described below. To describe the functional composition of seaweed quadrats, I classified assemblages as simple (only 'foliose' forms present), complex (only 'corticated terete' forms present), or mixed (all four functional groups present). The treatments described below are summarized in Table 2.2.

Treatment 1 (T1): S = 4, F = 4, FC = mixed. In the 'mixed polyculture' treatment, four seaweed species were included in each quadrat. One species was randomly selected from each seaweed functional group, ensuring all functional groups were represented. This treatment tested for the consequences of reduced species richness without the loss of functional richness.

Treatment 2 (T2): S = 1, F = 1, FC = foliose. In the 'simple monoculture' treatment, one species (per quadrat) was randomly selected from the six available species in the 'foliose' functional group. This treatment is comparable to the 'green tide' phenomenon, where seaweed assemblages are composed of fast growing, opportunistic algae typically from the Chlorophyte order Ulvales (Middelboe and Sand-Jensen 2000).

Treatment 3 (T3): S = 6, F = 1, FC = foliose. In the 'simple polyculture' treatment, polycultures were established using all six species selected from the 'foliose' morphotype. This treatment tests for the influence of a low functional richness but high species richness.

Treatment 4 (T4): S = 1, F = 1, FC = corticated terete. In the 'complex monoculture' treatment, one species (per quadrat) was randomly selected from the eight available species from the 'corticated terete' functional group. This treatment is comparable to a late-successional seaweed assemblage, where a slower-growing, competitively dominant, robust morphotype is found, such as the *Chondracanthus canaliculatus* monocultures described by Dean and Connell (1987b).

Treatment 5 (T5): S= 6, F = 1, FC = corticated terete. In the 'complex polyculture'

treament, polycultures were established with six species selected from the 'corticated terete' morphotype.

Treatment 6 (C): S = 8, F= 4, FC = mixed. Control quadrats were based on the communities encountered in the observational study, and each was composed of eight seaweed species randomly selected across four functional groups.

Treatments 1 and 2 were run in 2003 and treatments 3 to 5 were run in 2004, and n = 4 per treatment. Treatment 6 was run both 2003 and 2004, and n = 8 for 2003 and n = 12 for 2004.

2.2.5 Seaweed transplants

I used the transplant approach of Shaughnessy and DeWreede (2001) to create composite communities. To prepare for transplants, quadrats were first cleared of the existing flora and fauna, five holes were drilled into the rocky substratum, and masonry anchors were embedded. The anchors provided a means of attaching malleable wire grids to the intertidal. Seaweed thalli selected for transplanting were collected from within the study site and defaunated by dipping in fresh water and shaking, followed by visual inspection and manual removal of remaining epifauna (Kelaher 2002). Holdfasts of algae were woven into three-twist PVC rope, and then attached to the wire grids with nylon zip ties. Mean biomass of all transplanted quadrats was approximately equal (dry biomass = 10.25 g +/- 0.94 g) and was equivalent to the seaweed biomass of the observational quadrats (12.84 g +/- 2.00 g). Algal percent cover was greater than 95% in all quadrats.

Quadrats were established over three days and left for 30 days. Plants were then harvested by collecting the total biomass of each species from each quadrat into separate zippered collection bags. Samples were frozen for a minimum of 24 hours to euthanize epifauna before processing.

2.2.6 Sample processing

To remove the epifauna from the host alga, each frozen seaweed thallus was removed from its bag and thawed in a dish with 500 mL of seawater. Most epifauna sank to the bottom of the dish, but each sample was also rubbed and visually inspected to remove remaining epifauna. Thalli with dense branching or folding were processed with additional attention. This approach was highly effective, and visual inspection with a dissecting microscope revealed few, if any, epifauna remaining on the thalli. Because sessile invertebrate individuals were relatively scarce (typically bryozoans or barnacles) and difficult to quantify as a number of individuals (in the case of the colonial bryozoans), my analyses are limited to mobile epifauna. Samples were sieved through a 0.2 mm screen to retain epifauna, and then preserved in a 1.5 mL Eppendorf tube containing 95% ethanol. Invertebrates were then enumerated as morphospecies (Oliver and Beattie 1996) and later keyed to the lowest taxonomic level possible. Host thalli were dried at 80° C for 24 hours, and then weighed to the nearest 0.01 g to quantify host biomass.

2.2.7 Statistical analysis

Tests for the influence of seaweed species and functional richness were performed using ordinary least squares regression for the observational study, and one-way ANOVAs for the manipulative study, in both cases using invertebrate taxon richness and abundance as response variables. Groups of control quadrats were not different within year ($P > 0.25$) so controls were pooled across treatments within each year (Underwood 1997). Invertebrate assemblages associated with control plots were different ($P < 0.05$) between 2003 and 2004, so treatments were compared to control quadrats from the same year in which the treatment was done. To account for increased likelihood of Type 1 statistical errors, I used Bonferroni corrected critical alpha values in cases where multiple comparisons were performed (Zar 1999). For parametric tests, data were tested for normality (Anderson-Darling test) and for homogeneity of variance using Cochran's C (Underwood 1997). If data did not conform, appropriate

transformations were applied (Zar 1999). Parametric tests were carried out using JMP 4.0.4 (SAS Institute Inc.).

Non-parametric multivariate approaches (Clarke 1993) were used to test for the influence of seaweed taxonomic and functional composition on invertebrate composition. To down-weight the contribution of abundant taxa to measures of between-sample similarity (Clarke 1993), abundance data either fourth-root transformed (invertebrates) or root-transformed (seaweed). The degree of transformation differed between invertebrates and seaweeds because invertebrates were counted as individuals (ranging from zero to 1000) and seaweeds were sampled as percent cover (ranging from zero to 100). Similarity of species composition of invertebrate samples and seaweed transplant quadrats was calculated using Bray-Curtis similarities (Bray and Curtis 1957), which is a measure of sample similarity that ranges between zero (no species in common) and 100 (species composition and abundance are equivalent between samples). These sample similarities were then visualized using non-metric multidimensional scaling (nMDS). To calculate seaweed functional composition, total per-quadrat biomass of each seaweed species was summed into the appropriate functional group before applying root transformation and calculating Bray-Curtis similarity. Two techniques were used to assess the implications of the different treatments for invertebrate composition: a) for the manipulative experiment, direct comparisons between treatments and controls were made using Analysis of Similarities (ANOSIM; Clarke 1993), and b) for both the observational and manipulative components, assessments of overall congruence in multivariate similarity patterns between seaweed functional and species composition vs. invertebrate species composition were made using Mantel tests (Zar 1999); here I calculated Spearman rank correlation (Zar 1999) between similarity matrices.

Where significant differences between treatment and controls were indicated by the ANOSIM tests, the biota responsible for differences between groups were identified using Similarity Percentages (SIMPER; Clarke 1993). Multivariate analyses were carried out using PRIMER software (Version 5.2, Primer-E, www.primer-e.org).

2.3 Results

2.3.1 Observational study

For the observational collections, no significant correlations were observed between any of the measured variables, however no low-diversity seaweed quadrats were encountered; average seaweed species richness was 6.1 (+/- 0.49 SE) and average seaweed functional richness was 2.90 (+/- 0.23). There was no correlation between seaweed species richness and invertebrate species richness ($P = 0.64$, $r^2 = 0.17$) or invertebrate abundance ($P = 0.65$, $r^2 = 0.02$), or between seaweed functional richness and invertebrate richness ($P = 0.73$, $r^2 = 0.03$) and invertebrate abundance ($P = 0.57$, $r^2 = 0.04$). Further, no correlation was observed between invertebrate assemblage structure and either seaweed assemblage structure (Spearman rank correlation ($r_s = 0.111$, $P = 0.232$) or seaweed functional structure ($r_s = 0.019$, $P = 0.469$). An average of 301.7 (+/- 63.5 SE) invertebrates were found per quadrat, with a total of 3017 epifauna individuals across 61 invertebrate taxa across all quadrats.

2.3.2 Manipulative experiment

None of the five seaweed treatments resulted in differences in invertebrate richness or invertebrate abundance compared to control quadrats (ANOVA, $P_{2003} > 0.025$, $P_{2004} > 0.017$; critical alpha values determined by Bonferroni correction). Across all treatment quadrats, a total of 9593 invertebrate individuals were encountered across 66 taxa. Mean per-quadrat invertebrate taxon richness ranged from 15 to 25, and mean per-quadrat abundance ranged from 110 to 338 individuals.

Invertebrate composition in most of the treatments varied independently of seaweed composition. Invertebrate assemblages from mixed polycultures (T1) were not significantly different from the 2003 controls (ANOSIM $P > 0.025$), and simple polycultures (T3), complex monocultures (T4), and complex polycultures (T5) were not significantly different from the 2004 controls (ANOSIM $P > 0.017$; Fig. 2.1C and Table 2.3C). In only one treatment (simple monocultures, T2) did composition of invertebrate

assemblages depend on the identity of the seaweed treatment (ANOSIM, R = 0.520, P < 0.001; Fig. 2.1C and Table 2.3C). SIMPER analysis indicated that differences in the abundance of amphipods accounted for 42% of the observed assemblage dissimilarity between T2 and the control quadrats, followed by harpacticoid copepods (~16%), snails (~10%) and limpets, mites, and polychaetes, which each accounted for less than 5% of the differences (Table 2.4).

Overall patterns (i.e. rank order of similarity relationships within matrices) between seaweed taxonomic composition and invertebrate taxonomic composition (Fig. 2.1, Table 2.5) were not correlated in 2003 (r_s = 0.111, P = 0.239) or in 2004 (r_s = 0.103, P = 0.139). However, overall patterns of seaweed functional composition were correlated with patterns of invertebrate taxonomic composition in both 2003 (r_s = 0.275, P = 0.013) and 2004 (r_s = 0.196, P = 0.017).

2.4 Discussion

I found that many of the tested components of seaweed diversity had no observable influence on diversity of associated invertebrate epifauna. In all cases, invertebrate richness and abundance varied independently of the manipulated qualities of host algal assemblages. Invertebrate assemblage structure was different between control quadrats and algal assemblages composed of simple monocultures, but under none of the other test scenarios. Congruence of pairwise sample similarities was detected between algal functional structure and invertebrate assemblages, but not between algal taxonomic structure and invertebrate assemblages.

When compared at the species level, algae vary in quality of habitat provision for epifauna, with complexly branching algal species typically having a higher diversity of associated invertebrate epifauna as compared to algae with simple morphologies (Gee and Warwick, 1994, Chemello and Milazzo 2002). In this study I examined invertebrates associated with various types of seaweed communities. All seaweed quadrats composed of more than one species had associated invertebrate epifauna assemblages that were not different from control quadrats that contained eight seaweed species. When seaweed quadrats were composed of only one species, results of epifauna comparisons depended on the functional identity of the seaweed monoculture. This

latter result is consistent with previous investigations that link invertebrate diversity to seaweed host identity (Gee and Warwick 1994, Chemello and Milazzo 2002) and similar to those reported by Parker *et al.* (2001), who showed that within a subtidal Northeast Atlantic estuarine seagrass/drift seaweed community, plant composition was a strong predictor of invertebrate community structure, while plant richness showed only a weak positive correlation with diversity of invertebrate epifauna. My results contrast with similar studies undertaken in terrestrial habitats. Haddad *et al.* (2001) reported that insect species richness was positively correlated with plant species and functional richness in grassland ecosystems, and Perner *et al.* (2003) reported that after the cessation of pollution, herbivore richness was positively influenced by subsequent increases in plant species and functional richness.

Given that stronger relationships have been observed between diversity of plants and invertebrates in terrestrial systems, it is logical to ask why marine algal diversity and associated epifauna are not more tightly linked. Terrestrial insects are often specialized to their host (Janz *et al.* 2001), whereas marine invertebrates tend to be much more generalized in their host usage (Arrontes 1999), although examples of marine host specialization do exist (Sotka 2005). In the absence of widespread host-specialization, marine epifauna are likely more amenable than insects to switch to a new host when host composition or richness change.

Why did invertebrates associated with simple monocultures differ compared to the controls? The majority of studies relating host architectural complexity to epifauna diversity conclude that host plants that are better at providing predator-free space will have the highest associated invertebrate diversity (Arrontes 1999). The species included in the foliose functional group tend to be of low structural complexity, with many species lacking branches or specialized structures. This lack of complexity may provide fewer spaces for epifauna to hide from predators, which could explain the different composition of amphipods, harpacticoid copepods, gastropods, limpets, mites, and polychaete worms observed in simple monocultures compared to controls (Table 2.4). However, structural complexity can be difficult to define in a straightforward manner, and other characteristics besides branching may influence an algal host's ability to provide predator-free space. Several of the foliose seaweed species (e.g. *Porphyra* spp., *Ulva lactuca*) exhibit highly folded morphologies, which can also provide effective shelter for invertebrate epifauna. Figure 2.1C shows that several of the simple

monoculture quadrats had associated invertebrate epifauna assemblages that group closely with those from the control quadrats. This suggests that functional groupings, as currently defined, may not be the most reliable method of predicting a seaweed species performance as a host for invertebrate epifauna. Evidence exists to suggest that host species identity is particularly important when abiotic conditions are stressful. For example, Lilley and Schiel (2006) found that on New Zealand shores exposed to thermal stress, removal of a dominant canopy forming species, *Hormosira banksii* (Turner) Decaisne, had significant influence on assemblage structure of nearby and associated organisms.

2.4.1 Observational versus manipulative results

Results from my manipulative study suggest that only under particular scenarios of algal change will composition of associated epifauna be influenced. Therefore, it is not surprising that my observational study did not reveal any linkages between algal biodiversity and epifaunal diversity, because no low-diversity seaweed assemblages were encountered in observational quadrats.

2.4.2 Implications for invertebrates of changes in seaweed biodiversity

Under most scenarios, it appears that invertebrate epifauna assemblages are robust to changes in seaweed biodiversity. However, an interesting observation is that the 'simple monoculture' treatment, which harbored a lower diversity of invertebrate epifauna, is similar in composition to the increasingly field-observed 'green tide' phenomenon. This suggests that if green tides continue to become more widespread, there is potential for changes in seaweed biodiversity to alter local diversity and composition of invertebrate assemblages. It is also worth noting that even though host-specificity does not appear strong in this system, seaweeds do provide habitat for myriad invertebrates and if seaweed cover were to be entirely lost, this could be detrimental to associated invertebrate epifauna (Walker and Kendrick 1998), and to larger invertebrates and fish that feed on seaweed-associated epifauna.

Table 2.1: List of algal species included in this study, with functional group assignment and whether they were encountered in the observational study (O), used in the manipulative study (M) or both (B).

Taxon	Functional Group	Inclusion
Ahnfeltiopsis leptophyllus	Leathery	O
Analipus japonicus	Corticated terete	B
Callithamnion pikeanum	Filamentous	O
Ceramium pacificum	Corticated terete	O
Ceramium sp.	Corticated terete	O
Chondracanthus exasperatus	Leathery	M
Fucus distichus subsp. *evanescens*	Leathery	B
Gastroclonium subarticulatum	Corticated terete	M
Halosaccion glandiforme	Foliose	B
Mastocarpus jardinii	Leathery	M
Mastocarpus papillatus	Leathery	B
Mazzaella affinis	Corticated foliose	B
Mazzaella splendens	Corticated foliose	B
Microcladia borealis	Corticated terete	O
Microcladia coulteri	Corticated terete	O
Neorhodomela larix	Corticated terete	M
Odonthalia flocossa	Corticated terete	B
Osmundea spectabilis	Leathery	O
Porphyra sp.	Foliose	B
Prionitis lyallii	Corticated terete	B
Sargassum muticum	Corticated terete	M
Ulva lactuca	Foliose	B
Ulva intestinalis	Foliose	M
Ulva linza	Foliose	B
Ulva californica	Foliose	B

Table 2.2: Description of algal assemblage parameters used to compose control and experimental quadrats. N = 4 for each treatment; each treatment had four associated control quadrats.

Treatment Identity	Species Richness (S)	Functional Richness (F)	Functional Composition (FC)	Year
T1: Mixed Polyculture	4	4	Mixed	2003
T2: Simple Monoculture	1	1	Foliose	2003
T3: Simple Polyculture	6	1	Foliose	2004
T4: Complex Monoculture	1	1	Corticated terete	2004
T5: Complex Polyculture	6	1	Corticated terete	2004
C: Control	8	4	Mixed	2003 & 2004

Table 2.3: ANOSIM results for the manipulative experiment: Comparisons of specific treatments to control quadrats for algal taxonomic composition (A), algal functional composition (B), and composition of associated mobile invertebrate epifauna (C).

Treatment Compared to Control	A: Algal Species Composition		B: Algal Functional Composition		C: Invertebrate Species Composition	
	ANOSIM R	P value	ANOSIM R	P value	ANOSIM R	P value
T1	-0.012	0.476	-0.071	0.605	0.250	0.071
T2	0.865	0.005	0.317	0.043	0.520	0.001
T3	0.954	0.001	0.271	0.009	0.282	0.042
T4	0.896	0.001	0.733	0.002	0.213	0.149
T5	0.903	0.001	0.491	0.002	-0.055	0.573

Table 2.4: Summary of differences in abundance of major invertebrate taxa found on control quadrats compared to monocultures of foliose seaweed (Group T2).

Order	Control Average Abundance	Group T2 Average Abundance	Average Dissimilarity	Dissimilarity / SD	% contribution to overall dissimilarity
Amphipoda	198.17	118.25	19.83	1.38	42.15
Harpacticoida	39.50	19.25	7.41	1.44	15.75
Gastropoda	41.17	23.50	4.68	1.19	9.95
Patellogastropoda	13.50	2.50	2.21	1.60	4.71
Acarida	14.00	8.25	2.19	2.22	4.65
Polychaeta	9.50	6.75	1.93	2.60	4.10

Table 2.5: Spearman rank correlation values for tests of congruence between two seaweed assemblage descriptors compared to assemblage structure of associated invertebrate epifauna.

	Observational Collections		Manipulative Experiment			
Epifauna similarity compared to:	r_s	P	$r_{s\ (T1\text{-}T2)}$	$P_{(T1\text{-}T2)}$	$r_{s\ (T3\text{-}T5)}$	$P_{(T3\text{-}T5)}$
Seaweed taxonomic similarity	0.111	0.232	0.111	0.239	0.103	0.139
Seaweed functional similarity	0.19	0.469	0.275	0.013	0.196	0.017

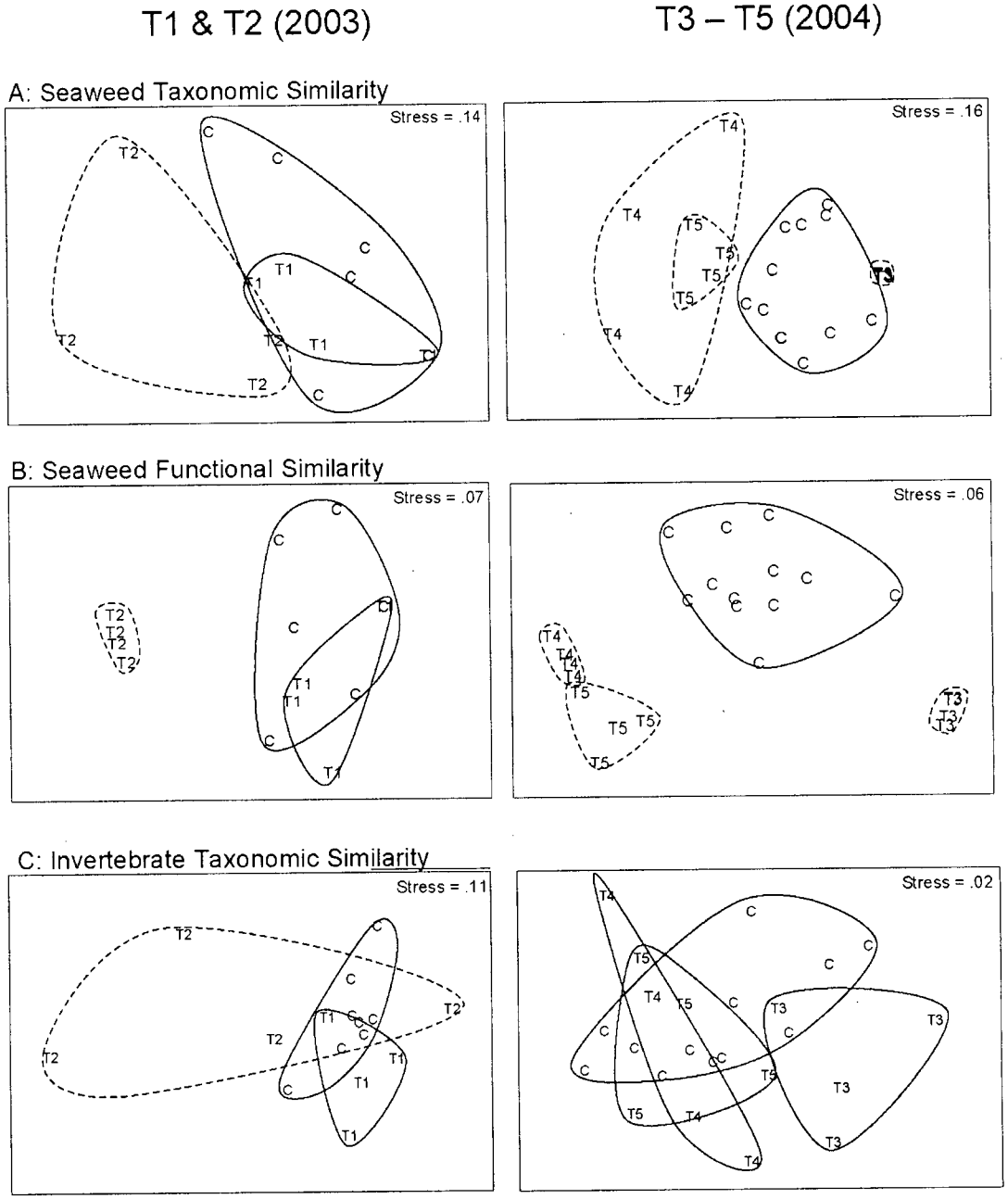

Figure 2.1: nMDS plots of Bray-Curtis Similarity based on: A) seaweed taxonomic composition, B) seaweed functional composition, and C) associated mobile invertebrate epifauna, from 2003 & 2004. C: Control, T1: mixed polyculture, T2: simple monoculture, T3: simple polyculture, T4: complex monoculture, T5: complex polyculture. Dashed line indicates that Treatment group is different from control group (ANOSIM $p < 0.05$; Table 2.4).

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Chapter 3: A comparison of host taxonomic relatedness and functional-group affiliation as predictors of seaweed-invertebrate epifaunal associations.

A version of this chapter will be submitted to *Marine Ecology Progress Series.*

3.1 Introduction

For small mobile invertebrates, seaweeds are a refuge from stressful conditions associated with life on rocky intertidal shores. Seaweed provide cool, wet, and protective canopies and interstices (Hayward 1980, 1988) and can ameliorate the influence of rapid changes in temperature, ultraviolet radiation, desiccation, and hydrodynamic forces caused by twice-daily emersion and immersion by seawater. At high tides, seaweeds can also offer shelter from predation by fish (Holmlund *et al.* 1990, Martin-Smith 1993, Norderhaug *et al.* 2005). Myriad invertebrate taxa use seaweeds as habitat (Colman 1939), and in some cases as a food source (Hawkins and Hartnoll 1983, Arrontes 1999). Epifauna composition, taxon richness, and abundance often differ across species of host seaweed (Colman 1939, Seed and O'Connor 1981, Taylor and Cole 1994). In this study, I explore several general frameworks that hold promise for predicting such patterns of invertebrate biodiversity based on seaweed traits.

Hayward (1988) stated that it is clear that distributions of epifauna result from behavioral choices by invertebrates to find and remain in the habitat most suitable. Criteria for epifauna host choice include factors internal to seaweeds: material properties such as cell structure and cell wall components, energetic storage products and defensive biochemistry (Hay *et al.* 1987, Graham and Wilcox 2000, Padilla and Allen 2000, Van Alstyne and Houser 2003). These properties can vary across seaweeds, resulting in differences in nutritive value and palatability (Paine and Vadas 1969, Hawkins and Hartnoll 1983). In addition to negatively acting to directly deter epifauna (Hay *et al.* 1987), algal defensive biochemistry can act positively, to promote epifauna by conferring associational defenses: e.g. unpalatable algae are avoided by omnivorous fishes, and epifauna therefore escape predation (Hay *et al.* 1990). Along with these internal seaweed features, epifauna also select seaweed hosts based on external features. Architectural complexity of overall seaweed form has widely been linked to abundance and richness of invertebrates (Dean and Connell 1987a, Gee and Warwick 1994, Taylor and Cole 1994, Davenport *et al.* 1996, Hull 1997, Chemello and Milazzo 2002). Compared to "simple" forms such as unbranched blades and crusts, "complex", highly branching seaweeds can better provide predator-free space for

epifauna (Duffy and Hay 1991), stay moist to limit desiccation effects (Ji and Tanaka 2002), and provide increased surface area and microhabitat variety (Christie *et al.* 2003, Norderhaug *et al.* 2005).

At present, scientific perception about the quality of different seaweeds as hosts for small mobile epifauna are based on a body of studies that compare performance of relatively few seaweed species, typically between two (Kraufvelin and Salovius 2004, Wikström and Kautsky 2004) and seven (Holmlund *et al.* 1990), but sometimes up to ten (Taylor and Cole 1994, Taylor and Steinberg 2005). However, a key goal of community ecology is to establish general principles that describe how biotic and abiotic factors structure biological assemblages (MacArthur 1972). To alleviate the need to compare the performance of particular algal species as hosts for epifauna, a more general predictive framework is desirable. The objective of the current study is to compare two such general frameworks: seaweed taxonomic relatedness and seaweed functional form groupings.

Ecologists are increasingly recognizing that taxonomic relationships between species can inform predictions about species performance in an ecological context (Webb *et al.* 2002). Species that are closely related are more likely to share traits (i.e. similarity by common descent), and thus perform similarly in ecological scenarios. Taxonomic relatedness may inform predictions of seaweed-host performance because internal features of seaweeds (material properties, nutritive value, defensive chemistry) tend to be conserved within taxonomic lineages. However, a property that could confound the use of seaweed taxonomic relatedness as a predictor of associated epifauna is that external morphology in seaweeds can vary seemingly independently of taxonomic affinity. Indeed, some genera such as *Codium* and *Caulerpa* contain a wide array of morphologies (Silva 1992), while convergent evolution has resulted in strikingly similar forms shared by algae classified as distantly as subkingdom (e.g. *Ulva lactuca,* a green alga from Subkingdom Viridiplantae and *Porphyra* spp., red algae from the Subkingdom Biliphyta) and kingdom (e.g. *Analipus japonicus,* a brown alga (Kingdom Chromista) and *Cumagloia andersonii,* a red alga (Kingdom Plantae). This similarity in morphology across taxonomic groupings has been formally recognized since the early 1980's, and led to the proposal of morphologically based "functional form" groupings under which predictions of ecological and ecophysiological performance of seaweeds could be made (Littler and Littler 1980, Steneck and Watling 1982, Steneck and Dethier

1994). The use of terrestrial plant functional groups has also become common in recent times (Lavorel *et al.* 1997, Diaz and Cabido 2001). In a recent review of the performance of algal functional groups, Padilla and Allen (2000) were critical of previous applications of seaweed functional form models, highlighting a lack of empirical support for most of the model predictions despite widespread acceptance of their use. They did, however, make a point of suggesting the promise of functional form groupings for predicting structure of habitat for associated organisms. This idea remains untested, although see Hacker and Steneck (1990) who discussed several habitat-providing algal species based on their functional group placement.

Inherent in the concept of using functional groupings to predict ecological or ecophysiological properties is the idea that species grouped together will perform similarly. This premise has been discussed in terms of 'functional redundancy' (Naeem 1998, Fonseca and Ganade 2001, Rosenfeld 2002, Loreau 2004). This concept is relevant to discussions about the consequences of changes in biodiversity because loss of particular species could be compensated for by functionally equivalent coexisting species. This buffering capacity of species rich assemblages has been viewed as a form of "biological insurance" (Thebault and Loreau 2006); however, to date, direct tests of the functional equivalence of seaweeds as hosts for invertebrates are limited to comparisons of only two seaweed taxa such as *Cladophora glomerata* and *Fucus vesiculosus* (Kraufvelin and Salovius 2004).

To test the efficacy of seaweed taxonomic relatedness and functional group affinity as predictors of seaweed – invertebrate epifauna associations, I ask three questions: a) is similarity of invertebrate assemblages positively correlated with algal host taxonomic relatedness; b) does invertebrate assemblage structure differ across seaweed functional groups; and c) is the performance of seaweed species as habitat for small mobile invertebrates similar within algal functional groups?

3.2. Materials and methods

3.2.1 Study Sites

Collections of host algae and associated invertebrates were taken at six rocky intertidal sites along southern Barkley Sound, British Columbia, Canada (Figure 1.3). Each site was sampled once per month over eleven months (March 2005 – January 2006) during spring tides.

3.2.2 Sample collections

At each sampling event (site per date), representatives of three to seven algal species were haphazardly collected along a horizontal belt transect that measured 1 m x 30 m, centred at 1 m above chart datum. I sampled eight individual thalli per algal species, and each thallus was sealed in a zippered collection bag. Algal species were selected if they were abundant at the site, and also to maximize taxonomic and functional representation within the overall data set. In total, 1652 algal thalli were collected across 32 algal species (Table 3.1). Samples were frozen to euthanize epifauna before processing, and then processed as described in section 2.2.6.

3.2.3 Algal taxonomy & taxonomic distance

Taxonomic affiliations of the 32 included species of host algae (Table 3.1) were obtained from Gabrielson *et al.* (2006). Taxonomic ranks ranged from specific epithets to Kingdom. Taxonomic distance between seaweed hosts was calculated by counting the number of "steps" through a dendrogram of the Linnaean taxonomic hierarchy (Figure 3.1). For several taxonomic ranks (Tribe, Subfamily, Subphylum, Infrakingdom, and Subkingdom) there was a) only one taxon in this data set classified to this level (e.g. Tribe Ceramiae), or b) lack of multiple subclades at that rank (e.g. Subkingdom). These ranks were not included in calculations of taxonomic distance.

3.2.4 Algal functional groups

Although several seaweed functional group classifications exist (Littler and Littler 1980, Steneck and Watling 1982, Steneck and Dethier 1994), the groupings are very similar. I chose to use the algal functional groups erected by Steneck and Dethier (1994) because they included eight groups compared to the other two models, which used six. Based on similarity in gross morphology, Steneck and Dethier grouped algae into microalgae, filamentous, foliose, corticated foliose, corticated terete, leathery, geniculate calcareous, and crustose. I use seven of these groups (microalgae are not considered), and functional group affiliation of each species is listed in Table 3.1.

3.2.5 Statistical analysis

All invertebrate abundances were fourth-root transformed before multivariate analyses to downweight the contribution of highly abundant invertebrate species to measures of sample similarity (Clarke 1993).

3.2.5.1 Taxonomic distance analyses

Pairwise comparisons of invertebrate assemblage similarity between algal thalli were calculated using the Bray-Curtis similarity measure (Bray and Curtis 1957). Analysis of Similarities (ANOSIM; Clarke 1993) was used to assess the degree of invertebrate assemblage similarity between host species. The ANOSIM test statistic (R) ranges between –1 and 1, with values close to zero indicating no difference between sample groups. Values closer to 1 indicate a greater difference between groups than within groups, whereas values closer to –1 indicate a greater difference within groups than between groups. The resultant R-values were then plotted against taxonomic distance of the two hosts being compared. The R-values were not normally distributed but exhibited homogeneous variances (Bartlett's test, $F = 0.47$ $p = 0.86$), so the nonparametric Wilcoxon signed-ranks procedure was used to test for differences in invertebrate assemblage similarity among taxonomic levels.

3.2.5.2 Functional group analyses

Across algal functional groups, I used ANOSIM to test for differences in composition of invertebrate assemblages and ANOVA to test for differences in invertebrate abundances and taxon richness. To control for richness differences caused by differences in invertebrate abundance, I rarefied species richness to 20 individuals (Magurran 1988). I used the mean of each algal species to replicate within functional group, and, because values of invertebrate abundance and rarefied richness violated assumptions of normality and homogeneity of variance, I used Monte Carlo randomization procedures (Manly 1991) to determine the level of significance of differences across functional groups. Specifically, identity of algal species was shuffled across functional groups, and the original F-statistic was compared to a null distribution of F-statistics created through 4999 of these randomized permutations.

Within functional groups, I used ANOSIM to test across algal species for differences in invertebrate assemblages. To test for differences in values of invertebrate abundance and rarefied richness, Monte Carlo randomization procedures (Manly 1991) were again used to test for between-species differences. Specifically I tested if, for each species comparison, Mean $_{\text{species X}}$ - Mean $_{\text{species Y}}$ (where (X, Y) represent all pairwise combinations of species within functional groups), differed significantly from a null distribution created through 4999 randomizations (with replacement) of the values for both groups.

Multivariate results and taxonomic distances were obtained using PRIMER software (Version. 6.1.6, Primer-E, www.primer-e.org). Parametric univariate analyses were performed using JMPin (Version 4.0.4, SAS Institute Inc.), and randomization procedures were achieved using PopTools (Hood 2006).

3.3 Results

3.3.1 General results

A total of 54,776 individuals were sampled across 98 taxa of mobile invertebrate epifauna. The majority of these individuals came from a small number of higher taxa,

including gammarid amphipods (47.9 %), harpacticoid and calanoid copepods (18.4 %), juvenile bivalve mollusks (12.2 %), gastropod mollusks (5.0 %), isopods (4.0 %), mites (3.6 %), polychaete worms (2.8 %) and nematodes (2.2 %).

3.3.2 Algal taxonomic distance

Similarity of invertebrate assemblages did not decrease as taxonomic distances between seaweed hosts increased; invertebrate assemblages were as similar between congeneric algal hosts as between algal species in different kingdoms (Wilcoxon, Chi-Square = 6.93, df = 7, $p = 0.44$; Figure 3.2).

3.3.3 Across algal functional groups

Invertebrate assemblages were different across most algal functional groups (ANOSIM R = 0.209, $p < 0.001$; Table 3.2). However, geniculate coralline algae had similar invertebrate composition to leathery, corticated terete, corticated foliose, and foliose functional groups. As well, crustose and corticated foliose functional groups harbored similarly sparse assemblages.

Invertebrate taxon richness was different across some, but not all, algal functional groups ($p < 0.002$, Figure 3.3, upper panel). The filamentous, foliose, corticated foliose, and corticated terete functional groups were not different ($p > 0.05$). The crustose group was different because it had few, if any, taxa associated with it, and the leathery and geniculate coralline functional groups were not different from either the former or the latter set of functional groups.

No differences across algal functional groups were noted for abundance of invertebrates (Figure 3.3, lower panel), although the results were marginally nonsignificant ($p = 0.081$).

3.3.4 Within algal functional groups

There was little evidence to support the prediction that algal species within the same functional group were functionally equivalent. Composition of invertebrate

assemblages (Table 3.3) was different for most pairwise comparison within most of the functional groups. Only five out of 28 possible pairwise comparisons were nonsignificant in the filamentous functional group. The corticated foliose group showed one nonsignificant result out of ten, corticated terete showed one out of 36, leathery showed one out of six. Within the foliose group and the geniculate coralline groups, all of the species had different invertebrate assemblages, whereas in the crustose group, the two species had the same type of assemblage.

For rarefied invertebrate taxon richness and invertebrate abundance (Figure 3.4), most algal species had a mean richness and abundance that differed from the functional group mean ($p < 0.05$). Notable exceptions include the filamentous group for which rarefied invertebrate richness was consistent with the functional group mean for most taxa, although *Polysiphonia senticulosa* and *Rhizoclonium riparium* were, respectively, well below and above the filamentous group mean. However, despite this relative consistency in taxon richness, invertebrate abundance was variable across the filamentous group. Rarefied richness and composition were the same for species within the coralline and crustose groups; however only two species were represented in each functional group.

3.4 Discussion

3.4.1 Taxonomic relatedness of seaweed host

Knowledge of the influence of host relatedness on associated fauna is potentially important to the estimation of global species diversity (Ødegaard *et al.* 2005), for predicting the ecological performance of host species, and understanding community assembly. However, although several recent studies examine the influence of genetic diversity on associated marine invertebrates within single host species (Hughes and Stachowicz 2004, Johnson *et al.* 2006), cross-species tests of linkages between host plant relatedness and associated fauna are not common (Farrell and Mitter 1990, Losos 1996, Kelly and Southwood 1999, Ødegaard *et al.* 2005, Weiblen *et al.* 2006). The results of the current study show that seaweed host taxonomic relatedness does not inform predictions about differences in diversity of associated small mobile

invertebrates. I found that mobile invertebrate assemblages were as different on sibling algal species as on hosts classified in different kingdoms (Figure 3.2).

Where host relatedness of terrestrial plants has been investigated as a predictor of diversity of associated phytophagous insects, some predictive value of host taxonomic relatedness has been demonstrated. Insect assemblages are more similar on plant hosts from the same genus and family, but not at higher taxonomic distances (Ødegaard *et al.* 2005, Weiblen *et al.* 2006), and host specificity is invoked as an explanation for this relationship. Congruence in patterns of diversification between host and herbivore clades indicate that specialization could be a result of coevolution between host plants and specialist feeders (Farrell and Mitter 1990). The relationship between host phylogeny and phytophagous insects makes sense because herbivorous insects prefer closely related plants that are similar in chemistry and resource provision. In the marine system examined in the current study, this is not the case; many seaweed epifauna do not consume their host (Arrontes 1999), and therefore tend to be more general in their host use patterns. As suggested in the introduction to this chapter, marine invertebrate epifauna select seaweed hosts based on internal and external features, yet seaweed form has been shown to be a stronger regulator of invertebrate epifauna than palatability or defensive chemistry (Dean and Connell 1987a, Norderhaug 2004). It is therefore not surprising that seaweed taxonomic relatedness was not congruent with observed patterns of associated invertebrates. Additional support for the lack of influence of host taxonomic relatedness on associated invertebrates is provided by the observation that a single species exhibiting an alternation of heteromorphic generations, *Mastocarpus papillatus,* shows that even within the same species, functionally different forms support different invertebrate assemblages (Figure 3.4).

It is important to note that seaweed taxonomy is currently in flux, and even major groups like the Rhodophyta are subject to substantial higher-level taxonomic rearrangement (Saunders and Hommersand 2004). Furthermore, genetic distances between seaweed taxa classified to the same taxonomic ranks are not always equal. However, given the often-demonstrated linkages between algal host morphology and invertebrate diversity (Martin-Smith 1993, Davenport *et al.* 1996, Attrill *et al.* 1999, Davenport *et al.* 1999, McAbendroth *et al.* 2005), it is unlikely that my conclusions would change given a revised algal taxonomy.

3.4.2 Seaweed functional groups

Differences were observed across several algal functional (i.e. morphological) groups for invertebrate composition, yet fewer between-group differences were noted for number of invertebrate taxa and no differences were seen for invertebrate abundance (Table 3.2, Figure 3.3). Morphologically based algal functional groups have had variable success for predicting seaweed-invertebrate interactions (Hawkins and Hartnoll 1983, Arrontes 1990, Duffy and Hay 1991, Wakefield and Murray 1998), and Padilla and Allen's (2000) suggestion that algal functional form groups could be applied to habitat provision was not well supported here. Observations of invertebrate richness across functional groups tend, on average, to follow common perceptions about relationships between algal thallus complexity and invertebrate diversity. Specifically, the complexly branching filamentous and corticated terete functional groups tended to have the most associated invertebrates, whereas simple groups (i.e. flat blades from the corticated foliose and leathery groups, and crustose groups) tended to have the least (Figure 3.3). However, there was substantial variation within functional groups (Figure 3.4), suggesting that functional group performance actually indicates little about the performance of the constituent species.

Hay (1994) suggested that if, in general, ecologically meaningful seaweed functional groups could be erected, these patterns of similarity could then lead naturally to discussions of species differences. However, based on my observations across a large number of species, it appears that invertebrate selection of seaweed host is largely dependant upon the identity of the host species, not the functional group. While there is no question that algal morphology influences diversity of associated invertebrates, it appears that the relationship between host morphology and invertebrate assemblages is not straightforward (i.e. increased architectural complexity does not directly lead to higher diversity of associated invertebrates), a phenomenon that is not uncommon when considering questions of functional morphology (Koehl 1996). Several possible explanations exist to explain the variable performance of host species within algal functional groups.

First, once invertebrates choose a host based on gross morphology, host selection decisions may be refined based on internal features of seaweeds. While I have not directly tested any internal variables here, I do show that complexly branching

algae with very similar external features can host different invertebrate assemblages. For example, species within filamentous and corticated terete groups (Figure 3.4), and even congeneric algae with very similar forms (e.g. *Acrosiphonia coalita* versus *Acrosiphonia arcta*) have a very different number of associated invertebrates. This latter result is similar to observations that the invasive species *Fucus evanescens* C. Ag. is utilized less by epifauna than the native congener *Fucus vesiculosus* L. along European coasts (Wikström and Kautsky 2004). These types of observations draw into question even the use of seaweed architectural complexity as a predictor of associated invertebrates; this often-cited regulator of seaweed-epifauna associations does not appear to be wholly reliable criterion for generalization.

Second, seaweed functional groups are traditionally delineated based on morphological features of individual thalli (Steneck and Dethier 1994). However, complexity of morphology is a parameter that can vary across scales of observation (Kingsford 1995, McAbendroth *et al.* 2005). For example, at the small (i.e. algal thallus) scale, architectural complexity may be considered as branching complexity (Chemello and Milazzo 2002), whereas at broader (i.e. seaweed stand) scales, arrangement of the individual thalli in space influences invertebrate habitat choices (Goodsell and Connell 2002, Goodsell *et al.* 2004, Goodsell and Connell 2005, Roberts and Poore 2005). These two scales of architectural complexity can differentially affect various types or sizes of seaweed-associated invertebrates (Hacker and Steneck 1990), or modify the effects of different abiotic and biotic stressors.

It is possible that the functional groups erected by Steneck and Dethier (1994) are not defined according to parameters that are relevant to habitat use by small mobile invertebrate epifauna. Padilla and Allen (2000) suggested that algal functional groups should be based not on gross morphology, but on particular functions, and then tested before being generally applied across taxa. However, in examining the suite of species tested here, it seems unlikely that meaningful functional groups could be defined; while there is an apparent gradient of habitat use by invertebrates, no clusters of similarly functioning algal species were observed (Figure 3.4). As such, replacements by 'equivalent' or 'redundant' taxa appear unlikely.

3.4.3 Is there hope for generalizations about seaweed-epifauna associations?

The two frameworks tested here (taxonomic relatedness and algal functional group affiliation) do not appear useful for informing predictions of habitat use by invertebrate epifauna. However, several options still exist as possibilities for generalizing about seaweed-epifauna associations; I offer here several suggestions for future research.

First, the marine system studied here embodies a much wider taxonomic breadth in both host plants and associated invertebrates compared to terrestrial insect – host plant systems. Invertebrate functional groups, based on feeding and bioturbation types, have been successful elsewhere (Mermillod-Blondin *et al.* 2002, Rabeni *et al.* 2005) and may offer some resolution in this marine system. For example, marine invertebrate mesoherbivores may show a stronger affinity for specific algal hosts than was revealed by the broad, community-wide assessment of invertebrate epifauna described here.

Second, given the observed gradient of host use across algal taxa, it would be interesting to look for particular algal traits that could be measured on a continuous scale, instead of discrete groups that integrate suites of algal traits. Chemello and Milazzo (2002) examined variation in nine morphological traits across six brown algal species, and showed that degree of branching alone explained over 60 % of the variation in plant-mollusc assemblages. This approach holds promise, although difficulties can arise when looking for morphological traits that are shared across a broad spectrum of algal morphologies.

Lastly, the small proportion of variance explained by the seaweed traits tested here suggests that factors other than seaweed traits are influencing habitat choices by small mobile invertebrates. It is highly likely that abiotic environmental conditions are also integrated into habitat choices by epifauna, and a major feature of intertidal existence is addressed in the next chapter: hydrodynamic regime.

Table 3.1: Functional group affiliations, number of collected thalli, and taxonomic hierarchy used to calculate taxonomic distances between seaweed species. Taxonomic authorities are available from Gabrielson *et al.* (2006)

Functional Group	N	Genus & Species	Family	Order	Subclass	Class	Phylum	Kingdom
filamentous	8	*Acrosiphonia arcta*	Acrosiphoniaceae	Codiolales		Ulvophyceae	Chlorophyta	Plantae
filamentous	8	*Acrosiphonia coalita*	Acrosiphoniaceae	Codiolales		Ulvophyceae	Chlorophyta	Plantae
leathery	54	*Alaria marginata*	Alariaceae	Laminariales		Phaeophyceae	Ochrophyta	Chromista
corticated	36	*Analipus japonicus*	Scytosiphonaceae	Ectocarpales		Phaeophyceae	Ochrophyta	Chromista
filamentous	42	*Ceramium pacificum*	Ceramiaceae	Ceramiales	Rhodymeniophycidae	Florideophycidae	Rhodophyta	Plantae
corticated foliose	107	*Chondracanthus exasperatus*	Gigartinaceae	Gigartinales	Rhodymeniophycidae	Florideophycidae	Rhodophyta	Plantae
filamentous	8	*Cladophora columbiana*	Cladophoraceae	Cladophorales		Cladophorophyceae	Chlorophyta	Plantae
corticated	46	*Codium fragile*	Codiaceae	Bryopsidales		Bryopsidophyceae	Chlorophyta	Plantae
coralline	8	*Corallina officinalis* var. *chilensis*	Corallinaceae	Corallinales	Rhodymeniophycidae	Florideophycidae	Rhodophyta	Plantae
coralline	16	*Corallina vancouveriensis*	Corallinaceae	Corallinales	Rhodymeniophycidae	Florideophycidae	Rhodophyta	Plantae
crustose	8	*Coralline Crust*	Corallinaceae	Corallinales	Rhodymeniophycidae	Florideophycidae	Rhodophyta	Plantae
leathery	8	*Costaria costata*	Costariaceae	Laminariales		Phaeophyceae	Ochrophyta	Chromista
corticated	39	*Cryptosiphonia woodii*	Dumontiaceae	Gigartinales	Rhodymeniophycidae	Florideophycidae	Rhodophyta	Plantae
corticated	8	*Desmarestia ligulata*	Desmarestiaceae	Desmarestiales		Phaeophyceae	Ochrophyta	Chromista
corticated	62	*Endocladia muricata*	Endocladiaceae	Gigartinales	Rhodymeniophycidae	Florideophycidae	Rhodophyta	Plantae
leathery	396	*Fucus distichus* subsp. *evanescens*	Fucaceae	Fucales		Phaeophyceae	Ochrophyta	Chromista
corticated	74	*Gastroclonium subarticulatum*	Champiaceae	Rhodymeniales	Rhodymeniophycidae	Florideophycidae	Rhodophyta	Plantae
corticated foliose	8	*Halosaccion glandiforme*	Palmariaceae	Palmariales	Rhodymeniophycidae	Florideophycidae	Rhodophyta	Plantae
corticated foliose	8	*Leathesia difformis*	Chordariaceae	Ectocarpales		Phaeophyceae	Ochrophyta	Chromista
corticated fol. / crustose	8 / 39	*Mastocarpus papillatus*	Phyllophoraceae	Gigartinales	Rhodymeniophycidae	Florideophycidae	Rhodophyta	Plantae
corticated foliose	84	*Mazzaella splendens*	Gigartinaceae	Gigartinales	Rhodymeniophycidae	Florideophycidae	Rhodophyta	Plantae
corticated	8	*Nemalion elminthoides*	Liagoraceae	Nemaliales	Nemaliophycidae	Florideophycidae	Rhodophyta	Plantae
corticated	35	*Neorhodomela larix*	Rhodomelaceae	Ceramiales	Rhodymeniophycidae	Florideophycidae	Rhodophyta	Plantae
filamentous	35	*Polysiphonia hendryi*	Rhodomelaceae	Ceramiales	Rhodymeniophycidae	Florideophycidae	Rhodophyta	Plantae
filamentous	15	*Polysiphonia paniculata*	Rhodomelaceae	Ceramiales	Rhodymeniophycidae	Florideophycidae	Rhodophyta	Plantae
filamentous	7	*Polysiphonia senticulosa*	Rhodomelaceae	Ceramiales	Rhodymeniophycidae	Florideophycidae	Rhodophyta	Plantae
foliose	64	*Porphyra abbottiae*	Bangiaceae	Bangiales	Bangiophycidae	Bangiophyceae	Rhodophyta	Plantae
corticated	80	*Prionitis lyallii*	Halymeniaceae	Halymeniales	Rhodymeniophycidae	Florideophycidae	Rhodophyta	Plantae
filamentous	8	*Rhizoclonium riparium*	Cladophoraceae	Cladophorales		Cladophorophyceae	Chlorophyta	Plantae
corticated	46	*Sargassum muticum*	Sargassaceae	Fucales		Phaeophyceae	Ochrophyta	Chromista
foliose	270	*Ulva lactuca*	Ulvaceae	Ulvales		Ulvophyceae	Chlorophyta	Plantae
foliose	8	*Ulva intestinalis*	Ulvaceae	Ulvales		Ulvophyceae	Chlorophyta	Plantae

Table 3.2: Results of ANOSIM test for differences in invertebrate epifauna assemblage across six algal functional groups. Boldface text indicates no difference between groups ($p > 0.05$).

Functional Group Comparison	R- Statistic	P-Value
foliose, leathery	0.122	< 0.001
foliose, corticated	0.113	< 0.001
foliose, corticated foliose	0.147	< 0.001
foliose, filamentous	0.358	< 0.001
foliose, crustose	0.542	< 0.001
foliose, coralline	0.090	< 0.048
leathery, corticated terete	0.208	< 0.001
leathery, corticated foliose	0.172	< 0.001
leathery, filamentous	0.419	< 0.001
leathery, crustose	0.200	< 0.001
leathery, coralline	0.067	**0.098**
corticated terete, corticated foliose	0.233	< 0.001
corticated terete, filamentous	0.151	< 0.001
corticated terete, crustose	0.593	< 0.001
corticated terete, coralline	0.041	**0.194**
corticated foliose, filamentous	0.373	< 0.001
corticated foliose, crustose	0.044	**0.088**
corticated foliose, coralline	0.036	**0.203**
filamentous, crustose	0.859	< 0.001
filamentous, coralline	0.320	< 0.001
crustose, coralline	0.884	< 0.001

Table 3.3: Results of ANOSIM tests comparing invertebrate epifauna assemblages across algal species within six functional groups. Boldface text highlights no difference between species ($p > 0.05$).

A. Filamentous (Global R = 0.431, p < 0.001)

Species comparisons	R- Statistic	P-Value
Polysiphonia senticulosa, Polysiphonia hendryi	0.321	< 0.001
Polysiphonia senticulosa, Acrosiphonia arcta	0.379	0.005
Polysiphonia senticulosa, Polysiphonia paniculata	0.133	**0.064**
Polysiphonia senticulosa, Acrosiphonia coalita	0.867	0.002
Polysiphonia senticulosa, Ceramium pacificum	0.881	< 0.001
Polysiphonia senticulosa, Rhizoclonium riparium	0.897	< 0.001
Polysiphonia senticulosa, Cladophora columbiana	0.995	< 0.001
Polysiphonia hendryi, Acrosiphonia arcta	0.007	**0.510**
Polysiphonia hendryi, Polysiphonia paniculata	0.237	< 0.001
Polysiphonia hendryi, Acrosiphonia coalita	0.012	**0.422**
Polysiphonia hendryi, Ceramium pacificum	0.374	< 0.001
Polysiphonia hendryi, Rhizoclonium riparium	0.256	0.007
Polysiphonia hendryi, Cladophora columbiana	0.419	< 0.001
Acrosiphonia arcta, Polysiphonia paniculata	0.073	**0.168**
Acrosiphonia arcta, Acrosiphonia coalita	0.575	< 0.001
Acrosiphonia arcta, Ceramium pacificum	0.702	< 0.001
Acrosiphonia arcta, Rhizoclonium riparium	0.594	< 0.001
Acrosiphonia arcta, Cladophora columbiana	0.963	< 0.001
Polysiphonia paniculata, Acrosiphonia coalita	0.133	**0.080**
Polysiphonia paniculata, Ceramium pacificum	0.56	< 0.001
Polysiphonia paniculata, Rhizoclonium riparium	0.173	0.038
Polysiphonia paniculata, Cladophora columbiana	0.296	0.015
Acrosiphonia coalita, Ceramium pacificum	0.178	0.024
Acrosiphonia coalita, Rhizoclonium riparium	0.442	< 0.001
Acrosiphonia coalita, Cladophora columbiana	0.881	< 0.001
Ceramium pacificum, Rhizoclonium riparium	0.607	< 0.001
Ceramium pacificum, Cladophora columbiana	0.697	< 0.001
Rhizoclonium riparium, Cladophora columbiana	0.74	< 0.001

B. Foliose (Global R = 0.113, p < 0.001)

Species comparisons	R- Statistic	P-Value
Ulva lactuca, Porphyra	0.12	< 0.001
Ulva lactuca, Ulva intestinalis	0.191	0.028
Porphyra, Ulva intestinalis	0.41	< 0.001

C. Corticated foliose (Global R = 0.269, P < 0.001)

Species comparisons	R- Statistic	P-Value
Mazzaella splendens, Chondracanthus exasperatus	0.176	< 0.001
Mazzaella splendens, Leathesia difformis	0.913	< 0.001
Mazzaella splendens, Mastocarpus papillatus	0.469	< 0.001
Mazzaella splendens, Halosaccion glandiforme	0.74	< 0.001
Chondracanthus exasperatus, Leathesia difformis	0.414	< 0.001
Chondracanthus exasperatus, Mastocarpus papillatus	0.067	**0.188**
Chondracanthus exasperatus, Halosaccion glandiforme	0.281	< 0.001
Leathesia difformis, Mastocarpus papillatus	0.966	< 0.001
Leathesia difformis, Halosaccion glandiforme	0.83	< 0.001
Mastocarpus papillatus, Halosaccion glandiforme	0.556	< 0.001

D. Corticated terete (Global R = 0.255, P < 0.001)

Species comparisons	R- Statistic	P-Value
Sargassum muticum, Gastroclonium subarticulatum	0.235	< 0.001
Sargassum muticum, Neorhodomela larix	0.272	< 0.001
Sargassum muticum, Codium fragile	0.431	< 0.001
Sargassum muticum, Prionitis lyallii	0.164	< 0.001
Sargassum muticum, Cryptosiphonia woodii	0.207	< 0.001
Sargassum muticum, Analipus japonica	0.259	< 0.001
Sargassum muticum, Endocladia muricata	0.361	< 0.001
Sargassum muticum, Nemalion elminthoides	0.736	< 0.001
Gastroclonium subarticulatum, Neorhodomela larix	0.158	< 0.001
Gastroclonium subarticulatum, Codium fragile	0.626	< 0.001
Gastroclonium subarticulatum, Prionitis lyallii	0.306	< 0.001
Gastroclonium subarticulatum, Cryptosiphonia woodii	0.282	< 0.001
Gastroclonium subarticulatum, Analipus japonica	0.347	< 0.001
Gastroclonium subarticulatum, Endocladia muricata	0.368	< 0.001
Gastroclonium subarticulatum, Nemalion elminthoides	0.831	< 0.001
Neorhodomela larix, Codium fragile	0.468	< 0.001
Neorhodomela larix, Prionitis lyallii	0.115	< 0.001
Neorhodomela larix, Cryptosiphonia woodii	0.132	< 0.001
Neorhodomela larix, Analipus japonica	0.255	< 0.001
Neorhodomela larix, Endocladia muricata	0.18	< 0.001
Neorhodomela larix, Nemalion elminthoides	0.791	< 0.001
Codium fragile, Prionitis lyallii	.04	**0.061**
Codium fragile, Cryptosiphonia woodii	0.322	< 0.001
Codium fragile, Analipus japonica	0.344	< 0.001
Codium fragile, Endocladia muricata	0.285	< 0.001
Codium fragile, Nemalion elminthoides	0.181	0.036
Prionitis lyallii, Cryptosiphonia woodii	0.097	0.005
Prionitis lyallii, Analipus japonica	0.143	0.003

Prionitis lyallii, Endocladia muricata	0.193	< 0.001
Prionitis lyallii, Nemalion elminthoides	0.165	0.037
Cryptosiphonia woodii, Analipus japonica	0.109	< 0.001
Cryptosiphonia woodii, Endocladia muricata	0.118	0.002
Cryptosiphonia woodii, Nemalion elminthoides	0.449	< 0.001
Analipus japonica, Endocladia muricata	0.132	0.003
Analipus japonica, Nemalion elminthoides	0.481	< 0.001
Endocladia muricata, Nemalion elminthoides	0.32	0.004

E. Leathery (Global R = 0.339, P < 0.001)

Species comparisons	**R- Statistic**	**P-Value**
Fucus distichus, Desmarestia ligulata	0.442	< 0.001
Fucus distichus, Alaria marginata	0.312	< 0.001
Fucus distichus, Costaria costata	0.434	< 0.001
Desmarestia ligulata, Alaria marginata	-0.095	**0.829**
Desmarestia ligulata, Costaria costata	0.763	< 0.001
Alaria marginata, Costaria costata	0.337	0.003

F. Geniculate coralline (Global R = 0.33, P = 0.003)

Species comparisons	**R- Statistic**	**P-Value**
Corallina vancouveriensis, Corallina officinalis	0.337	0.003

G. Crustose (Global R = -0.066, P = .100)

No species comparisons required

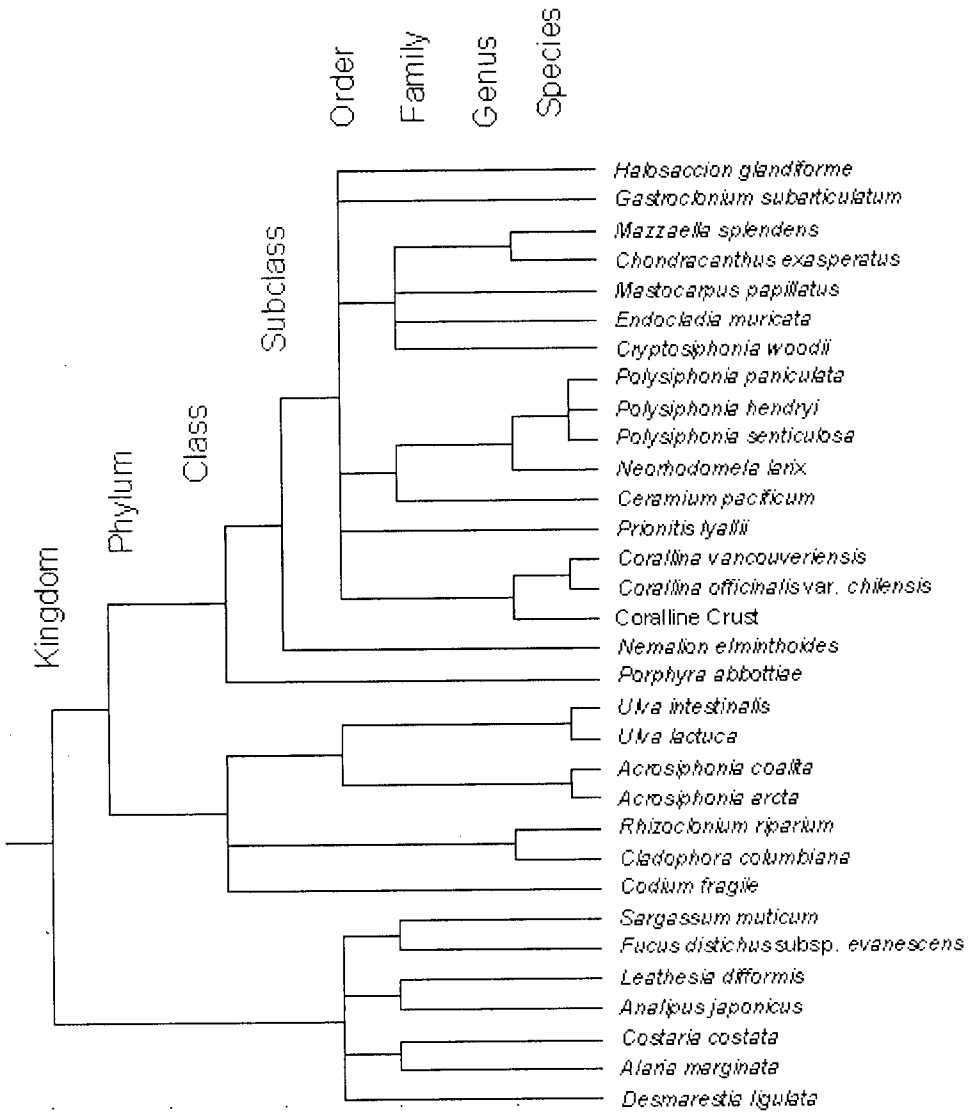

Figure 3.1: Dendrogram illustrating taxonomic relationships between algal species investigated as hosts for small mobile invertebrate epifauna. Taxonomic relationships follow Gabrielson *et al.* (2006).

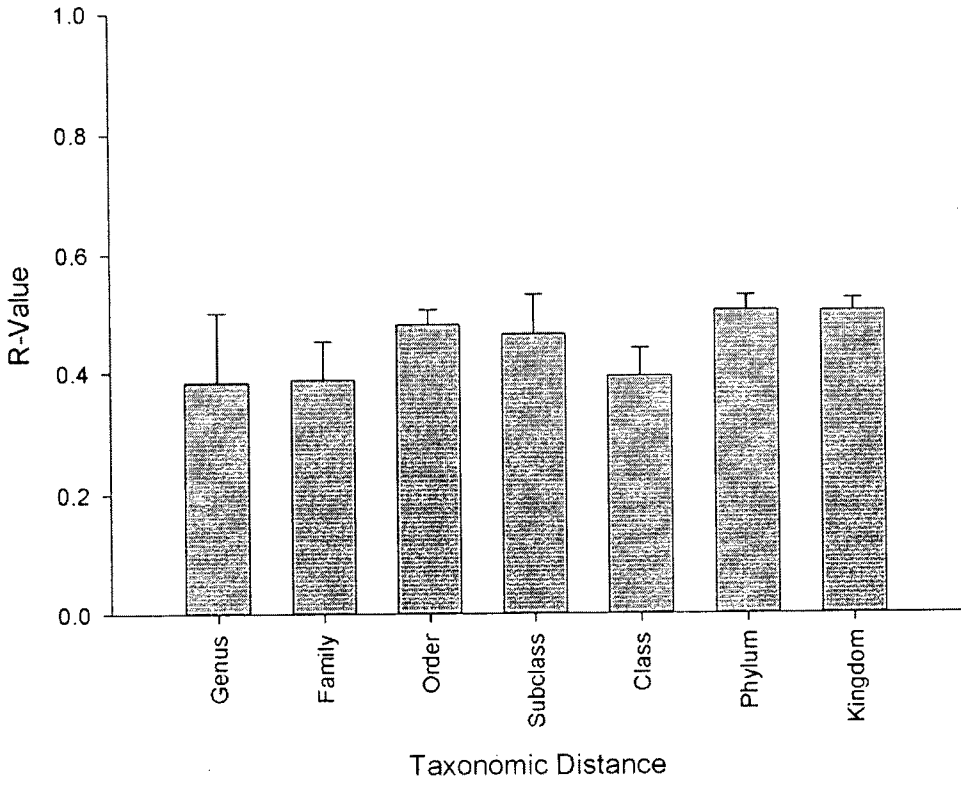

Figure 3.2: ANOSIM R-values indicating similarity of invertebrate assemblages between algal species within seven groups of increasing taxonomic distance. No differences were observed between groups ($p = 0.44$). Bars report mean values (+/- SE).

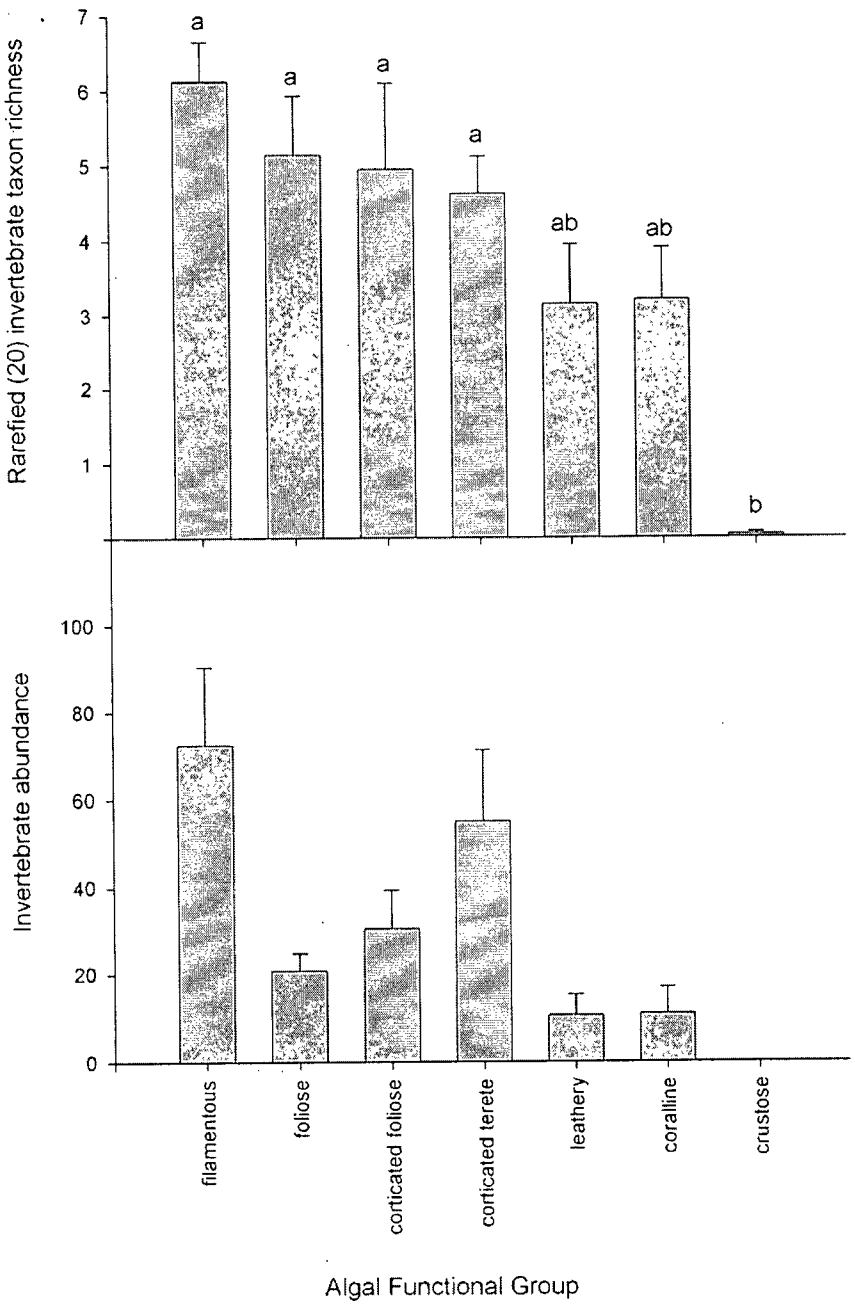

Figure 3.3: Comparisons of rarefied invertebrate taxon richness (upper panel) and invertebrate abundance (lower panel) across seven algal functional groups. Shared letters (upper panel) indicate no significant difference between groups ($p > 0.05$). Invertebrate abundance did not differ across algal functional groups ($p = 0.08$). Bars report mean values (+/- SE).

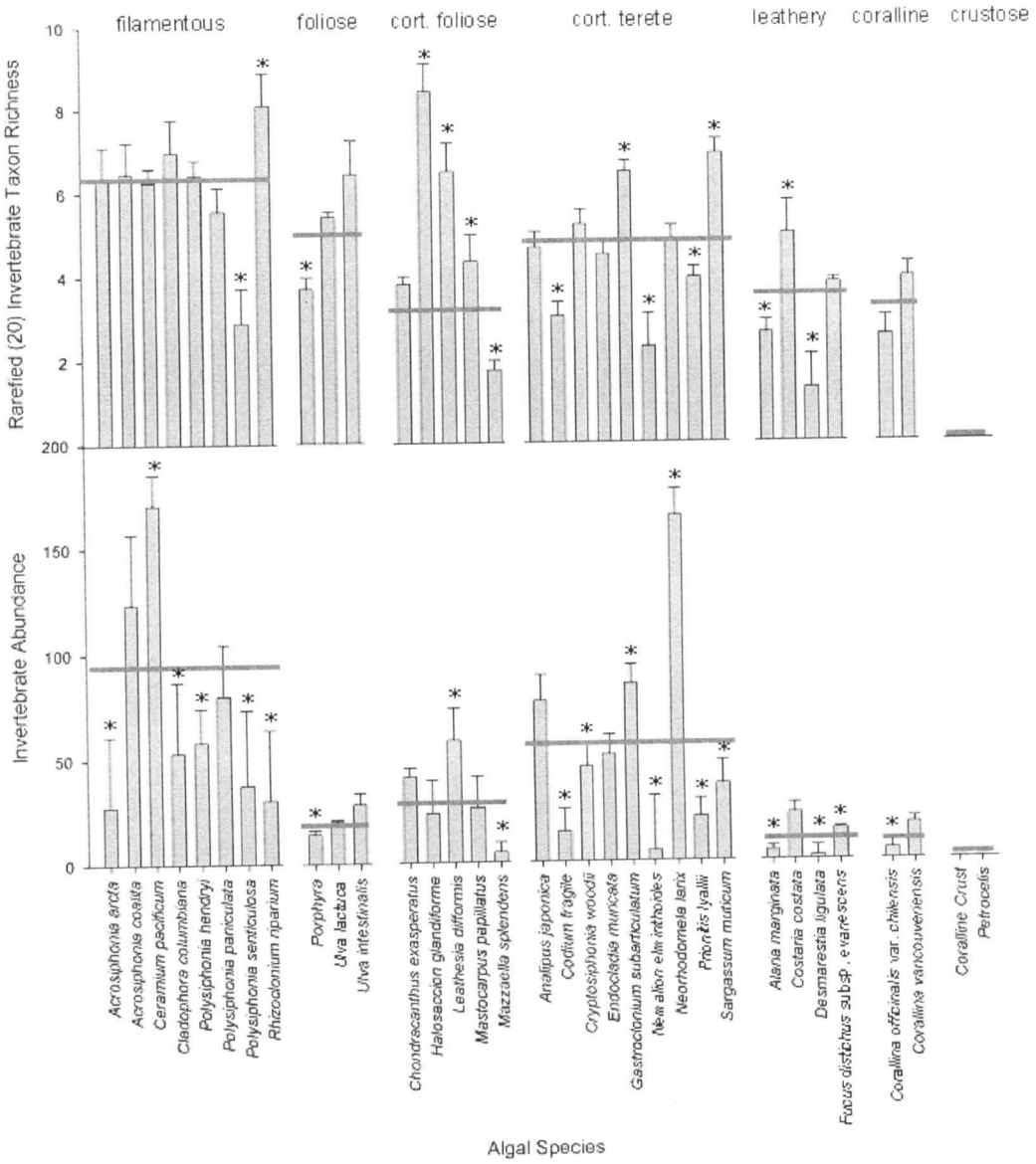

Figure 3.4: Comparisons of rarefied invertebrate taxon richness (upper panel) and invertebrate abundance (lower panel) for algal species within seven algal functional groups. Horizontal bars indicate the mean value for each functional group. Asterisk (*) indicates that the species mean differs from the functional group mean ($p < 0.05$). Bars report mean values (+/- SE).

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Chapter 4: Do facilitator traits interact with an environmental gradient to determine local species diversity?

A version of this chapter will be submitted to *Ecology*.

4.1 Introduction

4.1.1 Ecosystem engineering, species traits, & environmental gradients

Many habitat-providing organisms promote the coexistence of other species by directly or indirectly ameliorating the negative effects of inhospitable environments (Thompson *et al.* 1996, Kelaher *et al.* 2001, Bradshaw *et al.* 2003). This process, known as ecosystem engineering (Jones *et al.* 1994), can expand the realized niche of associated species (Crain and Bertness 2006, McGill *et al.* 2006), and provide a foundation for entire communities. These facilitative interactions are common in nature and although long recognized, ecologists have only recently begun to formally include facilitation into models of the major factors that structure biotic assemblages (Bruno and Bertness 2000, Menge 2000, Stachowicz 2001, Bruno *et al.* 2003). Given uncertainty about the consequences of changes in biodiversity of habitat-providing species (Benedetti-Cecchi *et al.* 2001, Hooper *et al.* 2005, Ewers and Didham 2006, Thebault and Loreau 2006, Winfree *et al.* 2007), the current challenge is to determine the circumstances under which ecosystem engineering is important (Crain and Bertness 2006). Several factors have been suggested to control the context under which species can act as habitat providers (Bruno and Bertness 2000, Crain and Bertness 2006, McGill *et al.* 2006), two of which I focus on here: host species traits and environmental gradients.

Species traits have recently been suggested as important regulators of habitat provision (Bruno and Bertness 2000), yet "...remarkably little work has been done on the traits involved in ecosystem engineering..." (Bouma *et al.* 2005). It makes sense that host species traits should influence ecosystem engineering, because not all habitat-providing species are created equal. To effectively ameliorate the influence of environmental stress, host species must possess traits that actually have an influence on prevailing stressors (Bruno and Bertness 2000). Some (McGill *et al.* 2006) have argued that a study of functional traits is a pragmatic approach to improving the predictive power of community ecology.

Environmental gradients may be determinants of the strength and importance of positive interactions (Bertness and Callaway 1994, Jones *et al.* 1997, Callaway et al.

2002, Crain and Bertness 2006, McGill *et al.* 2006) although the mechanisms of stress amelioration are hypothesized to differ depending on the level of environmental stress (Bruno *et al.* 2003). In harsh environments, ecosystem engineering is predicted to be important because of the amelioration of *abiotic* stressors (Bertness and Callaway 1994), whereas in benign environments, habitat-providing organisms tend to provide respite from 'negative' *biotic* interactions such as competition and predation (Crain and Bertness 2005, 2006). However, only a few studies (Wright and Jones 2004, Crain and Bertness 2005) have explicitly examined ecosystem engineering along stress gradients (Crain and Bertness 2006).

Species traits and environmental context undoubtedly work in concert to determine the outcome of positive interactions between coexisting species (McGill *et al.* 2006). Bruno and Bertness (2000) proposed a model summarizing their predictions about how trait values and stress levels might interact to determine local species diversity (Figure 4.1). They suggest that under low stress scenarios, by definition, stress is not acting to prevent associated species from inhabiting a particular patch. Therefore, facilitation is not required to maintain local species diversity. In moderately stressful scenarios, facilitating species that lack the traits appropriate to ameliorate stressors should have a lower diversity of associated organisms compared to facilitators with high trait values. Lastly, in high stress scenarios, Bruno and Bertness (2000) predict that associated organisms will be absent from patches unless facilitators with traits sufficient to ameliorate stress are present.

The objective of the current study is to test how ecosystem engineering is influenced by facilitator traits along a stress gradient in a multi-species intertidal seaweed-epifauna system. Specifically, I examine how the stresses imposed by crashing waves interact with seaweed morphology to determine habitat provision for small mobile invertebrate epifauna.

4.1.2 Wave action as a moderator of algal-invertebrate interactions

Wave action is a major force driving the ecology and evolution of nearshore benthic organisms (Bell and Denny 1994, Denny and Gaylord 2002, Koehl 2006). Water movement experienced at a site can influence organismal size and morphology

(Gutierrez and Fernandez 1992, Blanchette 1997, Milligan and DeWreede 2000, Denny and Gaylord 2002), physiology (Hurd 2000), large and small-scale organismal distributions (Bustamante and Branch 1996, DeFelice and Parrish 2001, Guerra-Garcia 2001, Hovel *et al.* 2002), and mortality, survival and population structure (Carrington 1990, McQuaid and Lindsay 2000, Duggins *et al.* 2001, Pratt and Johnson 2002).

For small mobile invertebrates, which can include amphipods, isopods, gastropods, and copepods, among other taxa, bare rock substrate provides little refuge from hydrodynamic forces imposed by crashing waves (Thompson *et al.* 1996). However, biogenic structures such as mussel beds and algal cover can provide protection for a wide array of invertebrate epifauna. Quality of habitat provision varies across algal hosts (Chapter 3), and evidence exists to suggest that morphological properties of host algae can underpin observed differences in diversity of associated invertebrates (Colman 1939, Seed and O'Connor 1981, Taylor and Cole 1994). Habitat provision by single host algal species across wave gradients has been investigated several times (Dommasnes 1968, Fenwick 1976, DeFelice and Parrish 2001, Arroyo *et al.* 2004), however no cross-species comparisons have been undertaken.

To test if facilitator traits (i.e. algal morphology) and an environmental gradient (i.e. wave action) interact to regulate local species diversity (of small mobile invertebrates), I ask here three questions: a) how do individual algal species perform as habitat-providing organisms across a wave exposure gradient; b) how does habitat use by invertebrate epifauna compare across host algal species as wave impact increases; and c) do these observations fit the predictions made by Bruno and Bertness (2000) regarding how facilitator traits and environmental stress could interact to determine local species diversity?

4.2 Materials and methods

4.2.1 Study sites

Algae and associated invertebrates were collected monthly from February 2005 to March 2006 at six rocky intertidal sites in southern Barkley Sound, British Columbia.

Study areas were delineated as 30 m of rocky intertidal shore at a sheltered and exposed site at each of Dixon Island, Scott's Bay, and Nudibranch Point (Figure 1.3).

4.2.2 Measurement of maximum wave forces

As waves move into Barkley Sound there is, in general, a gradient of decreasing wave height, although wind direction and local topography can greatly influence realized wave impact on different shores. At each of my study sites, wave impact was measured by deploying five maximum wave-force dynamometers (Bell and Denny 1994) 24 hours prior to collection of algae and associated invertebrates. Dynamometers were placed along a 30 m transect at 1 m above chart datum (the same area as the biotic collections, described below). Dynamometers indicate only the strongest wave to impact the shore during the period of deployment, so I fitted each apparatus with a spring of one of three strengths: weak (0.21 +/- 0.02 N/mm), medium (0.78 +/- 0.04 N/mm), or strong (1.8 +/- 0.21 N/mm), chosen according to prevailing wave conditions. Apparati that were stretched to the maximum spring extension were not included in the analysis (this occurred only five times out of 295 dynamometer measurements). Spring extensions were converted to maximum wave velocities using equations from Bell & Denny (1994). To minimize effects of within-site (topographic) variation in wave exposure, drogues were not deployed nor were algal collections made within 2 meters on either side of the entrance to surge channels.

4.2.3 Sampling of seaweeds and epifauna

Twelve different algal species were examined (Figure 4.2). It was not possible to achieve a fully crossed design (i.e. all species from all sites at all dates) owing to patchy algal distributions and seasonality. Species included were: *Alaria marginata* Postels & Ruprecht (54 individuals), *Chondracanthus exasperatus* (Harvey & Bailey) J.R. Hughey (107), *Codium fragile* (Suringar) Hariot (46), *Cryptosiphonia woodii* (J. Agardh) J. Agardh (39), *Endocladia muricata* (Endlicher) J. Agardh (62), *Fucus distichus* subsp. *evanescens* (C. Agardh) H.T. Powell (396), hereafter referred to as *Fucus distichus*,

Gastroclonium subarticulatum (Turner) Kützing (74), the 'Petrocelis' phase of *Mastocarpus* (39), *Mazzaella splendens* (Setchell & N.L. Gardner) Fredericq (84), *Prionitis lyallii* Harvey (80), *Polysiphonia spp.* (57), and *Ulva lactuca* Linnaeus (270). In total, 1308 algal thalli were collected, and the only algal species collected at all sites on all sampling dates was *Fucus distichus*. These twelve species comprise an array of morphologies that can be arranged in order of increasing architectural complexity. The least complex species is an epilithic crust ('Petrocelis' in Figure 4.2), and complexity increases with several corticated foliose blades (*A. marginata*, *C. exasperatus*, *M. splendens*), a thin and highly folding blade (*U. lactuca*), several coarsely branching species (*C. fragile*, *F. distichus*, *G. subarticulatum*, *P. lyallii*), and the most complex thalli are represented by three more highly branching species (*C. woodii*, *E. muricata*, *P. hendryi*).

When encountered, eight individuals of each study species were collected at low tide from each site, each month during spring tides. Algal individuals were haphazardly selected along a 1 m x 30 m horizontal band transect, horizontally centered at one meter above chart datum. To minimize the variation caused by vertical shifts in abiotic and biotic structuring factors, species typical of the upper intertidal zone (e.g. *Fucus*) were collected from the bottom of their vertical range, and lower species (e.g. *Mazzaella* and *Chondracanthus*) were collected at the upper reaches of their distribution. Upright thalloid algae were collected by plucking from the base and each was immediately placed into an individual zippered plastic bag. Care was taken not to select individuals with epiphyte cover, and no individuals were selected from tidepools. Invertebrate samples were taken from 'Petrocelis' crusts by visually assessing a 10 cm x 10cm patch for macroinvertebrates, then rubbing the same area with a cotton swab to gather any microscopic epifauna. After collection, all samples were labeled and frozen for a minimum of 3 days to euthanize epifauna and preserve samples until processing could take place. Samples were processed and invertebrate epifauna were removed from algae and identified according to procedures described in section 2.2.6.

4.2.4 Statistical analyses

Maximum wave velocity measurements were averaged across the five dynamometer measurements from each site on each collection date. For each algal host species, invertebrate abundance and taxon richness (rarefied to 20 individuals) were plotted against maximum wave velocity. Significance of these relationships was tested using a mixed-model univariate ANOVA with one fixed factor (maximum wave velocity) and two random factors (site and collection month). Composition of epifauna assemblages was also examined using nonparametric multivariate approaches (Clarke 1993). Epifaunal abundances were fourth-root transformed to downweight the contribution of abundant taxa (Clarke 1993), and similarities were assessed using the Bray-Curtis similarity measure (Bray and Curtis 1957). To test for differences in composition of invertebrate epifauna as wave action increases, wave velocities were grouped into six categories (< 2.00, 2.00 – 2.99, 3.00 – 3.99, 4.00 – 4.99, 5.00 - 5.99, and > 6.00 meters per second), and then for each algal host, invertebrate assemblages from adjacent categories (i.e. < 2.00 versus 2.00 – 2.99; 2.00 – 2.99 versus 3.00 – 3.99 and so on) were compared using Analysis of Similarities (ANOSIM; Clarke 1993). To determine which higher invertebrate taxa were most influenced by wave action on each algal host species, I compared, using Similarity Percentages (SIMPER; Clarke 1993), epifauna assemblages at the lowest and highest wave velocities available for each host. This analysis identified which invertebrate taxa were responsible for 90% of the variability in invertebrate assemblage structure across the gradient of wave velocity. I then plotted the change in average abundances of these invertebrate taxa for each algal host along the wave exposure gradient. Univariate analyses were done using SPSS (Version 12, SPSS Inc.) and multivariate analyses were done using PRIMER (Version. 6.1.6, Primer-E Ltd., www.primer-e.org).

4.3 Results

4.3.1 Invertebrate abundance and taxon richness

Increased wave velocity resulted in a decrease in invertebrate abundance on *Fucus distichus,* but not on any of the other tested hosts (Figure 4.3; Table 4.1). Wave velocity decreased invertebrate taxon richness on only three of the tested seaweed hosts (Figure 4.4; Table 4.1). Based on this latter result, three groups of habitat-providing algae were identified, and these were congruent with the relative architectural complexity of the hosts: low, moderate, and high complexity thalli.

Richness of epifauna found on seaweeds of low complexity (i.e. crusts or unbranching blades such as 'Petrocelis', *Alaria marginata*, and *Mazzaella splendens*; Figure 4.2 h, a, i) and high complexity (i.e. highly folded, papillated, or branched thalli such as *Ulva lactuca*, *Chondracanthus exasperatus Cryptosiphonia woodii*, *Endocladia muricata*, and *Polysiphonia* spp; Figure 4.2 l, b, d, e, j) was not affected by wave velocity. Alternatively, invertebrates living on several seaweeds of moderate architectural complexity (i.e. coarsely or sparsely branching species: *Fucus distichus, Gastroclonium subarticulatum,* and *Prionitis lyallii* (Figure 4.2 f, g, k) were reduced in invertebrate taxon richness as wave velocity increased. One exception to this latter grouping was *Codium fragile*, which is a coarsely branching green alga (Figure 4.2 c); invertebrate taxon richness on *C. fragile* was not influenced by increased wave velocity.

Invertebrate taxon richness was more influenced by increasing wave velocity than was invertebrate abundance; for two seaweed hosts *Prionitis lyallii* and *Gastroclonium subarticulatum* (Figure 4.2 k, g), invertebrate taxon richness decreased with increasing wave velocity (Figure 4.3), whereas invertebrate abundance (Figure 4.4) did not (Table 4.1).

4.3.2 Invertebrate composition

As seen for invertebrate taxon richness and abundance, the influence of wave velocity on invertebrate composition (i.e. the identities of epifauna taxa) depended on the identity of the host seaweed (Table 4.2 and Figure 4.5). Invertebrate composition on

algal hosts with simple morphologies ('Petrocelis', *Alaria*, and *Mazzaella*) was not influenced by wave velocity. For several species, *Cryptosiphonia woodii*, *Prionitis lyallii* and *Ulva lactuca*, changes in invertebrate composition were seen at lower wave velocities, but assemblages stabilized and did not change above wave velocities of 3 m/s. For the remaining species, the assemblages appear to stabilize at higher wave velocities (above 5 m/s).

The most abundant invertebrate taxa found on most host species were amphipods, copepods, and bivalves (Figure 4.5). The influence of increased wave velocity on each of these invertebrate taxa was variable for each host alga, and no monotonic relationships were observed. Amphipods, the most abundant group, increased in abundance on *Chondracanthus exasperatus,* but decreased on *Fucus distichus*. Bivalves (typically juvenile mussels, *Mytilus* spp.) were abundant on only a few algal hosts, and appeared either unaffected by increasing wave velocity (e.g. on *Cryptosiphonia woodii*) or increased in abundance (e.g. on *Endocladia muricata*). Many of the other invertebrate taxa were present in small numbers and appeared resilient to changes in wave velocity.

4.4 Discussion

The results presented here support the view that traits of habitat-providing species can interact with an environmental gradient to moderate the importance of ecosystem engineering. I found that the taxon richness of associated invertebrates depended on the interaction between architectural complexity of host species and the wave exposure intensity. Three 'groups' of host species were identified, and these groups were congruent with the relative architectural complexity of the seaweed host: a) 'simple' thalli that were minimally utilized as habitat under any of the tested circumstances, b) thalli that were coarsely branched and were utilized by diverse invertebrate assemblages under relatively benign wave conditions but became less utilized under higher wave action, and C) more complex or highly folding algal hosts that appeared to provide equivalent habitat to diverse invertebrate assemblages under all tested wave conditions. To understand how morphology of seaweed hosts can interact

with wave exposure to regulate invertebrate diversity, it is useful to review how seaweeds have adapted to cope with wave action.

4.4.1 How do seaweeds protect invertebrates from wave action?

The behavior of crashing waves on a shore is complex, but two major forces are experienced by algae: brief, but intense, impingement forces, as well as drag forces (Denny and Gaylord 2002). To cope with wave action, many algal species have evolved flexible thalli that let them reconfigure in flow, allowing the alga to experience lower forces than would more rigid organisms (Denny and Gaylord 2002). In *Chondrus crispus*, two facets of thallus reconfiguration have been identified: a bending of the stipe to allow the alga to flatten against the substrate as well as a compaction of the crown (Boller and Carrington 2006). When the algal host flattens down this lowers the associated invertebrate assemblage to the substrate where, in theory, the velocity of water should be slower as compared to higher positions in the water column. However, for turbulent flows and shallow water (< 5 meters) the differences in velocity between the substrate and water column is negligible (Denny and Gaylord 2002), so this mechanism is unlikely to contribute to the observed relationships between invertebrate diversity and wave velocity.

The algal host's propensity to undergo crown compaction is much more likely to directly influence epifaunal invertebrates. This crown compaction serves to streamline the alga by 'bringing together' parts of the thallus and, in doing so, can protect the invertebrates from being dislodged by the water flow. However, the degree to which this compaction can protect the invertebrates is dependant upon the morphology of the host alga (Boller and Carrington 2007). While I have not directly demonstrated that my seaweed study species can undergo crown compaction, a recent cross-species comparison of reconfiguration for ten northwest Atlantic seaweeds (Boller and Carrington 2007) showed that intertidal algae with similar morphologies reconfigure to a comparable extent. It is therefore reasonable to generalize to the taxa tested in this study.

Algal crusts (i.e. the 'Petrocelis' phase of *Mastocarpus*) cannot, of course, undergo crown compaction, so they do not provide cover from wave action. As a result,

there is a sparse (i.e. typically non-existent) invertebrate assemblage associated with 'Petrocelis' (Figures 4.3-5). For simple blades (i.e. *Alaria* and *Mazzaella*), which are not well utilized by invertebrate epifauna even at low wave velocities, reconfiguration of the crown is accomplished by an 'inrolling' of the blade (Boller and Carrington 2007). Invertebrates on the 'inside' of the rolled blade have the potential to be protected from wave action (M. Boller, personal communication). For coarsely branched algae, interstitial spaces are relatively large, so crown compaction is unlikely to prevent water from flowing through the interstices of the thallus. As a result, invertebrates inhabiting species such as *Fucus distichus*, *Gastroclonium subarticulatum,* and *Prionitis lyallii* are likely increasingly dislodged as water motion becomes faster (Figure 4.3 and 4.4). Further, Boller and Carrington (2007) showed that these coarsely branching algae reconfigured to a lesser extent as compared to bladed forms, so the algae tended to experience higher drag. For highly branching taxa such as *Polysiphonia* spp. and *Cryptosiphonia woodii,* interstitial spaces are relatively small, so crown compaction results in a cohesive cover that forms over the invertebrates. Similarly, *Ulva lactuca* is a highly folded blade that can buffer invertebrates from wave force, so taxon richness and abundance of associated invertebrates appear robust to elevated water velocity.

Another shape-change mechanism that algae use to cope with wave action is phenotypic plasticity (Norton *et al.* 1982); algae found in wave-exposed areas tend to be smaller than counterparts found in wave-sheltered areas (Blanchette 1997, Fowler-Walker *et al.* 2006). Differences in morphology across a wave exposure gradient can occur through differential growth (Fowler-Walker *et al.* 2006) or through tattering of the thallus (Blanchette 1997). Although this reduction in surface area could lead to a loss of space for use by invertebrates, this might not directly translate to a loss of invertebrate diversity, for two reasons. Firstly, effects of habitat complexity can act independently of surface area (Johnson *et al.* 2003, Becerra-Munoz and Schramm 2006). For example, Beck (2000) found that gastropod diversity increased with topographic complexity of substrate when surface area was held constant. Secondly, damage to thalli can result in increased adventitious branching (Van Alstyne 1989) and thus tattering may eventually lead to increased thallus complexity. This latter idea remains untested, however the consequences of algal phenotypic plasticity for invertebrate habitat choice are an interesting area for future study.

The observation that groups of invertebrate taxa were differentially influenced by wave exposure (Figure 4.5) suggests that, in addition to facilitator traits, traits of the facilitated organisms are also important for determining the outcome of positive interactions in this system. Dommasnes (1968) studied the influence of wave exposure on the meiofauna inhabiting *Corallina officinalis*, and suggested that if epifaunal invertebrates had appendages that were well matched to the morphology of their host seaweed, this would improve their ability to withstand dislodgement. This idea appears to be supported here, particularly for the amphipods. With increasing wave velocity, amphipod abundance decreased on wide-bladed hosts like *Fucus distichus* and *Mazzaella spendens*, but remained similar (albeit variable) on more finely branching hosts (e.g. *Endocladia muricata* and *Cryptosiphonia woodii*), likely reflecting the ability of amphipods to better grasp onto the thinner axes of the complexly branching host algae. Above wave velocities of 5 m/s, invertebrate assemblages appeared to stablize on many of the host algae. However, it is difficult to assess stability because collections taken above 6 m/s were not available for several host species, and there is potential for assemblage change at higher wave velocities than were measured in this study.

4.4.2 Performance of the Bruno and Bertness model

Bruno and Bertness (2000) proposed a conceptual model that outlined how facilitator traits could interact with ambient stress levels to determine local species diversity (Figure 4.1). In general their predictions were supported. However, my results did not match the shape of their predicted relationships in all cases. The model performed well for predicting the influence of seaweed morphology on invertebrate diversity at high levels of wave impact; host species with simple architecture were less able to buffer invertebrates from dislodgement as compared to host species with more complex morphologies. However, at low levels of stress, Bruno and Bertness (2000) predicted that local species diversity should be the same on all facilitators. On the contrary, at low levels of wave impact, the shape of the relationship I observed was similar to that at high wave stress; complex seaweed forms performed better than simple forms. There are at least two reasons why the predictions of Bruno and

Bertness' model did not work for predicting importance of ecosystem engineering in low wave stress areas.

In intertidal environments, stressors rarely act alone; covarying stressors confound tests of individual stress gradients. When considering water motion, I have focused so far only on the negative implications of increasing hydrodynamic forces. However, at the lower end of the water motion gradient, organisms are subjected to stresses associated with desiccation, such as water stress and high temperatures (Helmuth *et al.* 2002). These additional stressors may explain why, at low wave velocities, simple algal forms had a low diversity of associated invertebrates compared to more complex forms. Another factor confounding the predictions of the Bruno and Bertness model is the assumption that the stressor doesn't influence the habitat-providing species (Bruno and Bertness 2000). This assumption is clearly violated in this study system because wave action can modify the morphology of host algae.

4.4.3 Implications

One predicted consequence of global climate change is an increased frequency and intensity of storms, and thus of wave action (Carter and Draper 1988, Hoozemans and Wiersma 1992). These increases in wave action can in turn influence the survival and distribution of seaweeds (Vadas *et al.* 1990, Diez *et al.* 2003, Jonsson *et al.* 2006). The findings of the current study suggest that in some cases, these shifts in seaweed composition will have ramifications for invertebrates that use seaweeds as habitat, potentially leading to changes in composition and abundance of food sources for birds and fish that feed on seaweed-dwelling invertebrates (Kendall *et al.* 2004, Vandendriessche *et al.* 2007).

If scientists and managers hope to determine which, and under what circumstances, ecosystem engineering is important, it is unlikely that simple models will effectively describe the context specificity of such positive interactions. My findings suggest that the relationships between facilitator traits and environmental gradients are not straightforward, and that knowledge of several key features will be required, including details about the dominant stressors acting in the system, the mechanisms

through which these stressors negatively influence organisms present, and how habitat-providing organisms ameliorate the effects of these stressors.

Table 4.1: Relationships between maximum wave velocity (ranging from ~1 m/s – 6 m/s) versus invertebrate abundance and rarefied invertebrate richness associated with twelve seaweed species. Boldface text indicates significant ($p < 0.05$) influence of wave velocity, and all significant relationships are negative.

Host Algal Species	Invertebrate Abundance		Invertebrate Richness	
	F	p	F	p
Alaria marginata	0.095	0.761	0.247	0.624
Chondracanthus exasperatus	0.976	0.344	3.525	0.064
Codium fragile	5.352	0.090	2.642	0.182
Cryptosiphonia woodii	0.203	0.683	0.114	0.764
Endocladia muricata	0.282	0.614	0.095	0.769
Fucus distichus s. evanescens	**24.12**	**< 0.001**	**32.20**	**< 0.001**
Gastroclonium subarticulatum	0.159	0.700	**23.49**	**< 0.001**
Mastocarpus ('Petrocelis' phase)	0.079	0.828	0.123	0.735
Mazzaella splendens	0.325	0.572	0.325	0.572
Polysiphonia spp.	1.147	0.352	0.365	0.580
Prionitis lyallii	3.255	0.109	**20.04**	**0.002**
Ulva lactuca	4.234	0.054	0.003	0.959

Table 4.2: Results of ANOSIM tests for differences in composition, across a gradient of maximum wave velocity, for invertebrates associated with twelve host algal species. Boldface R-values indicate a significant difference ($p < 0.05$).

Global R	Host Seaweed Species	< 2 m/s versus 2 - 2.9 m/s	2 - 2.9 m/s versus 3 - 3.9 m/s	3 - 3.9 m/s versus 4 - 4.9 m/s	4 - 4.9 m/s versus 5 - 5.9 m/s	5 - 5.9 m/s versus > 6 m/s
0.057	*Alaria marginata*	-	-	-	-	-
0.158	*Chondracanthus exasperatus*	**0.109**	**0.18**	nd	nd	0.122*
0.254	*Codium fragile*	nd	nd	**0.527**	**0.364**	0.117
0.479	*Cryptosiphonia woodii*	**0.544**	**0.403**	nd	0.117*	nd
0.537	*Endocladia muricata*	**0.473**	0.12	**0.924**	nd	nd
0.183	*Fucus distichus s. evanescens*	**0.131**	0.014	**0.268**	0.023	0.121
0.276	*Gastroclonium subarticulatum*	**0.329**	**0.19**	**0.571**	**0.283**	nd
-0.033	*Mastocarpus* (Petrocelis phase)	-	-	-	-	-
0.024	*Mazzaella splendens*	-	-	-	-	-
0.36	*Polysiphonia sp.*	nd	**0.385**	**0.8**	**0.259**	nd
0.078	*Prionitis lyallii*	nd	**0.308**	-0.119	-0.135	0.133
0.086	*Ulva lactuca*	**0.282**	0.065	-0.075	0.044	0.173

(-) indicates that no comparison is necessary due to a nonsignificant Global ANOSIM test.
(nd) indicates that no data are available for the comparison.
(*) indicates that comparison was done for closest available (lower) wave velocity group.

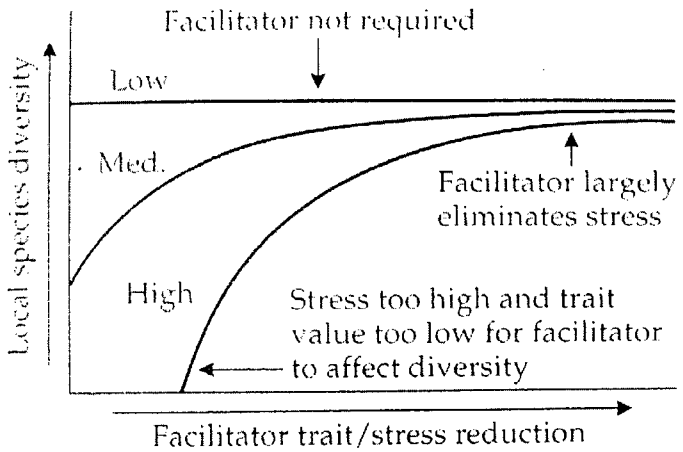

Figure 4.1: Conceptual model illustrating how three levels of ambient stress (low, medium, and high) and facilitator traits are proposed to interact to determine levels of local species diversity. Figure reproduced from Bruno and Bertness (2001), used with permission from Sinauer Associates, Inc.

Figure 4.2: Photographs of twelve seaweed species studied as hosts for small mobile invertebrates: a) *Alaria marginata*, b) *Chondracanthus exasperatus*, c) *Codium fragile*, d) *Cryptosiphonia woodii,* e) *Endocladia muricata*, f) *Fucus distichus* subsp. *evanescens*, g) *Gastroclonium subarticulatum,* h) *Mastocarpus* ('Petrocelis' phase), i) *Mazzaella splendens*, j) *Polysiphonia hendryi,* k) *Prionitis lyallii,* and l) *Ulva lactuca.*

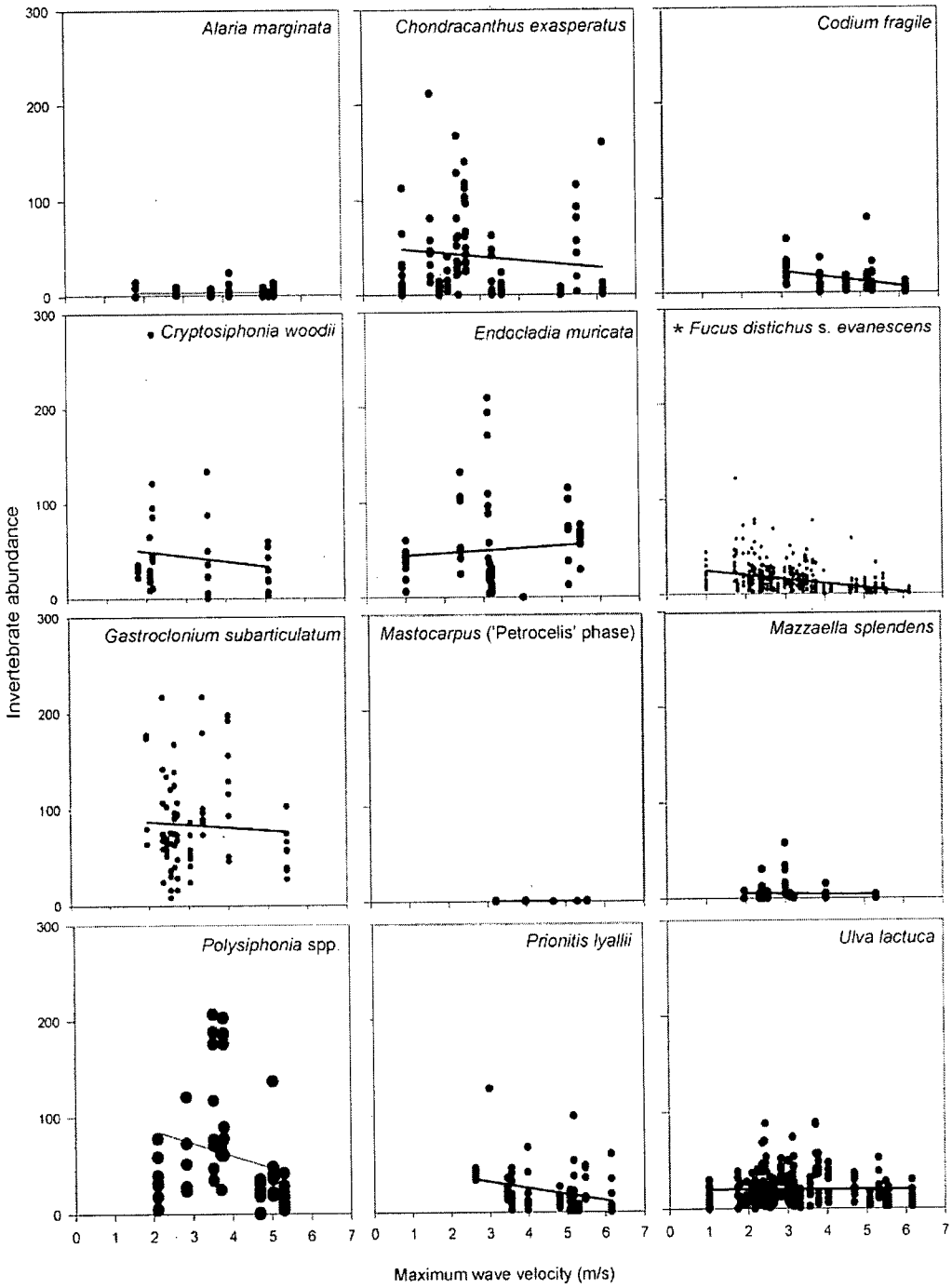

Figure 4.3: Relationship between maximum wave velocity (over a 24 hour period) and abundance of small mobile invertebrates associated with twelve species of host seaweed. An asterisk (*) identifies a significant influence of wave velocity.

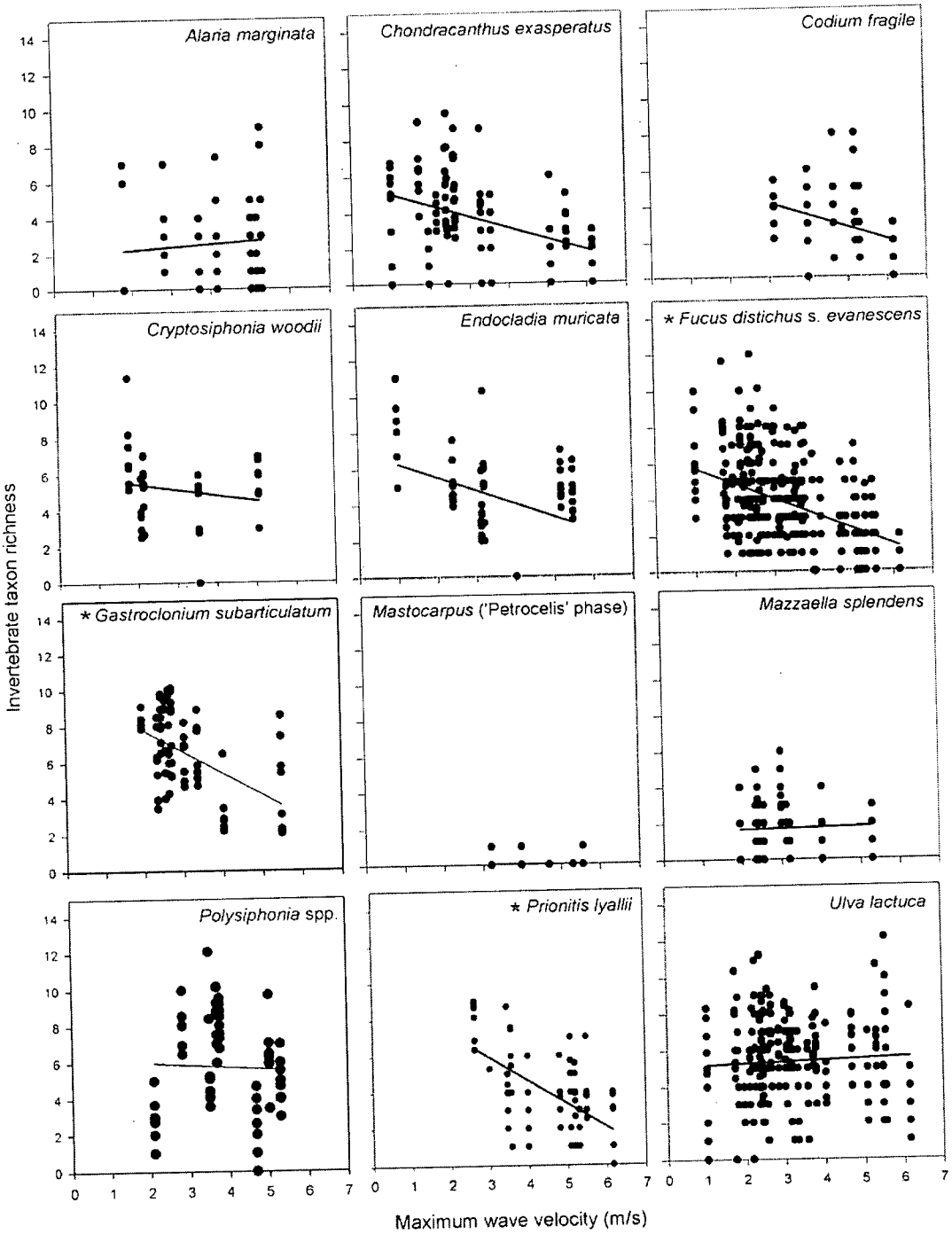

Figure 4.4: Relationship between maximum wave velocity (over a 24 hour period) and taxon richness (rarefied to 20 individuals) of small mobile invertebrates associated with twelve species of host seaweed. An asterisk (*) identifies a significant influence of wave velocity.

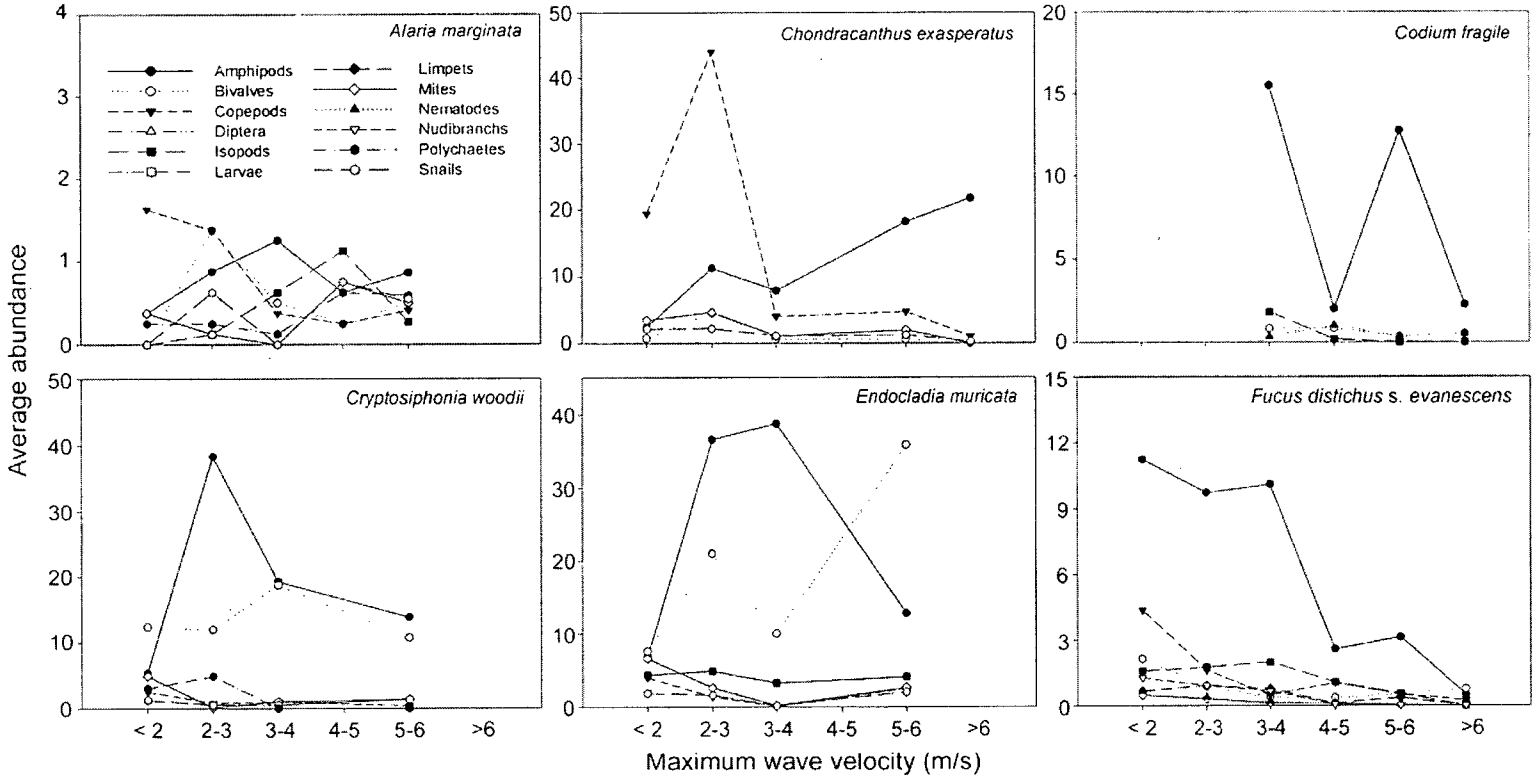

Figure 4.5A: Changes in average abundance of invertebrate taxa associated with six host seaweed species across a maximum wave velocity gradient. Error bars were omitted and lines joining points were added for clarity. Note the different Y-axes scales.

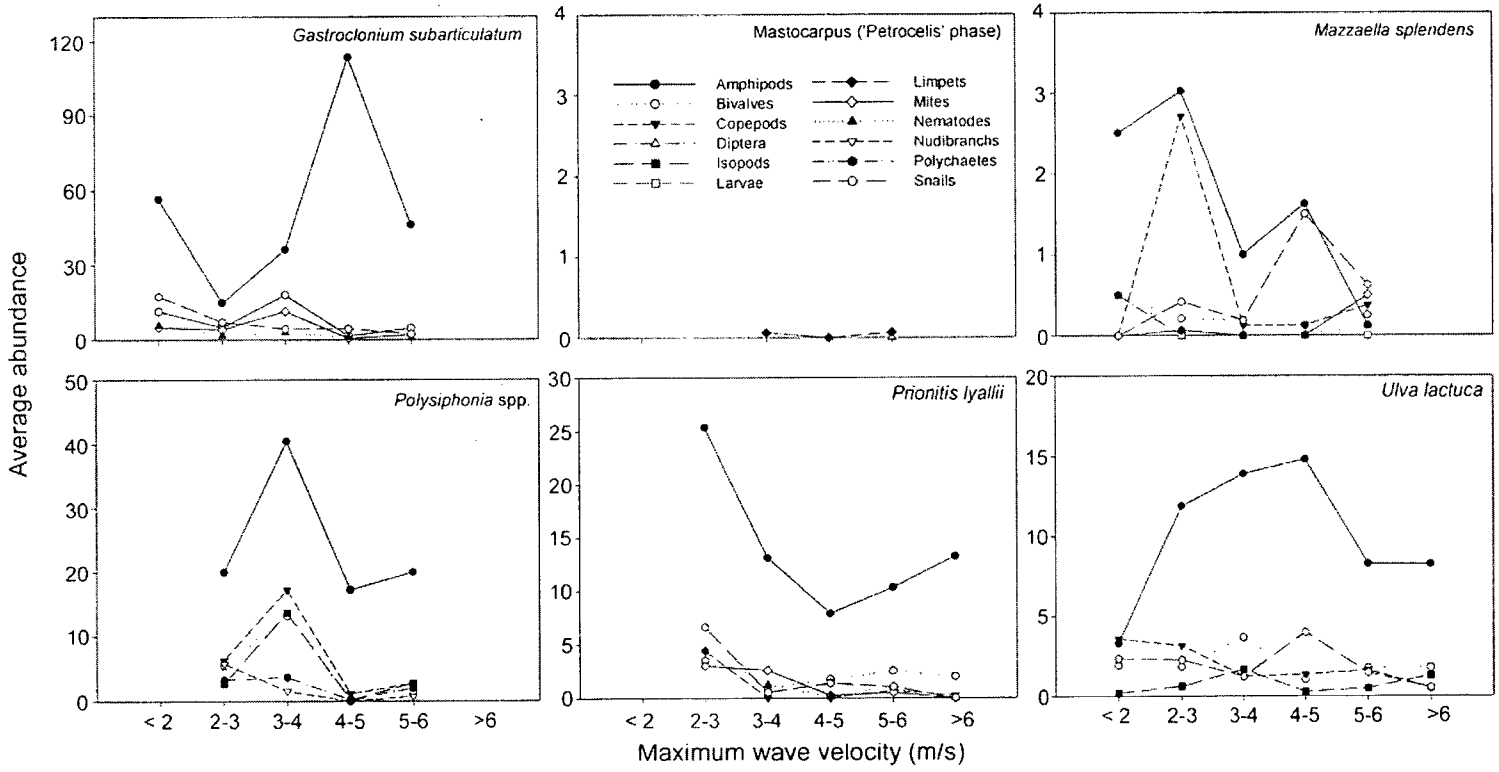

Figure 4.6B: Changes in average abundance of invertebrate taxa associated with six host seaweed species across a maximum wave velocity gradient. Error bars were omitted and lines joining points were added for clarity. Note the different Y-axes scales.

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Chapter 5: General Summary

5.1 Recapitulation of thesis objectives

In response to personal (Bates 2002, Bates et al. 2005, 2007) and published (Schramm and Nienhuis 1996, Scott and Tittley 1998) observations of anthropogenic changes in seaweed biodiversity, the objective of my Ph.D. research was to investigate the possible consequences of these floristic shifts for small mobile invertebrate epifauna that use seaweeds as habitat. Accordingly, I examined how seaweed traits at the assemblage level (i.e. seaweed biodiversity (Chapter 2)) and the species level (taxonomic relatedness and functional group affinity (Chapter 3)) influenced associated invertebrate epifauna. As well, I examined how an abiotic environmental gradient (i.e. maximum wave velocity) interacted with seaweed morphology to determine the outcome of such habitat-use (Chapter 4).

5.2 Summary of study findings

The major conclusions of Chapter 2, "Do changes in seaweed biodiversity influence invertebrate epifauna?" were that:

a) changes in richness of algal species and functional groups do not influence invertebrate richness or abundance;
b) most floristic changes at the seaweed assemblage level did not influence invertebrate composition; only when algal assemblages were composed just of foliose species did I observe differences in the associated invertebrate assemblages.

In Chapter 3, "A comparison of host taxonomic relatedness and functional-group affiliation as predictors of seaweed-invertebrate epifauna associations", I found that:

a) taxonomic relatedness of seaweed hosts was not correlated with similarity in invertebrate composition;

b) the performance of seaweed host species as habitat was variable within seaweed functional groups. This high variation within functional groups led to my conclusion that species identity is more useful than functional group identity for predicting seaweed performance as habitat;
c) in general, prevailing perspectives about the relationship between seaweed architectural complexity and invertebrate habitat usage were upheld, however architectural complexity was not a wholly reliable criterion for generalizing about algal host performance; species with the same morphology can have very different assemblages of associated invertebrates.

The major conclusions of Chapter 4, "Do facilitator traits interact with an environmental gradient to determine local species diversity?" were:

a) facilitator traits (i.e. algal morphology) do interact with an environmental gradient (i.e. maximum wave velocity) to determine local species diversity (of associated invertebrate epifauna).
b) three classes of algal host were identified: those that were not utilized by invertebrates under any of the tested wave exposure regimes, those that were well utilized under low velocities but invertebrate diversity decreased as wave velocity increased, and hosts that were well utilized under all of the tested wave velocities.
c) simple models that describe the interactions between environmental stress and trait-based stress amelioration are unlikely to forecast local species diversity. In particular, the model that I tested (Bruno and Bertness 2000) was not consistent with my observations of invertebrate biodiversity at low wave velocities.

5.3 Consequences for small mobile invertebrate epifauna of changes in seaweed biodiversity

At the outset of my Ph.D. research, I hypothesized tight linkages between invertebrates and their seaweed hosts, and therefore I anticipated that changes in

seaweed biodiversity would result in shifts in biodiversity of epifaunal invertebrates. However, neither of these ideas was strongly supported by my observations or manipulations. It appears that, although individual seaweeds supported different assemblages of associated invertebrates (Figure 3.4), there was community-level buffering of small-scale changes in seaweed assemblage structure (Figure 2.1). This result suggests that small-scale changes in algal biodiversity are unlikely to influence invertebrate epifaunal diversity. One exception to this conclusion might occur when larger areas of algal cover are lost or reduced to "coralline pavement", as is the case when sea urchins denude algal cover into "urchin barrens" (Hart and Scheibling 1988). Algal crusts support few or no small mobile invertebrates (Figure 3.4).

The intertidal environment is a dynamic and sometimes harsh environment, where algal assemblages change dramatically throughout the year and environmental conditions fluctuate substantially. This tumultuous environment may have selected invertebrates to be host-generalists. Invertebrates using algae as habitat are likely adapted to unpredictable circumstances, so the types of changes that I examined are within the spectrum of conditions to which epifaunal invertebrates have been exposed.

5.4 Community ecology as a predictive science

While studying these seaweed-epifauna interactions, I attempted to address the criticism that community ecology has failed as a predictive science because it lacks general laws (Lawton 1999, McGill et al. 2006), and the results of ecological studies are typically organism- and environment-specific. I incorporated several advances in community ecology theory to allow a comparison of general versus species-identity based approaches in this seaweed-epifauna study system. These general approaches included a study of biodiversity-ecosystem function relationships, functional group diversity, phylogenetic / taxonomic perspectives in community ecology, and the study of functional trait performance along an environmental gradient.

I found that, even within this seaweed-epifaunal study system, the potential for generalizing about host-epibiont interactions was low. My attempts to depart from the use of seaweed species identity (e.g. by grouping them into functional groups, or assuming seaweed species equivalence by invoking species richness) were not successful for predicting biodiversity of associated invertebrate epifauna (Chapters 2 and 3). Only in Chapter 4 did I observe some congruence across host species, where seaweeds with like morphologies responded in similar ways to changes in water motion, resulting in similar patterns of invertebrate richness and abundance. As a result, it appears that most predictions about seaweed-invertebrate interactions would suffer if seaweed species identity were not taken into account.

5.5 Byproducts

By studying a large number of invertebrate and seaweed taxa, some useful 'byproducts' were generated. The Convention on Biological Diversity, of which Canada is a signatory nation, states that participatory nations must identify and monitor their biological resources. Few studies of seaweed epifauna are available for the Pacific coast of Canada. My data sets document invertebrate habitat usage across a wide array of host seaweeds. This work documents baseline information about the dynamics of invertebrate habitat use across space and time. I have voucher collections that I can contribute to museum collections, and I have collection records, so if invertebrate biologists are interested in finding particular taxa, I can, at the very least, indicate which algal host or collection site to start looking at.

5.6 Hindsight and future directions

There are several shortcomings that are worthy of mention here, things that I would do differently if I could start again.

As with most ecological studies, the level of replication could have been increased. In the study described in chapter 3, there are numerous algal species that

were collected only a few times, so results of comparisons to well replicated species could be driven by idiosyncrasies related to collection methods, uncontrolled factors, or random chance. I would make an attempt to more evenly replicate all algal study species.

In this thesis, I frequently discuss the implications of algal morphology for invertebrate habitat usage, but my estimates of morphological complexity are qualitative; I do not quantitatively address specific morphological features. Over the course of my Ph.D., I undertook several attempts to morphometrically quantify differences in algal morphology, but the intricacies of comparing algae with such a wide array of feature sets became statistically complex. The landmark morphometric methods popular today (Monteiro et al. 2000) do not easily accommodate missing data (e.g. where features such as branching are not shared by all taxa under comparison). Landmark morphometrics are better suited to comparing phenotypic plasticity or development within taxa. Quantification of across-species algal morphology remains of interest to me, and will be part of my ongoing future research.

Due to cryptic features and complex taxonomy for some invertebrate taxa, the level of identification for epifauna for some taxa (e.g. nematodes, some amphipods) was coarse. The consequence of studying such a wide array of taxa (both for seaweeds and for invertebrates) is that ecological details of invertebrates were not considered in detail. My conclusions of invertebrate habitat generalism are potentially overstated; if I integrated the autecology of the invertebrates, my conclusions about the implications of changes in seaweed biodiversity might be different. Furthermore, interactions between the epifauna were not addressed, nor were the influence of epifauna on the seaweed hosts. While I do not regret that I studied such a wide array of taxa, I think there would be value in returning to subsets of taxa to examine them in more detail.

5.7 Literature cited

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Appendices

Appendix A: Taxonomic affiliations of invertebrate voucher specimens collected for the studies described in this thesis.

Appendix A: Taxonomic affiliations of invertebrate voucher specimens collected for the studies described in this thesis. The listed numbers are my voucher identifier codes. If specific epithet or genus is not indicated, affiliation is listed at the level of P = Phylum; C = Class; SC = Subclass; O = Order; F = Family.

1) Harpacticoida (O)
2) Gammaridea (O)
3) Polychaeta (C)
4) Flabellifera (SO)
5) Polyplacophora (C)
6) Orthogastropoda (SC)
8) Orthogastropoda (SC)
11) Amphipoda (O)
12) Polychaeta (C)
13) Patellogastropoda (O)
14) Orthogastropoda (SC)
16) Majidae (F)
17) Asteroidea (C)
19) Orthogastropoda (SC)
20) Paguridae (F)
21) Polychaeta (C)
23) Acariformes (O)
24) Patellogastropoda (O)
25) Nudibranchia (SO)
26) Harpacticoida (O)
27) Acariformes (O)
28) Gammaridea (O)
29) Asteroidea (C)
30) Diptera (O)
31) Acariformes (O)
32) Nematoda (P)
33) Gammaridea (O)
35) Acariformes (O)
36) Harpacticoida (O)
37) Polychaeta (C)
38) Gastropoda (O)
39) Caprellidea (SO)
40) Polyplacophora (C)
41) Polychaeta (C)
45) Gastropoda (O)
46) Gammaridea (O)
47) Diptera (O)
48) Acariformes (O)
49) Polychaeta (C)
50) Coleoptera (O)
51) Orthogastropoda (SC)
52) Orthogastropoda (SC)
54) Gammaridea (O)
55) Gammaridea (O)
56) Polychaeta (C)
58) *Pugetia producta*
59) Calanoida (O)
60) Acariformes (O)
62) *Idotea wosnosenskii*
63) Polychaeta (C)
64) Pantopoda (O)
66) Polychaeta (C)
68) Harpacticoida (O)
69) Gammaridea (O)
70) Polychaeta (C)
71) Diptera (O)
72) Orthogastropoda (SC)
74) Orthogastropoda (SC)
76) Gammaridea (O)
77) Orthogastropoda (SC)
78) Polyplacophora (C)
79) Idoteidae (F)
80) Polychaeta (C)
81) Polychaeta (C)
82) Polychaeta (C)
83) *Mytilus* spp.
84) Orthogastropoda (SC)
85) Gammaridea (O)
86) Polychaeta (C)
87) Orthogastropoda (SC)
88) Bivalvia (C)
89) Harpacticoida (O)
90) Orthogastropoda (SC)
91) Majidae (F)
92) Ophiuroidea (C)
93) Bivalvia (C)
94) Unknown
95) Orthogastropoda (SC)
96) Unknown
97) Bivalvia (C)
98) Orthogastropoda (SC)
99) Orthogastropoda (SC)
100) Unknown
101) Coleoptera (O)
102) Orthogastropoda (SC)
103) Pantopoda (O)
104) Bivalvia (C)
105) Pseudoscorpionida (O)
106) Idoteidae (F)
107) Orthogastropoda (SC)
108) Orthogastropoda (SC)
109) Polychaeta (C)
110) Isopoda (SO)
111) Isopoda (SO)
112) Holothuroidea (C)
113) Platyhelminthes (P)
114) Platyhelminthes (P)
115) Epicaridea (SO)
116) Orthogastropoda (SC)
117) Unknown
118) Orthogastropoda (SC)
119) Flabellifera (SO)
120) Cumacea (O)
121) Orthogastropoda (SC)
122) *Anisodoris nobilis*