Factors governing interactions among species in a complex marine ecosystem

by

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Abstract

Species interactions take a variety of forms, from weak to strong, and negative to positive, each with unique consequences for local community structure. These interactions are contingent on biotic, abiotic, and scale-dependent variables, and this makes them difficult to predict. In this dissertation I describe three empirical intertidal studies aimed at understanding the dependency of species interactions on environmental and ecological context.

First I present a test of the relative importance of six variables known to affect the sign and strength of species interactions, using perturbation experiments across a range of habitats in New Zealand and North America. I observe that species interactions in communities are typically weak, with a balance of positive and negative effects. Interaction strengths are related to traits of species, such as body size and trophic level, but are relatively insensitive to environmental conditions.

The second study has two parts. First, I examine the prevalence of nonlinear species interactions, using experimental gradients in abundance of three focal species. Then I assess how well linear and nonlinear interaction coefficients, estimated in the first experiment, predict the outcome of a second set of perturbations. I find that interactions are typically linear across focal species densities, and that predictions regarding the outcome of short-term perturbations are not significantly improved by nonlinear estimates.

Lastly, I investigate the relative impacts of biotic interactions, abiotic stress, and the interactive effects of the two factors, on community diversity. The results demonstrate that although environmental stress alters certain species interactions, it does not change the overall distribution of weak and strong effects. This is, in part, because biotic processes mitigate the effects of abiotic stress and allow the community to maintain its functioning even under harsh conditions.

Abstract

Together the results demonstrate how empirically-based interaction coefficients can be used to explain species diversity and the responses of ecosystems to environmental change. Interactions are directly related to population density, relatively insensitive to environment conditions, and strongly tied to species' allometric properties. This exhibits the potential for future research to predict ecosystem dynamics without detailed information on communities.

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Statement of co-authorship

The research presented in Chapter 2 was born of collaboration with Stacie A. Lilley, David R. Schiel, and Jonathan B. Shurin. All authors contributed to the design of the study. S.A.L. and S.A.W. conducted the field experiments. S.A.W. analysed the data. S.A.W. and J.B.S. wrote the manuscript.

Chapter 3 is co-authored with Dieta R. Lund, who helped collect and analyse the data. S.A.W. designed the study and wrote the manuscript.

All parts of Chapter 4, including design, data collection, analysis, and writing, were done by S.A.W.

Preface

Knowledge,
it excites prejudices to call it science,
is advancing as irresistibly, as majestically, as remorselessly
as the ocean moves in upon the shore.

Oliver Wendell Holmes

Chapter 1

Introduction

1.1 Background

Species interactions present one of the greatest sources of uncertainty to ecologists trying to understand patterns of diversity and predict the responses of ecosystems to environmental change. Interactions can take a wide range of forms from negative (Connell 1961) to positive (Bruno et al. 2003). Some are readily observable, like when a sea star eats a mussel (Paine 1966), while others are subtle yet potentially important. For example, the presence of larval dragonflies can change the feeding behavior of small bullfrogs (Peacor and Werner 2001). These intricacies make species interactions extremely difficult, time consuming, and costly to study in any detail. To further complicate matters, interactions themselves often change in time and space in conjunction with the environment and other community members (Menge and Sutherland 1976, Chesson and Huntly 1997). As a result, ecologists have only a rudimentary understanding of the relative importance of different species interaction types, including direct and indirect (Menge 1995), positive and negative (Bertness and Callaway 1994), and linear and nonlinear (Abrams 2001). My thesis aims to understand what level of detail is necessary to predict the response of populations to each other and to changes in the environment.

A great debate has historically surrounded the importance of species interactions in communities. Early biologists recognized that species respond individually to environmental factors such as water or light, and viewed assemblages as collections of species with similar needs (von Humbolt 1805, Tansley 1920, Gleason 1926). Other ecologists meanwhile believed that the interrelationships between species had a more powerful influence on community structure (White 1789, Warming and Vahl 1909, Elton 1927). This debate continued through the 20$^{\text{th}}$ century with research that either downplayed the importance of species interactions (Hutchinson 1941,

Whittaker 1956, Caswell 1976) or relied heavily on interactive processes to explain community dynamics (Hutchinson 1959, Paine 1980, Oksanen et al. 1981). Most recently, a similar dispute has centered around the importance of local biotic interactions in light of non-interactive processes such as dispersal that operate at the regional scale (Caley and Schluter 1997). In one prior study, I quantified the impact of regional processes on local scale diversity by comparing species richness across scales in the intertidal (Russell et al. 2006). I found that regional richness explained between 10% and 90% of local community diversity, depending on the degree of environmental stress. The results supported the theory that local interactions can structure communities, particularly in stressful habitats, and they called for further simultaneous tests of the impacts of local species interactions and the abiotic environment on patterns of diversity.

In community ecology, a balance must be struck between approaches that are detailed enough to describe population dynamics, yet general enough to apply to communities in different environments. At one end of the spectrum are studies that use dynamical models to relate population abundances to interspecific interactions through time. Several authors have observed that interactions between species are nonlinear relative to their abundance, in part because of species' adaptive behaviors and functional responses to predators (Messier 1994, Sarnelle 2003). Such nonlinearities make the dynamics of systems difficult to predict, particularly as species are added or lost, or as environmental conditions change (Abrams 2001). At the other end of the spectrum, a second approach exchanges such precise measures of interaction strength for topological models, such as food webs, that assume a uniform interaction intensity. By ignoring some of the biological detail, these models are more adept at coarser community-level and cross-habitat comparisons with empirical data. Although such models have been used to accurately predict the structure of food webs in marine and terrestrial ecosystems (Williams and Martinez 2000), without information on interaction strengths they cannot always explain patterns of abundance or the ubiquitous distribution of many weak and few strong interactions in communities (Paine 1980, Raffaelli and Hall 1996). The level of detail required of ecological models depends on the desired specificity and precision of the predictions. If the goal is to predict species abundances in communities, it will require an intermediate approach that can incorporate weighted species links and higher-

order interactions, but still be generalized to diverse communities across a variety of contexts (Polis 1994).

Throughout this dissertation I use experimental methods to estimate the strength of interactions between species in the rocky intertidal. Specifically, I measure the per-capita impact of one individual of a focal species on an entire population of a target species. Interactions are quantified in the field using 'species removal' and 'press' experiments (Bender et al. 1984, Laska and Wootton 1998, Berlow et al. 1999), in which the abundance of the focal species is altered in a manipulated plot. Changes in the abundance of the target population in the manipulated plot are compared to an untreated control plot, to compute the response of the target species to the focal species over time. The magnitude and direction of these interactions are then used as response variables in further analyses. Many analyses in this dissertation use multilevel models that account for interdependencies between nested sampling units (e.g. repeated measurements of populations from a single plot). A brief introduction to multilevel modeling is given in Appendix A.

The interaction coefficients I measure are an amalgamation of all the direct and indirect interactions between species (Bender, et al. 1984, Laska and Wootton 1998). Indirect effects pose unique problems to experimentalists; because they are a combination of many direct interactions though many pathways, the outcomes of experiments can be sensitive to slight variations in these direct effects (Yodzis 1988). Additionally, the direct, not the indirect, effects are the currency of most theoretical models. However, ecologists know that indirect effects can have large influences on community structure (Kerfoot and Sih 1987, up to 60% in Menge 1995) and are particularly interested in this combined effect of one species on another in a community. Yodzis (1994) refers to this joint impact of direct and indirect effects as "a very complicated system response" (p. 195), one that may not be interpretable from a reductionistic view and instead only wholly understood from a systems perspective (Costanza et al. 1993). If, with each new level of complexity, new system properties emerge (Anderson 1972), then community-wide analyses will be necessary to distill the network of species interactions into a common currency for assessing the importance of interspecific interactions on patterns of diversity in different environments.
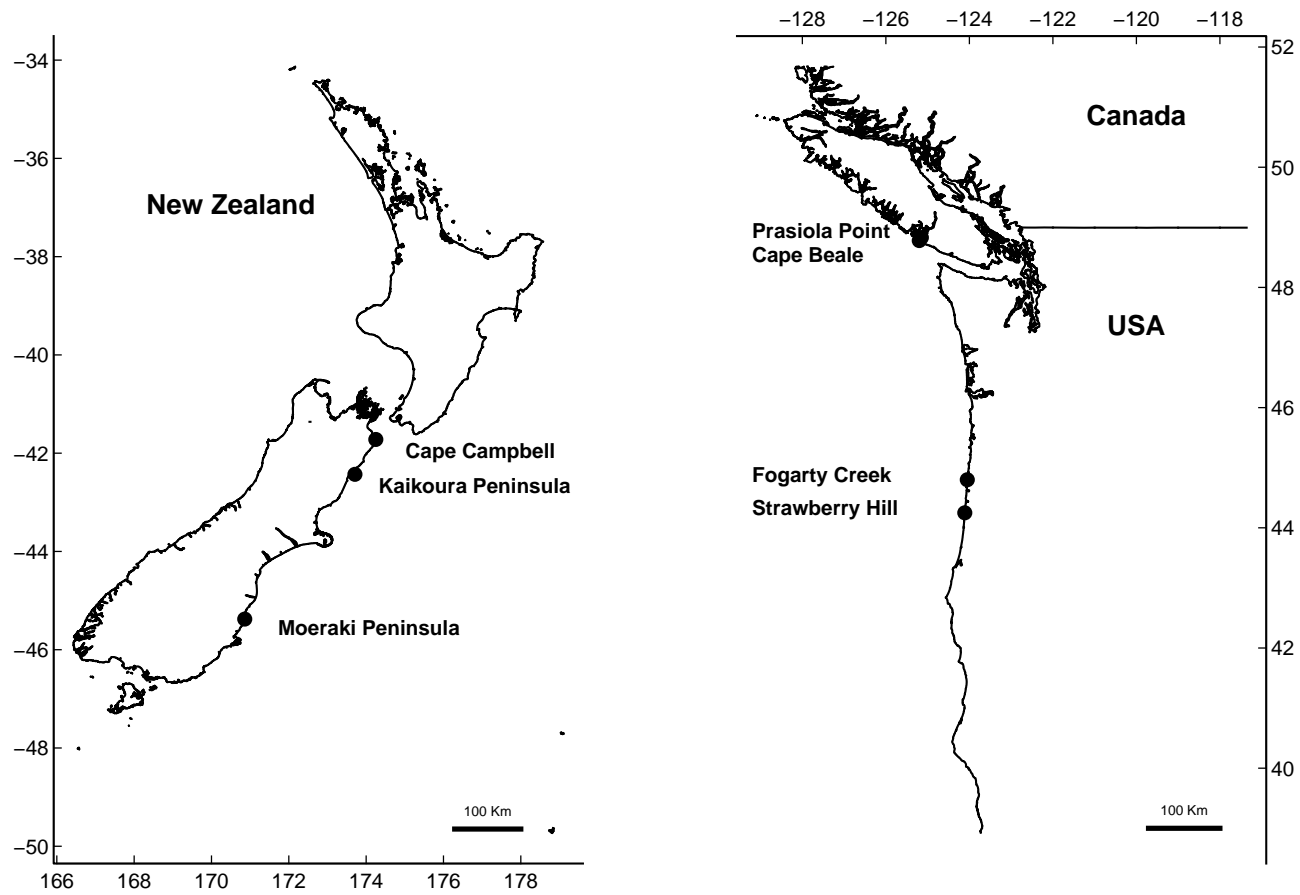
Figure 1.1: Map of the study sites in New Zealand and North America referred to throughout this dissertation.

(a) Cape Campbell, NZ

(b) Moeraki Peninsula, NZ

(c) Prasiola Point, BC

(d) Cape Beale, BC

Figure 1.2: Photographs of four study sites in New Zealand and British Columbia referred to throughout this dissertation.

1.2 Dissertation overview

Chapter 2

This thesis research first asks how species interactions are distributed in communities and the contingency of their sign and strength on the environment and the species present. A variety of factors, such as diversity, environmental stress, temporal and

spatial scale, and species traits, have been suggested to determine interactivity. In Chapter 2 I test the influence of these variables on the magnitude and direction of species interactions, with 29 species removal experiments across a range of intertidal habitat types in New Zealand and North America (Figure 1.1, 1.2). Previous research has shown that most interactions between species are weak (Figure 1.3, Paine 1992, Fagan and Hurd 1994, de Ruiter et al. 1995), but little is known about how this varies across environments or at different local scales. The sign of species interactions is also expected to vary across habitats (Bertness and Callaway 1994), with more facilitative interactions in more stressful environments. However, no synthesis to date has thoroughly assessed these hypotheses with entire communities. My results show that contrary to predictions, positive and negative effects are equally prevalent. In accordance with previous studies most interactions are weak, with only a few strong effects. I also find that although the sign and strength of species interactions is unaltered by most ecological factors, including environmental stress, organismal traits such as body size can predict interactivity. This is a promising result which suggests that easily measurable features of organisms can be used to predict community dynamics.

Chapter 3

Studies using species removal and press experiments to estimate interaction coefficients often assume that the per-capita effects of focal species are linear across a range of densities. This simplification allows experiments at one density to be used to infer species' interaction strengths at higher or lower levels of abundance. However, the validity of this assumption has been questioned (Abrams 2001). Studies in the intertidal (Ruesink 1998) and other ecosystems (Sarnelle 2003) have shown that species can have nonlinear effects, with dramatic changes at threshold levels of abundance. Nonetheless, a number of other studies have found that linear interaction coefficients are sufficient to predict community dynamics (Pfister 1995, Schmitz 1997, Wootton 1997, Berlow 1999, Emmerson and Raffaelli 2004, Novak 2008). In Chapter 3 I investigate this dichotomy by first quantifying the prevalence of nonlinear interactions in one high intertidal community. Then I assess the performance of a linear and three nonlinear interaction strength estimates by their capacity to pre-
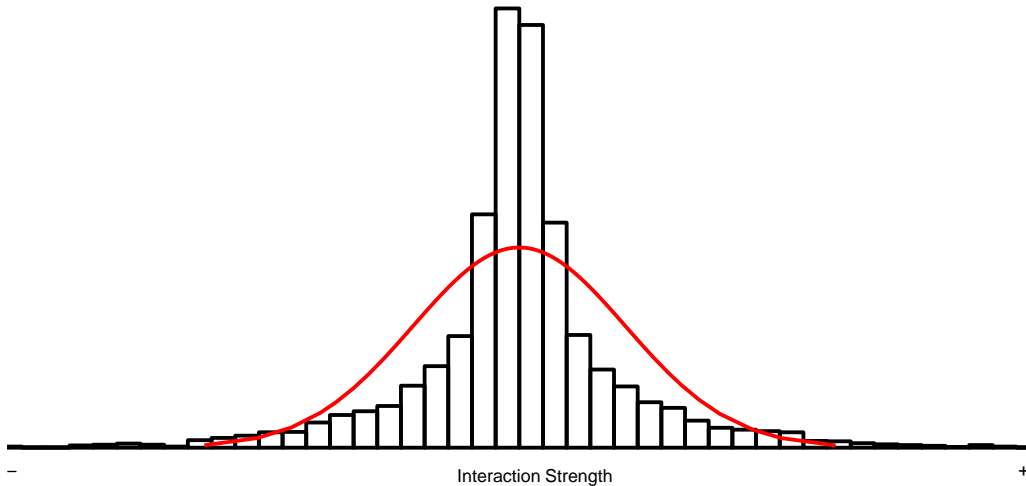
Figure 1.3: The expected distribution of interaction strengths with many weak and few strong pairwise effects between species. Studies in this dissertation test the importance of factors hypothesized to alter the strength and sign (positive versus negative) of the interactions that form this distribution. The red line depicts a Gaussian distribution.

dict the outcome of a second perturbation experiment. I find that most pairwise interactions are best described by a linear function and that the nonlinear forms do not improve the accuracy of the model predictions.

Chapter 4

In the final study, I draw connections between the biotic and abiotic processes structuring communities by examining how environmental stress alters species interactions in the high intertidal zone. Heat stress is a major environmental force structuring high shore communities (Hutchins 1947, Southward 1958, Tsuchiya 1983, Helmuth et al. 2006), and one that may intensify with global warming (Fields et al. 1993, Helmuth et al. 2002, Harley et al. 2006). For this reason, I carried out a field experiment to measure changes in species interactions in communities subjected to varying levels of heat stress. Past research has sought to determine how individual interactions are impacted by environmental stress, but few studies (e.g. Post and

Pedersen 2008) have used community-wide comparisons of changes in interspecific interactions under different stress regimes. Interestingly, I find that although abiotic stress alters community composition, and can affect the sign and strength of individual species interactions, it does not change the community-wide distribution of interaction types; the balance of positive versus negative and weak versus strong effects is maintained across the stress gradient. In Chapter 4 I discuss the potential for environmental heterogeneity and feedbacks between biotic interactions and abiotic processes to modify these results.

Summary

The following three chapters describe the patterns of interaction strengths across entire communities and explore the processes that shape them. These studies serve as rigorous experimental tests of the many factors suspected to alter species' interactivity. They also confirm the utility of species interaction coefficients for future comparisons of the relative influence of multiple factors on patterns of diversity in communities. The thesis concludes with a general discussion of the results and potential for further research on these topics.

1.3 Bibliography

Abrams, P.A. 2001. Describing and quantifying interspecific interactions: a commentary on recent approaches. Oikos 94:209–218.

Anderson, P.W. 1972. More is different: broken symmetry and nature of hierarchical structure of science. Science 177:393–396.

Bender, E.A., T.J. Case, and M.E. Gilpin. 1984. Perturbation experiments in community ecology: theory and practice. Ecology 65:1–13.

Berlow, E.L. 1999. Strong effects of weak interactions in ecological communities. Nature 398:330–334.

Berlow, E.L., S.A. Navarette, C.J. Briggs, M.E. Power, and B.A. Menge. 1999. Quantifying variation in the strengths of species interactions. Ecology 80:2206–2224.

Bertness, M.D. and R. Callaway. 1994. Positive interactions in communities. Trends in Ecology and Evolution 9:191–193.

Bruno, J.F., J.J. Stachowicz, and M.D. Bertness. 2003. Inclusion of facilitation into ecological theory. Trends in Ecology and Evolution 18:119–125.

Caley, M. and D. Schluter. 1997. The relationship between local and regional diversity. Ecology 78:70–80.

Caswell, H. 1976. Community structure: a neutral model analysis. Ecological Monographs 46:327–354.

Chesson, P. and N. Huntly. 1997. The roles of harsh and fluctuating conditions in the dynamics of ecological communities. American Naturalist 150:519–553.

Connell, J.H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. Ecology 42:710–723.

Costanza, R., L. Wainger, C. Folke, and K.G. Maler. 1993. Modeling complex ecological economic systems: toward an evolutionary, dynamic understanding of people and nature. Bioscience 43:545–555.

de Ruiter, P.C., A.M. Neutel, and J.C. Moore. 1995. Energetics, patterns of interaction strengths, and stability in real ecosystems. Science 269:1257–1260.

Elton, C. 1927. Animal Ecology. Sidgwick and Jackson, London.

Emmerson, M.C. and D. Raffaelli. 2004. Predator-prey body size, interaction strength and the stability of a real food web. Journal of Animal Ecology 73:399–

409.

Fagan, W.F. and L.E. Hurd. 1994. Hatch density variation of a generalist arthropod predator: population consequences and community impact. Ecology 75:2022–2032.

Fields, P.A., J.B. Graham, R.H. Rosenblatt, and G.N. Somero. 1993. Effects of expected global climate change on marine faunas. Trends in Ecology and Evolution 8:361–367.

Gleason, H.A. 1926. The individualistic concept of the plant association. Bulletin of the Torrey Botanical Club 53:7–26.

Harley, C.D.G., A.R. Hughes, K.M. Hultgren, B.G. Miner, C.J.B. Sorte, C.S. Thornber, L.F. Rodriguez, L. Tomanek, and S.L. Williams. 2006. The impacts of climate change in coastal marine systems. Ecology Letters 9:228–241.

Helmuth, B., B.R. Broitman, C.A. Blanchette, S. Gilman, P. Halpin, C.D.G. Harley, M.J. O'Donnell, G.E. Hofmann, B. Menge, and D. Strickland. 2006. Mosaic patterns of thermal stress in the rocky intertidal zone: implications for climate change. Ecological Monographs 76:461–479.

Helmuth, B., C.D.G. Harley, P.M. Halpin, M. O'Donnell, G.E. Hofmann, and C.A. Blanchette. 2002. Climate change and latitudinal patterns of intertidal thermal stress. Science 298:1015–1017.

Hutchins, L. 1947. The bases for temperature zonation in geographical distribution. Ecological Monographs 17:325–335.

Hutchinson, G.E. 1941. Ecological aspects of succession in natural populations. American Naturalist 55:406–418.

Hutchinson, G.E. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? American Naturalist 93:145–159.

Kerfoot, W.C. and A. Sih. 1987. Predation: Direct and Indirect Impacts on Aquatic Communities. University Press of New England, Hanover.

Laska, M.S. and J.T. Wootton. 1998. Theoretical concepts and empirical approaches to measuring interaction strength. Ecology 79:461–476.

Menge, B. 1995. Indirect effects in marine rocky intertidal interaction webs: patterns and importance. Ecological Monographs 65:21–74.

Menge, B.A. and J.P. Sutherland. 1976. Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. American

Naturalist 110:351–369.

Messier, F. 1994. Ungulate population models with predation: a case study with the North American moose. Ecology 75:478–488.

Novak, M. 2008. Trophic omnivory and the structure, strength, and nonlinear nature of species interactions across a productivity gradient. PhD Thesis. University of Chicago, Chicago.

Oksanen, L., S.D. Fretwell, J. Arruda, and P. Niemela. 1981. Exploitation ecosystems in gradients of primary productivity. American Naturalist 118:240–261.

Paine, R.T. 1966. Food web complexity and species diversity. American Naturalist 100:65–75.

Paine, R.T. 1980. Food webs: linkage, interaction strength and community infrastructure. Journal of Animal Ecology 49:667–685.

Paine, R.T. 1992. Food-web analysis through field measurement of per-capita interaction strength. Nature 355:73–75.

Peacor, S.D. and E.E. Werner. 2001. The contribution of trait-mediated indirect effects to the net effects of a predator. Proceedings of the National Academy of Sciences of the United States of America 98:3904–3908.

Pfister, C.A. 1995. Estimating competition coefficients from census data: a test with field manipulations of tidepool fishes. American Naturalist 146:271–291.

Polis, G.A. 1994. Food webs, trophic cascades and community structure. Australian Journal of Ecology 19:121–136.

Post, E. and C. Pedersen. 2008. Opposing plant community responses to warming with and without herbivores. Proceedings of the National Academy of Sciences of the United States of America 105:12353–12358.

Raffaelli, D. and S. Hall. 1996. Assessing the relative importance of trophic links in food webs. Pages 185–191 in G.A. Polis and K.O. Winemiller, editors. Food Webs: Integration of Patterns and Dynamics. Chapman and Hall, New York.

Ruesink, J.L. 1998. Variation in per capita interaction strength: thresholds due to nonlinear dynamics and nonequilibrium conditions. Proceedings of the National Academy of Sciences of the United States of America 95:6843–6847.

Russell, R., S.A. Wood, G. Allison, and B.A. Menge. 2006. Scale, environment, and trophic status: the context dependency of community saturation in rocky intertidal communities. American Naturalist 167:E158–E170.

Sarnelle, O. 2003. Nonlinear effects of an aquatic consumer: causes and consequences. American Naturalist 161:478–496.

Schmitz, O.J. 1997. Press perturbations and the predictability of ecological interactions in a food web. Ecology 78:55–69.

Southward, A.J. 1958. Note on the temperature tolerances of some intertidal animals in relation to environmental temperatures and geographical distribution. Journal of the Marine Biological Association of the United Kingdom 37:49–66.

Tansley, A.G. 1920. The classification of vegetation and the concept of development. Journal of Ecology 8:118–149.

Tsuchiya, M. 1983. Mass mortality in a population of the mussel *Mytilus edulis* L. caused by high temperature on rocky shores. Journal of Experimental Marine Biology and Ecology 66:101–111.

von Humboldt, A. and A. Bonpland. 1805. Essai sur la Geographie des Plantes. Chez Levrault, Schoell et Compagnie, Paris.

Warming, E. and M. Vahl. 1909. Oecology of Plants: an Introduction to the Study of Plant-communities. Clarendon Press, Oxford.

White, G. 1789. The Natural History of Selborne. T. Bensley, for B. White and Son, London.

Whittaker, R.H. 1956. Vegetation of the Great Smoky Mountains. Ecological Monographs 26:1–69.

Williams, R.J. and N.D. Martinez. 2000. Simple rules yield complex food webs. Nature 404:180–183.

Wootton, J.T. 1997. Estimates and tests of per capita interaction strength: diet, abundance, and impact of intertidally foraging birds. Ecological Monographs 67:45–64.

Yodzis, P. 1988. The indeterminacy of ecological interactions as perceived through perturbation experiments. Ecology 69:508–515.

Yodzis, P. 1996. Food webs and perturbation experiments: theory and practice. Pages 192–200 in G.A. Polis and K.O. Winemiller, editors. Food Webs: Integration of Patterns and Dynamics.

Chapter 2

An empirical assessment of the factors regulating species interactions in intertidal communities [§]

2.1   Introduction

Species interactions come in a variety of forms, from weak to strong, and negative or positive, each with unique consequences for local community structure. Recently, the characteristic community-wide distribution of many weakly and few strongly interacting species has emerged as a ubiquitous yet poorly understood pattern in nature (Paine 1992, Fagan and Hurd 1994, Raffaelli and Hall 1996, Berlow 1999). Theoretically, this interaction distribution confers stability in ecological systems (Yodzis 1981, de Ruiter et al. 1995, Roxburgh and Wilson 2000, Neutel et al. 2002), however, its origins are unclear. Many environmental, organismal and scale-dependent variables have been suggested to dictate the nature of species interactions in communities. Competing theories have also proposed that interaction strength is related to species richness (Margalef 1968, Keitt 1997). Now the challenge is to discern the relative importance of these factors for the frequency of strong versus weak, and positive versus negative, interactions in communities (Agrawal et al. 2007).

   The morphological, physiological, behavioral, and ecological traits of species may affect the strength of their interactions with associated community members (Soule et al. 2005). Evidence suggests that interaction strength is scaled to body size in food

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webs (Emmerson and Raffaelli 2004) and thereby correlated with several allometric species traits including metabolism, home range, abundance, and trophic status (Brown et al. 2004, Woodward et al. 2005). Larger, more mobile, or abundant species have greater potential to interact with other species and thus may have stronger effects (Duffy 2003). Often top trophic consumers, for example, have strong interactions that cascade down through other community members to lower trophic levels (Shurin et al. 2002) and may destabilize food webs (Bascompte et al. 2005). However, recent studies have also shown that large mobile consumers can dampen oscillatory dynamics caused by strong interactions between lower trophic groups, by coupling spatially compartmentalized subwebs (McCann et al. 1998, McCann et al. 2005). An understanding of the mechanistic basis of species interactivity in terms of organismal traits could allow for more general predictions of dynamics without detailed information on particular species or communities.

Gradients of environmental stress may also shift the relative importance of positive versus negative interactions (Bertness and Callaway 1994, Brooker and Callaghan 1998). Negative interactions often dominate under less stressful conditions while positive interactions are more prevalent under stressful regimes (Stachowicz 2001, Tirado and Pugnaire 2005). A recent meta-analysis of 11 alpine plant removal experiments, for example, showed a shift from competitive to facilitative plant–plant interactions with increasing stress along an elevation gradient (Callaway et al. 2002). Other studies, however, have shown that this relationship is context dependent. Pennings et al. (2003) found that the relationship between interaction type and environmental severity in salt marsh plants depended on geographic scale and the coexistence of particular plant species. Their results point to a need for studies that explore the environmental control of interaction distributions across habitats and regions varying in levels of physical stress (Brooker et al. 2008).

The temporal and spatial scales of resolution may also influence the sign and strength of species interactions. Direct and indirect interactions between species are believed to act on disparate time scales, with indirect effects unfolding more slowly as they are transmitted along chains of direct interactions (Yodzis 1988). At broad temporal and spatial scales, interactions may be weaker due to segregation of species. Larger study areas include more heterogeneous habitats and greater species richness (Palmer and White 1994) in part because coexistence is possible at larger

scales where spatial niche segregation weakens interactions that would otherwise lead to exclusion (Connell 1961, Grace and Wetzel 1981). Differences in organisms' home ranges, as well as habitat edges, should act as barriers to the movement of mobile organisms and thereby limit interactivity (Wootton and Emmerson 2005). The magnitude of these scale effects, relative to other factors, has not been fully explored.

There is a clear need for studies that examine the relative influences of multiple factors on species interactivity. In this synthesis, we test the relative roles of diversity, environmental stress, experimental scale, and species traits in shaping the community-wide distribution of species interaction strengths. We use an unprecedented dataset of empirically derived interaction coefficients, based on specific responses to the removal of dominant intertidal taxa in the northern (Oregon and British Columbia) and southern (New Zealand) Pacific Ocean. Our goal is to identify features of organisms, communities and environments that influence interaction sign and magnitude and shape the distribution of weak and strong interactions.

2.2 Methods

Field techniques

Data from 29 independent field experiments were used to assess the community-wide distribution of species interactions. Each experiment consisted of replicated 'removal' and unmanipulated control plots of equal size, arrayed in one intertidal habitat. The experiments were done on the east coast of New Zealand and the west coast of North America at various times between 2002 and 2008 (Table 2.1). A single focal species was eliminated from the manipulated plots and continually excluded for the duration of the study (a PRESS experiment, Bender et al. 1984; see Lilley and Schiel 2006 for further descriptions of the experimental protocol). Focal species were abundant algae and invertebrates that were dominant community members known to have numerous strong direct trophic and nontrophic effects on other species (Lilley and Schiel 2006). Thus, our data may be biased towards focal species with less variable (Berlow 1999) and disproportionately strong interactions in the community. This bias limits our ability to generalize interactivity to the other

community members, but does not restrict comparisons between experiments. The abundances of all associated, non-manipulated target species found in the study plots were monitored throughout the experiment. Individuals of mobile organisms were enumerated. Abundances of sessile taxa were measured by visually estimating percent coverage. Focal species density (individuals $\cdot$ m^{-2}) was also measured. Plots were monitored at varying intervals, typically every three to six months, for up to three years after the experiment was initiated.

Interaction metric

The interaction coefficient between focal and target species was calculated using the log ratio of the response in density of the target species in the removal treatment unit relative to the untreated control (Wootton 1997, Osenberg et al. 1997). The data were bootstrapped to produce all possible removal-control plot pairs (Paine 1992), for a total of 81,075 pairwise species interaction estimates. The measure,

$$DI_{ij} = \frac{ln\dfrac{\left(\dfrac{C_{i,p}}{C_{i,p-1}}\right)}{\left(\dfrac{E_{i,p}}{E_{i,p-1}}\right)}}{\Delta t \cdot Y} \tag{2.1}$$

gives the per-capita impact of the focal species j on the population trajectory of target species i, DI_{ij}, where $C_{i,p}$ is the abundance of the target organism in the presence of the focal species and $E_{i,p}$ is its abundance in the absence of the focal species at monitoring period p. The time between sample periods, Δt, is expressed in days. Density of the focal species in the control plot, Y, is expressed in individuals per square meter to facilitate comparisons among different plot sizes. Because this metric is a log ratio it cannot be calculated with abundance values of zero. In such cases, one individual per square meter is added to all E and C values (Wootton 1997). The log ratio is distributed around zero; species whose abundances decline in the absence of the focal species, relative to the control, will have positive interaction coefficients, while those that increase will have negative coefficients.
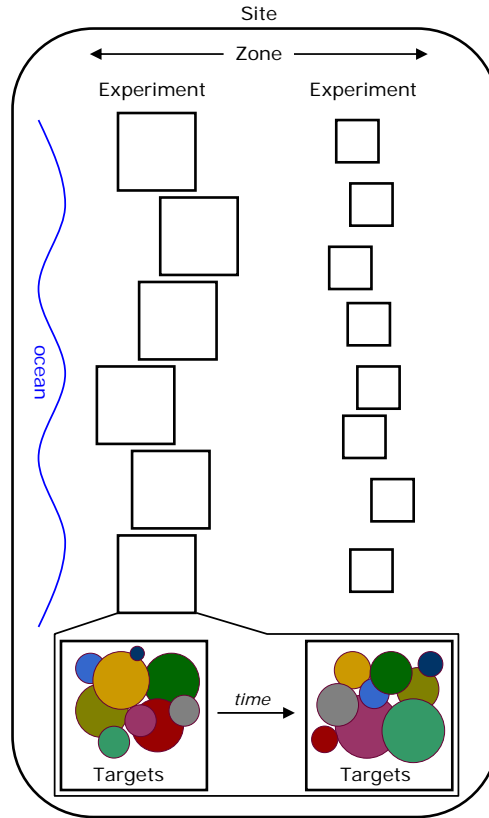
Figure 2.1: Each experiment consisted of replicate control and removal plots, of the same size, in one intertidal zone at a site. The abundances of all target species were measured at time intervals over the duration of the experiment.

Region	Site	Species Removed	Trophic	Size (g)	Density ($\#\cdot m^{-2}$)	Zone	Scale (m^2)	Dates (yr/mo)
New Zealand	Cape Campbell	*Durvillaea antarctica*	Producer	734	20	Low	0.25	2002/10-2003/10
New Zealand	Cape Campbell	*Hormosira banksii*	Producer	17.3	331	Mid	0.25	2002/09-2003/10
New Zealand	Kaikoura Peninsula	*Cystophora torulosa*	Producer	33	294	Low	0.25	2002/12-2003/10
New Zealand	Kaikoura Peninsula	*Durvillaea antarctica*	Producer	427	29	Low	0.25	2002/09-2003/10
New Zealand	Kaikoura Peninsula	*Hormosira banksii*	Producer	26.5	918	Mid	0.025	2002/09-2003/10
New Zealand	Kaikoura Peninsula	*Hormosira banksii*	Producer	26.5	510	Mid	0.25	2002/09-2003/10
New Zealand	Kaikoura Peninsula	*Hormosira banksii*	Producer	26.5	534	Mid	1.25	2002/07-2004/08
New Zealand	Kaikoura Peninsula	*Corallina officinalis*	Producer	0.45	4800	Mid	0.025	2002/09-2003/10
New Zealand	Kaikoura Peninsula	*Corallina officinalis*	Producer	0.45	11378	Mid	0.25	2002/12-2003/10
New Zealand	Moeraki Peninsula	*Cystophora torulosa*	Producer	31.5	282	Low	0.25	2002/12-2003/10
New Zealand	Moeraki Peninsula	*Hormosira banksii*	Producer	12.8	567	Mid	1.25	2002/07-2004/08
New Zealand	Moeraki Peninsula	*Corallina officinalis*	Producer	0.45	8676	Mid	0.25	2002/12-2003/10
North America	Cape Beale	*Postelsia palmaeformis*	Producer	133	42	Mid	0.25	2006/09-2008/08
North America	Fogarty Creek	*Fucus gardneri*	Producer	29.8	149	High	0.25	2002/04-2003/04
North America	Fogarty Creek	*Laminaria setchellii*	Producer	62.4	107	Low	0.25	2002/04-2003/04
North America	Fogarty Creek	*Pelvetiopsis limitata*	Producer	2.28	436	High	0.25	2002/04-2003/04
North America	Fogarty Creek	*Balanus glandula*	Suspension	0.164	7555	High	0.025	2002/04-2003/04
North America	Prasiola Point	*Katharina tunicata*	Herbivore	20	10	Low	0.25	2008/03-2008/09
North America	Prasiola Point	*Lottia digitalis*	Herbivore	0.165	82	High	0.025	2005/05-2007/05
North America	Prasiola Point	*Lottia digitalis*	Herbivore	0.165	293	High	0.025	2006/05-2008/04
North America	Prasiola Point	*Lottia pelta*	Herbivore	0.598	16	High	0.025	2005/05-2007/05
North America	Prasiola Point	*Pisaster ochraceus*	Carnivore	99.5	8	Low	0.25	2008/03-2008/09
North America	Prasiola Point	*Fucus gardneri*	Producer	5.49	1010	High	0.025	2005/05-2008/05
North America	Prasiola Point	*Fucus gardneri*	Producer	5.49	636	High	0.25	2005/05-2007/05
North America	Prasiola Point	*Fucus gardneri*	Producer	5.49	393	High	1.00	2005/05-2007/05
North America	Prasiola Point	*Laminaria setchellii*	Producer	36	83	Low	0.25	2005/06-2006/07
North America	Prasiola Point	*Balanus glandula*	Suspension	0.164	5509	High	0.025	2005/05-2008/05
North America	Strawberry Hill	*Fucus gardneri*	Producer	11.3	51	High	0.25	2002/04-2003/04
North America	Strawberry Hill	*Pelvetiopsis limitata*	Producer	2.28	603	High	0.25	2002/04-2003/04

Table 2.1: The 29 experiments conducted as part of this study. Figure 1.1 gives a map showing the locations of the study sites. Photos of four of the research sites are shown in Figure 1.2. The average size and density of the focal taxon is given, along with the shore elevation, plot size, and date of the experiment.

Analytical procedures

Our analyses consider three response variables. For each pairwise interaction between a focal and target taxa, we are interested in the sign (positive or negative) and strength of the interaction coefficient, DI_{ij} (Equation 2.1). To assess interaction sign, we reduce the coefficients into binary positive versus negative responses to be analyzed using a logistic regression. Interaction strength is calculated as the absolute value of the interaction coefficient. As such, interaction strength is always a positive value. Otherwise, strong positive and negative interactions on both sides of zero could be averaged to give an overall weak community-wide effect (Dodds and Nelson 2006). Thirdly, we measure the kurtosis of the distribution of coefficients from each experiment to describe the ratio of weak:strong interactions. Kurtosis is computed using Pearson's technique (Zar 1984). The values are averages per experiment across monitoring periods.

Multilevel models are used to test the hypotheses that the sign and strength of species interactions are related to local scale, diversity, shore height, and experimental duration, as well as the body size of the focal species, and trophic identity of both the target and focal species. The dependent variable in every case is the interaction coefficient computed for a focal-target species combination, averaged across all replicate pairs of removal and control plots in each experiment. We employ a three level model (level 1: repeated measures; level 2: target populations; level 3: experiments [the 'community-wide' response]) with random slopes and intercepts at all levels (see Appendix A on multilevel modeling). Predictors at all levels test for effects of the fixed factors (level 1: Time; level 2: Target; level 3: Focal, Richness, Zone, Scale, Mass). Time refers to the sampling date. Target and Focal represent trophic types (producer, suspension feeder, herbivore, carnivore, or omnivore) of the response and manipulated populations respectively. Richness is the maximum richness measured in an experiment across all sampling times. These estimates do not differ significantly from jacknifed experiment-level richnesses (Heltshe and Forrester 1983, Gotelli and Colwell 2001). Zone is an ordered factor with three levels (low, middle, and high), used as a proxy for degree of environmental stress. In the intertidal, there is a clear gradient in heat and desiccation stress across zones (Bertness and Leonard 1997), much like the elevation gradient in alpine ecosystems

(Callaway et al. 2002). Scale represents the quadrat size, and ranges from 0.025 m^2 to 1.25 m^2. Finally, Mass indexes the body mass of the focal species excluded in the removal experiments. Numerical predictors were centered by subtracting the mean value so that the model tests for differences under average conditions (Kreft and de Leeuw 1998). The model also includes tests for cross-level Target · Richness, Target · Stress, Target · Scale, Target · Mass, and Target · Focal interactions.

The above multilevel framework was used to assess the effects of predictors on the sign and strength of the species interactions. To model interaction sign we performed a logistic multilevel regression using a logit link function expressing interaction sign as a probability of being positive. To test interaction strength, a linear multilevel model was used. Data were log transformed to meet assumptions of normality. We assessed the benefit of including an autoregressive order one correlation to account for the inherent correlation between sample times (Pinheiro and Bates 2000), but it did not improve the model fit. Regressions were performed using the nlme and lme4 packages for R (R Development Core Team 2008). P-values for the main effects were generated using Markov Chain Monte Carlo methods, using the mcmcsamp function in the lme4 package.

To test the hypothesis that kurtosis is related to species richness we used a simple linear regression. For each experiment, average kurtosis was regressed against average species richness. Both variables were log transformed.

2.3 Results and discussion

Our synthesis of intertidal removal experiments indicates that traits of species play a dominant role in determining the strength, but not the sign, of interactions among organisms (Table 2.2). Positive and negative interactions were equally prevalent in all cases, regardless of tidal height, temporal or spatial scale of the experiment, species richness of the community, or the types of species examined. The first of these observations is most surprising as it suggests that the increase in facilitative interactions with environmental stress occurs in some taxa but is not a general feature of interactions across all members of the community. Individual carnivores exert greater impacts on communities than herbivores, which in turn are stronger interactors than suspension feeders. However, since these larger organisms with

higher trophic positions are less numerically abundant, their population-level effects are equivalent. Population densities decline with increasing body size, and these two changes combine to yield a comparable population-level impact on other community members across a range of sizes.

a)

Factor	df	SS	MS	p
Time	1	0.087	0.087	0.690
Target Trophic Type	4	4.058	1.014	0.573
Zone	1	0.235	0.235	0.284
Scale	1	0.977	0.977	0.845
Richness	1	0.856	0.856	0.954
Body Size	1	0.010	0.010	0.355
Focal Trophic Type	3	4.899	1.633	0.158
Target Trophic Type · Zone	4	8.730	2.183	0.324
Target Trophic Type · Scale	4	2.245	0.561	0.448
Target Trophic Type · Richness	4	5.137	1.284	0.481
Target Trophic Type · Body Size	4	3.014	0.753	0.511
Target Trophic Type · Focal Trophic Type	12	7.078	0.590	0.746

b)

Factor	df	SS	MS	p
Time	1	0.059	0.587	0.948
Target Trophic Type	4	132.8	33.21	<.001
Zone	1	13.18	13.18	0.810
Scale	1	11.12	11.12	0.175
Richness	1	0.428	0.428	0.563
Body Size	1	13.01	13.01	0.003
Focal Trophic Type	3	23.71	7.902	0.006
Target Trophic Type · Zone	4	14.50	3.624	0.540
Target Trophic Type · Scale	4	41.58	10.39	0.440
Target Trophic Type · Richness	4	3.993	0.998	0.447
Target Trophic Type · Body Size	4	10.36	2.591	0.334
Target Trophic Type · Focal Trophic Type	12	20.31	1.692	0.748

Table 2.2: Results of an analysis of variance testing the effects of factors on the sign (a) and strength (b) of species interactions.

Body size

Our study provides empirical evidence that large taxa have stronger community-wide effects than small-bodied species (Figure 2.2, Table 2.2b). Measured here as body mass, size spans three orders of magnitude from barnacles (< 1 g) to the large alga *Durvillaea antarctica* (< 1 Kg, max c. 30 Kg, Table 2.1). This property relates to a

wide range of organismal traits determining abundance, population growth, feeding ecology and range size, and therefore predicts the outcome of interactions at the community level (Woodward et al. 2005, Wootton and Emmerson 2005). Recent studies have shown that predator:prey size ratios reflect the strength of trophic interactions (Emmerson and Raffaelli 2004, Berlow et al. 2009). In this study we find that some of the strongest per-capita effects are actually nontrophic impacts by the algal prey species *D. antarctica*. An individual *D. antarctica* excludes understory species by whipping its fronds against the substrate (Santelices et al. 1980), while also providing habitat for dozens of macroinvertebrate grazers in its holdfast (Edgar and Burton 2000), in the same way that trees harbor communities of smaller-bodied consumers (Southwood 1961). Sessile species like *D. antarctica*, that can reach lengths of 10 m, are able to interact with organisms over scales greater than the home ranges of their associated mobile invertebrate consumers. Interestingly, although the two species are separated biogeographically, one sessile *D. antarctica* spans an area comparable to the typical foraging range of the infamous predatory sea star *Pisaster ochraceus* (Robles et al. 1995). So although mobility is undoubtedly important, particularly in food webs, so too are the strong, often nontrophic, positive and negative effects of sessile organisms. Our results show that body size serves as the best surrogate measure of the potential for species of all trophic types to engage in direct interactions that result in particularly strong community-wide effects.

Trophic type

The results show that even after accounting for body size predators have stronger per-capita effects on communities than lower trophic species (Figure 2.2, 2.3a, Table 2.2b). The community-wide effect of harvesting a predator, such as a sea star, is many times greater than the loss of an equivalent number of suspension feeding mussels. Thus it appears that the top-down effect of an individual predator is greater than the bottom-up effect of its prey in complex multi-trophic communities, as found previously (Yodzis 1981, de Ruiter et al. 1995, Moore et al. 1996, Borer et al. 2006). However, herbivores and primary producers have equal impacts (Table 2.3, Figure 2.3a) because they encompass a wide and overlapping range of sizes, spanning a 100- and 1000-fold size range, respectively (Figure 2.2).
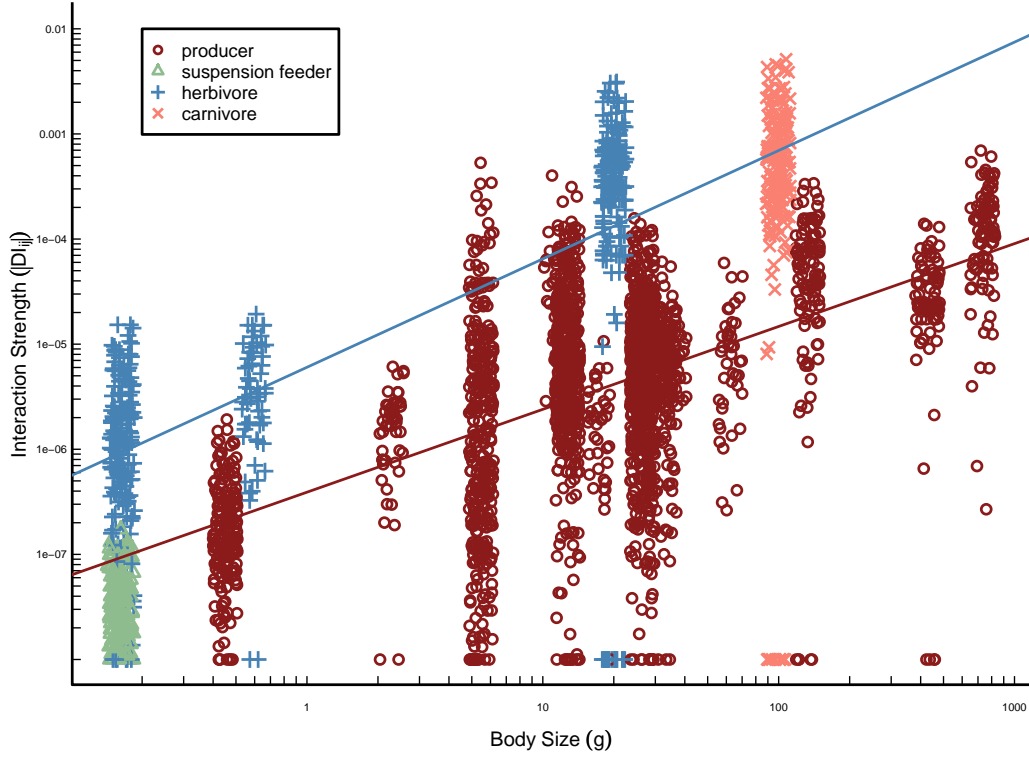
Figure 2.2: The relationship between focal species body size and per-capita interaction strength. Each point symbolizes one pairwise interaction. Colors and symbols represent different trophic types of the focal species removed. Points have been jittered to ease visualization. Lines were fit to the producer and herbivore data using ordinary least squares. Interactions measured by Wootton (1997) for predatory American Black Oystercatchers (480 g, $D\bar{I}_{ij} = 0.004$), Glaucous-winged Gulls (1130 g, $D\bar{I}_{ij} = 0.018$), and Northwestern Crows (620 g, $D\bar{I}_{ij} = 0.014$) also conform to these patterns.

We find that no trophic group of species exerts predominantly positive or negative effects on other species (Table 2.2a). For instance, consumer species are equally likely to benefit or suffer in interactions with producer species. Paine (1992) likewise found that intertidal herbivores had comparable positive and negative effects on one species of prey, *Alaria marginata*. Such results may not be predicted by simple food webs and emphasize the need to consider an assortment of interaction types, including trophic and nontrophic, as well as direct and indirect effects (Jones et al. 1997). In our experiments, interactions between predators and prey often elicit a complex response of both positive and negative effects. For example, by removing the barnacle *Balanus glandula* we are able to detect its direct positive effects on other invertebrates, such as the grazing snail *Littorina spp.*, for which it creates habitat (Harley 2006). Meanwhile, through inhibition of grazing by limpets, it also has indirect positive effects on macroalgae (Farrell 1991), but direct negative effects on species such as *Chthamalus dalli*, a smaller barnacle that it out-competes for space (Dayton 1971). Ultimately, positive responses balance negative responses, and through the complex assortment of indirect and nontrophic interactions the sign of the outcome is unpredictable based strictly on trophic type.

Species richness

Our results further indicate the importance of weak interactions by showing that the pattern of many weak and few strong effects is more pronounced in species-rich communities ($F_{1,27} = 4.710$, p = 0.039, Figure 2.4). In this study, with up to 62 taxa, more speciose communities have more leptokurtotic distributions of interactions with greater proportions of weak interactors. This is not accompanied by a corresponding change in interaction strength (Table 2.2b). The interplay among richness, interaction strength, and stability is complex. Competing theories have suggested that richness and interaction strength are directly (Margalef 1968, May 1973, Kokkoris et al. 2002) or inversely (Keitt 1997, Wilson et al. 2003) related. Stability on the other hand is not dependent on the mean interaction strength; it arises in communities with many weakly and few strongly interacting species (de Ruiter et al. 1995). This distribution of interactions has been observed in the rocky intertidal (Paine 1992) and elsewhere (Raffaelli and Hall 1996) for subsets of species, and again here in
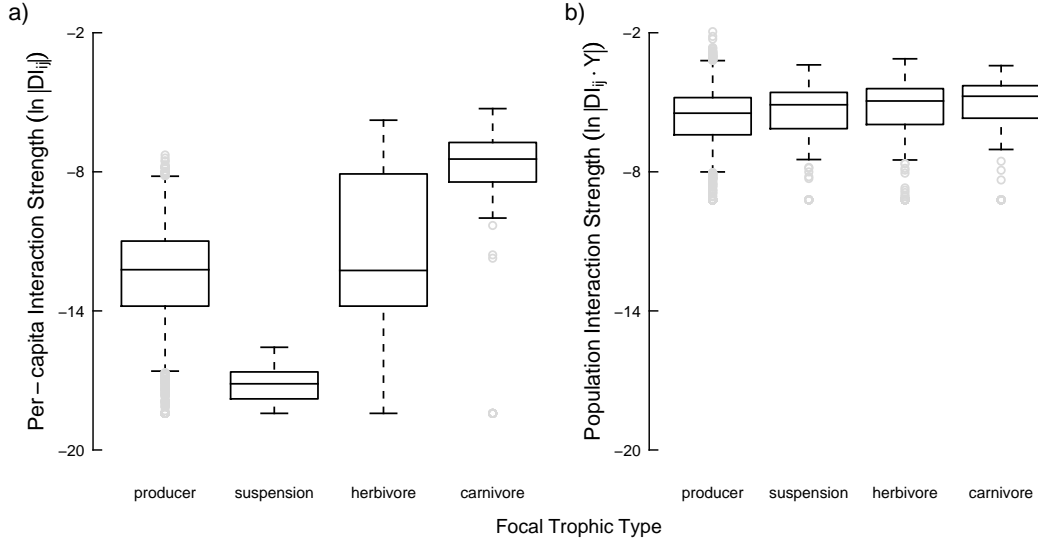
Figure 2.3: The strength of per-capita (a) and population-level (b) effects of focal species grouped by trophic type.

this community-wide study. We build on these studies by showing that disproportionate numbers of weakly interacting species are required to balance the effects of the added strong interactors and maintain a constant community-wide interaction strength. This is new empirical evidence that the distribution of many weakly and few strongly interacting species provides the stability required for diverse communities to persist.

Environmental stress

Based on previous studies (e.g. Bertness and Leonard 1997), we predicted that the community-wide distribution of species interactions would shift from more negative to positive in communities from the low to high intertidal. Surprisingly, however, we find no evidence for such a shift (Table 2.2a). The strength of interactions also does not vary across habitats along the environmental stress gradient (Table 2.2b). In our multilevel models, we analyze the impact of factors such as stress on interactions over time. In these time series, pairwise interactions between any two species are
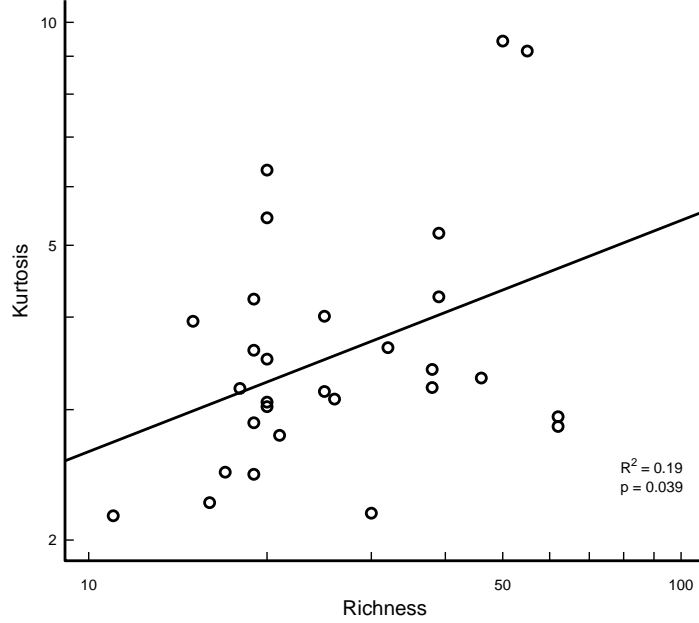
Figure 2.4: The relationship between species richness and kurtosis of the community-wide distribution of per-capita interaction strengths. Kurtosis is a measure of the ratio of weak to strong species interactions. As richness increases, the proportion of weak interactions also increases, possibly to balance the impact of the few strong effects.

rarely constant, and often alternate signs. This temporal variability may originate from a number of biotic and abiotic factors. Environmental fluctuations at daily (Foster 2002) to annual (Greenlee and Callaway 1996) time scales have been shown to reverse the direction of species interactions. Indirect interactions (Yodzis 1988) and ontogenic shifts (Miriti 2006) can also switch interaction signs. We integrate across these sources of variability in search of persistent generalities. While species show differences in interactivity within experiments at static points in time, there are no long term trends explainable by environmental stress.

There may be other explanations for why facilitation does not increase with stress. At any point along a stress gradient, a community represents a collection of species existing within a niche defined by their tolerance limits. Consider, for

example, a habitat modification by a high intertidal species that reduces temperature. This may have a facilitative effect on organisms living at their upper thermal limits (cf. Bruno et al. 2003). However, the environment will be modified in other ways, potentially leading to reduced light availability (e.g. from canopies) or water flow. Other species will be inhibited by these modifications, and register them as negative interactions. Biotic processes will be similarly altered and these changes can, through indirect effects, have positive and negative community-wide consequences. Ultimately, in the face of such complexity, the effects of environmental stressors are felt differently by different species. It is possible that species from one trophic group may exhibit comparable responses to stressors, and thus show coordinated shifts that are masked at the community level. In fact, most prior evidence for stress-interaction gradients has come from single trophic level studies on plant-plant interactions (Brooker et al. 2008). However, our results show that while some individual taxa can shift from negative to positive effects, trophic types do not consistently vary in the sign or strength of their interactions across the stress gradient (Table 2.3).

While our experimental approach benefits from being relatively tractable, one limitation is that direct and indirect effects cannot be distinguished. Theory holds that indirect interactions are slower to manifest, and have larger effects, than direct interactions (Bender et al. 1984, Yodzis 1988, Abrams 1992), hence, interaction strength should increase over time. However, we find no long-term trend in interaction magnitude or direction, suggesting that indirect effects are not slower to propagate or that indirect interactions are similar in strength and sign as direct ones. Other investigations in the rocky intertidal (Menge 1995, 1997) have reached similar conclusions, that direct and indirect interactions operate simultaneously, and can have comparably strong effects. Thus, research that estimates direct effects independently of indirect ones (e.g. de Ruiter et al. 1995) will be beneficial. Such approaches will provide further insight into the associations between the separate and combined measures (Schmitz 1997), and serve as more direct tests of many theoretical predictions.

Spatial and temporal scales

We find no impact of either the size of the experimental unit or the duration of the study on the sign or strength of species interactions (Table 2.2). The plot sizes in our study were not large enough to encompass the variety of habitats necessary to generate spatial segregation that would reduce the community-wide interaction strength. It does not appear that our study, nor previous intertidal experiments on species interactions spanning these local scales and time periods, are dramatically biased by artifacts arising from spatial and temporal extent.

Per-capita versus population effects

On a per-capita basis, mobile consumers exert stronger effects on other species than suspension feeders (Figure 2.3a), however, population level differences among focal groups ($DI_{ij} \cdot Y$; 'species impact' in Wootton 1997) are comparatively small (Figure 2.3b). Differences among populations of target taxa are also slight, though predators and suspension feeding invertebrates show less response to removals than producers, which are themselves less affected than herbivores (Table 2.3b). These patterns are independent of the species type being removed, as indicated by the non-significant Target · Focal trophic type interaction (Table 2.2). The per-capita effects of predators and herbivores are large because their numerical densities are low compared to producers. This pattern of lower abundance with higher trophic levels and body sizes is common in many ecosystems (Damuth 1981, Cohen et al. 2003). The inverse scaling relationships between body size and both population abundance and individual mass-specific metabolic rates led Damuth (1987) to propose that population energy use is invariant, since the increasing metabolism of larger taxa is offset by their lower abundance. Our results suggest an interesting corollary: although effects span many orders of magnitude, species impacts on other community members increase with size and trophic position on an individual basis, but are more uniform at the population level.

These results hold a number of important implications for ecology and conservation. First, they indicate that measurable ecological traits of individuals such as body size can be used to predict community-wide impact. Interaction intensity may be a function of metabolic rate, reflecting the ability of species to monopolize re-

sources including food or space. Second, this guides predictions about the secondary consequences of species loss for ecosystems. Although population-level effects of removals are constant across trophic levels, large species with high trophic positions are more vulnerable to extinction (Duffy 2003). Removal of these populations will have community-wide effects comparable to extinctions of the most dominant low trophic species. Our study did not experiment with rare, small-bodied taxa, but others have shown these species can have sizable influences on community structure (Berlow 1999, Lyons and Schwartz 2001). Finally, species introductions may also follow equivalent rules. Levin et al. (2002) found that invasions by algae and suspension feeding bryozoans had commensurate community-wide impacts. As in our deletion experiments, the introduced focal species had many weak and few strong effects that were evenly positive and negative.

Conclusion

The unpredictability and context-dependency of species interactions presents one of the greatest challenges to predictions of ecosystem dynamics (Agrawal et al. 2007). Our results highlight three important points about the factors regulating the sign and magnitude of interactions. First, the data support the idea that weak interactions are important stabilizing elements that favor greater diversity. Communities with more species have more kurtotic interaction distributions, indicating that diversity is associated with a greater prevalence of weak interactions. Second, we find that species traits predict interaction strength, and are relatively insensitive to environmental conditions such as tidal height or the species richness of the community. This is a promising result with regard to developing predictive models of community dynamics. It suggests that measurable features of organisms, such as body size, provide an indication of their per-capita impact on other species. Finally, although mobile consumers exert stronger impacts on others at the individual level, their population level effects are equivalent across trophic groups. This indicates that interaction intensity arises out of use of resources such as food or space that show similar allometric relationships. Thus, although large individuals and those with higher trophic position exert greater impacts on other taxa, extinctions of populations at any trophic level can have community-wide consequences.
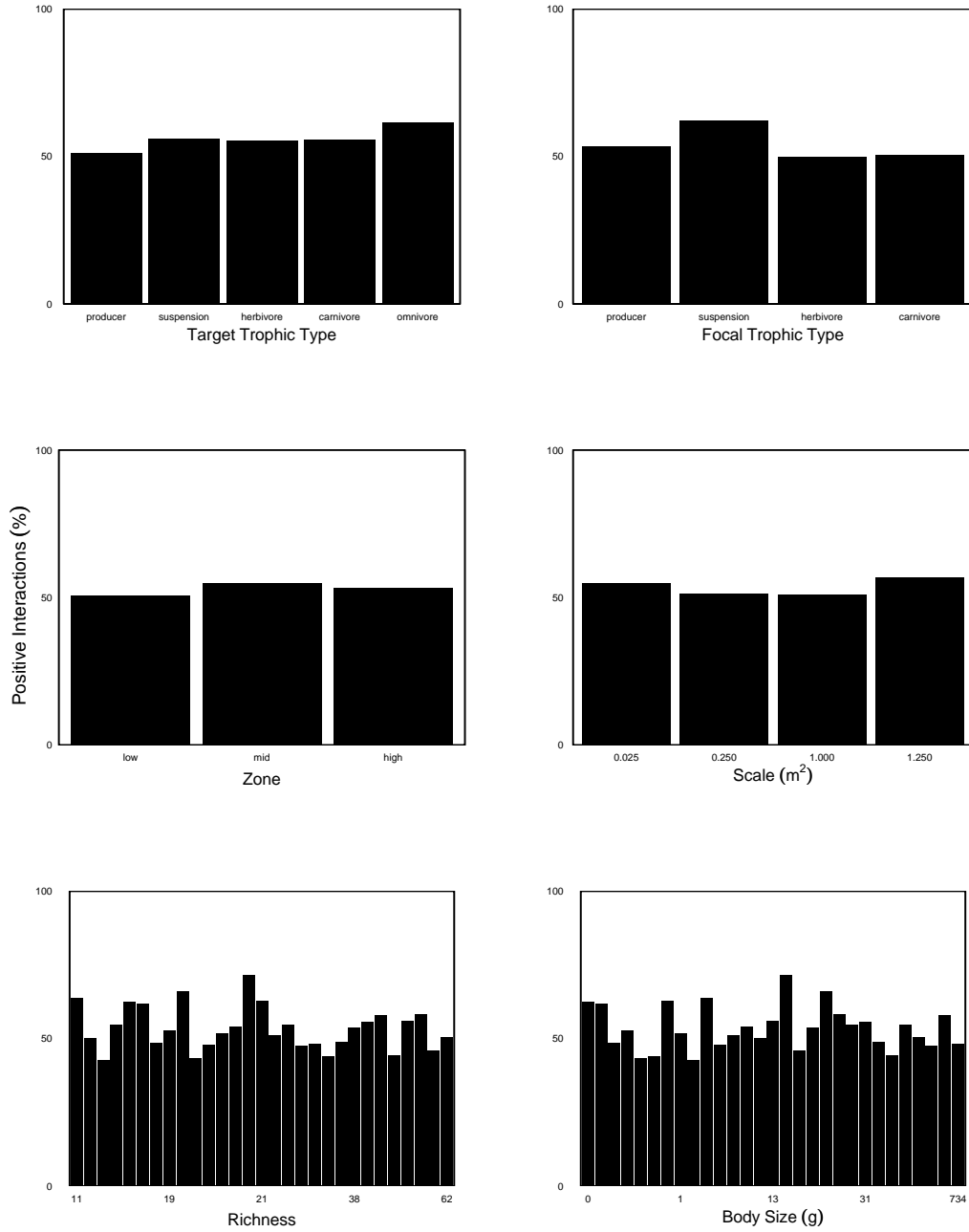
Figure 2.5: Plots showing relationships between predictors and interaction sign. Values presented are arithmetic means of all lower-level data.
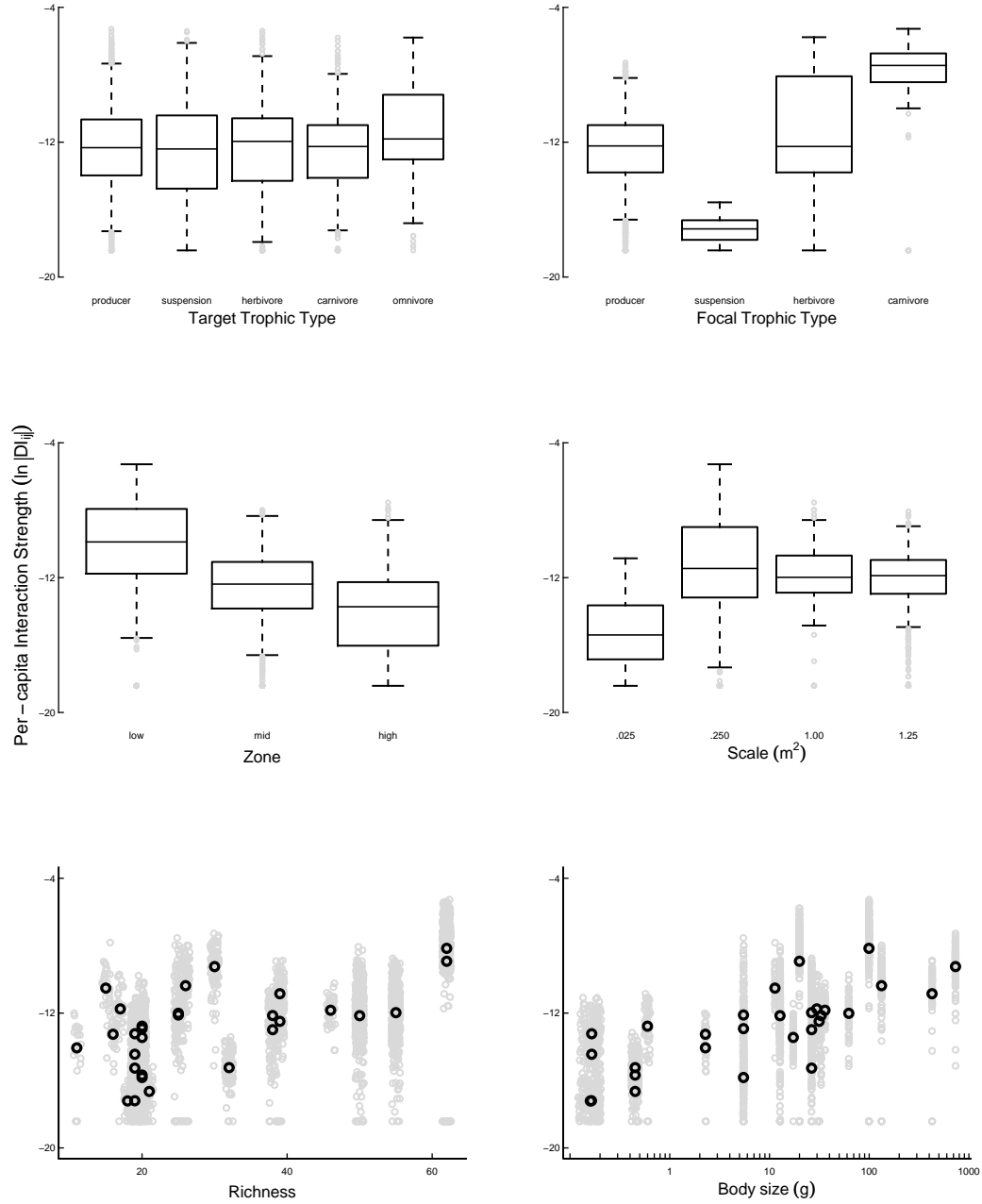
Figure 2.6: Plots showing relationships between predictors and interaction strength. Values presented are arithmetic means of all lower-level data.

	a)			b)		
Factor	Estimate	Std. Error	p	Estimate	Std. Error	p
Intercept	0.189	0.083	0.022	-12.20	0.919	<.001
Time	0.000	0.000	0.984	0.000	0.001	0.945
Target Species Type						
Suspension	0.002	0.155	0.986	-0.490	0.142	0.001
Herbivore	0.152	0.129	0.239	0.396	0.119	0.001
Carnivore	0.250	0.184	0.175	-0.348	0.159	0.036
Omnivore	0.222	0.317	0.485	0.004	0.277	0.943
Zone	-0.152	0.186	0.413	0.223	1.330	0.808
Scale	0.025	0.311	0.935	3.120	2.530	0.160
Richness	0.011	0.012	0.352	-0.009	0.087	0.526
Body Size	-0.001	0.001	0.343	0.012	0.005	0.002
Focal Species Type						
Suspension	-0.617	0.327	0.059	-3.490	2.220	0.012
Herbivore	-0.122	0.252	0.628	-0.419	1.840	0.575
Carnivore	-0.082	0.387	0.832	7.940	3.370	0.018
Target Species Type · Zone						
Suspension · Zone	-0.282	0.363	0.438	-0.261	0.327	0.453
Herbivore · Zone	0.550	0.313	0.079	0.255	0.285	0.313
Carnivore · Zone	0.286	0.404	0.478	-0.232	0.353	0.584
Omnivore · Zone	0.515	0.739	0.486	0.501	0.651	0.413
Target Species Type · Scale						
Suspension · Scale	1.170	0.565	0.038	0.028	0.510	0.987
Herbivore · Scale	0.195	0.482	0.686	0.755	0.441	0.127
Carnivore · Scale	0.241	0.651	0.712	0.808	0.566	0.200
Omnivore · Scale	0.832	1.150	0.470	0.368	0.965	0.774
Target Species Type · Richness						
Suspension · Richness	-0.036	0.022	0.099	-0.006	0.020	0.778
Herbivore · Richness	-0.005	0.019	0.799	0.000	0.018	0.893
Carnivore · Richness	-0.019	0.025	0.450	-0.042	0.022	0.070
Omnivore · Richness	-0.025	0.044	0.569	-0.003	0.038	0.986
Target Species Type · Body Size						
Suspension · Body Size	0.001	0.002	0.445	-0.002	0.002	0.239
Herbivore · Body Size	0.002	0.001	0.219	0.002	0.001	0.172
Carnivore · Body Size	-0.002	0.004	0.539	-0.002	0.003	0.461
Omnivore · Body Size	0.001	0.004	0.763	0.002	0.003	0.576
Target Species Type · Focal Species Type						
Suspension · Suspension	0.311	0.581	0.592	0.468	0.499	0.362
Herbivore · Suspension	-0.245	0.516	0.634	0.194	0.432	0.726
Carnivore · Suspension	-0.517	0.828	0.533	0.287	0.645	0.668
Omnivore · Suspension	-1.060	1.230	0.388	-0.154	1.160	0.871
Suspension · Herbivore	0.580	0.430	0.177	0.102	0.391	0.877
Herbivore · Herbivore	-0.078	0.394	0.844	0.154	0.352	0.791
Carnivore · Herbivore	-0.238	0.559	0.670	1.040	0.480	0.043
Omnivore · Herbivore	0.936	0.968	0.334	1.090	0.787	0.197
Suspension · Carnivore	0.477	0.639	0.455	0.147	0.603	0.840
Herbivore · Carnivore	0.566	0.656	0.389	0.525	0.628	0.451
Carnivore · Carnivore	-0.541	0.838	0.519	1.290	0.747	0.099
Omnivore · Carnivore	0.776	1.150	0.499	0.891	0.996	0.408

Table 2.3: Parameter estimates from the multilevel model testing the effects of factors on the sign (a) and strength (b) of species interactions. Continuous numerical predictors are centered to test differences between average conditions. Target and Focal trophic type are categorical factors and tested using linear contrasts against primary producers. Analysis of variance is used to test for effects of the main factors (Table 2.2).

2.4 Bibliography

Abrams, P.A. 1992. Predators that benefit prey and prey that harm predators: unusual effects of interacting foraging adaptations. American Naturalist 140:573–600.

Agrawal, A.A., D.D. Ackerly, F. Adler, A.E. Arnold, C. Caceres, D.F. Doak, E. Post, P.J. Hudson, J. Maron, K.A. Mooney, M. Power, D. Schemske, J. Stachowicz, S. Strauss, M.G. Turner, and E. Werner. 2007. Filling key gaps in population and community ecology. Frontiers in Ecology and the Environment 5:145–152.

Bascompte, J., C.J. Melian, and E. Sala. 2005. Interaction strength combinations and the overfishing of a marine food web. Proceedings of the National Academy of Sciences of the United States of America 102:5443–5447.

Bender, E.A., T.J. Case, and M.E. Gilpin. 1984. Perturbation experiments in community ecology: theory and practice. Ecology 65:1–13.

Berlow, E.L., J.A. Dunne, N.D. Martinez, P.B. Stark, R.J. Williams, and U. Brose. 2009. Simple prediction of interaction strengths in complex food webs. Proceedings of the National Academy of Sciences of the United States of America 106:187–191.

Berlow, E.L., S.A. Navarrete, C.J. Briggs, M.E. Power, and B.A. Menge. 1999. Quantifying variation in the strengths of species interactions. Ecology 80:2206–2224.

Bertness, M.D. and R. Callaway. 1994. Positive interactions in communities. Trends in Ecology and Evolution 9:191–193.

Bertness, M.D. and G.H. Leonard. 1997. The role of positive interactions in communities: lessons from intertidal habitats. Ecology 78:1976–1989.

Borer, E.T., B.S. Halpern, and E.W. Seabloom. 2006. Asymmetry in community regulation: effects of predators and productivity. Ecology 87:2813–2820.

Brooker, R.W. and T.V. Callaghan. 1998. The balance between positive and negative plant interactions and its relationship to environmental gradients: a model. Oikos 81:196–207.

Brooker, R.W., F.T. Maestre, R.M. Callaway, C.L. Lortie, L.A. Cavieres, G. Kunstler, P. Liancourt, K. Tielborger, J.M.J. Travis, F. Anthelme, C. Armas, L. Coll, E. Corcket, S. Delzon, E. Forey, Z. Kikvidze, J. Olofsson, F. Pugnaire,

C.L. Quiroz, P. Saccone, K. Schiffers, M. Seifan, B. Touzard, and R. Michalet. 2008. Facilitation in plant communities: the past, the present, and the future. Journal of Ecology 96:18–34.

Brown, J.H., J.F. Gillooly, A.P. Allen, V.M. Savage, and G.B. West. 2004. Toward a metabolic theory of ecology. Ecology 85:1771–1789.

Bruno, J.F., J.J. Stachowicz, and M.D. Bertness. 2003. Inclusion of facilitation into ecological theory. Trends in Ecology and Evolution 18:119–125.

Callaway, R.M., R.W. Brooker, P. Choler, Z. Kikvidze, C.J. Lortie, R. Michalet, L. Paolini, F.I. Pugnaire, B. Newingham, E.T. Aschehoug, C. Armas, D. Kikodze, and B.J. Cook. 2002. Positive interactions among alpine plants increase with stress. Nature 417:844–848.

Cohen, J.E., T. Jonsson, and S.R. Carpenter. 2003. Ecological community description using the food web, species abundance, and body size. Proceedings of the National Academy of Sciences of the United States of America 100:1781–1786.

Connell, J.H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. Ecology 42:710–723.

Damuth, J. 1981. Population-density and body size in mammals. Nature 290:699–700.

Damuth, J. 1987. Interspecific allometry of population density in mammals and other animals: the independence of body mass and population energy-use. Biological Journal of the Linnean Society 31:193–246.

Dayton, P. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecological Monographs 41:351–387.

de Ruiter, P.C., A.M. Neutel, and J.C. Moore. 1995. Energetics, patterns of interaction strengths, and stability in real ecosystems. Science 269:1257–1260.

Dodds, W.K. and J.A. Nelson. 2006. Redefining the community: a species-based approach. Oikos 112:464–472.

Duffy, J.E. 2003. Biodiversity loss, trophic skew and ecosystem functioning. Ecology Letters 6:680–687.

Edgar, G.J. and H.R. Burton. 2000. The biogeography of shallow water macrofauna at Heard Island. Papers and Proceedings of the Royal Society of Tasmania 133:23–26.

Emmerson, M.C. and D. Raffaelli. 2004. Predator-prey body size, interaction strength and the stability of a real food web. Journal of Animal Ecology 73:399–409.

Fagan, W.F. and L.E. Hurd. 1994. Hatch density variation of a generalist arthropod predator: population consequences and community impact. Ecology 75:2022–2032.

Farrell, T.M. 1991. Models and mechanisms of succession: an example from a rocky intertidal community. Ecological Monographs 61:95–113.

Foster, B.L. 2002. Competition, facilitation, and the distribution of *Schizachyrium scoparium* along a topographic-productivity gradient. Ecoscience 9:355–363.

Gotelli, N.J. and R.K. Colwell. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4:379–391.

Grace, J.B. and R.G. Wetzel. 1981. Habitat partitioning and competitive displacement in cattails (Typha): experimental field studies. American Naturalist 118:463–474.

Greenlee, J.T. and R.M. Callaway. 1996. Abiotic stress and the relative importance of interference and facilitation in montane bunchgrass communities in Western Montana. American Naturalist 148:386–396.

Harley, C.D.G. 2006. Effects of physical ecosystem engineering and herbivory on intertidal community structure. Marine Ecology Progress Series 317:29–39.

Heltshe, J. and N. Forrester. 1983. Estimation species richness using the jackknife procedure. Biometrics 39:1–11.

Jones, C.G., J.H. Lawton, and M. Shachak. 1997. Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78:1946–1957.

Keitt, T.H. 1997. Stability and complexity on a lattice: coexistence of species in an individual-based food web model. Ecological Modelling 102:243–258.

Kokkoris, G.D., V.A.A. Jansen, M. Loreau, and A.Y. Troumbis. 2002. Variability in interaction strength and implications for biodiversity. Journal of Animal Ecology 71:362–371.

Kreft, I. and J. de Leeuw. 1998. Introducing Multilevel Modeling. Sage Publications, Thousand Oaks.

Levin, P.S., J.A. Coyer, R. Petrik, and T.P. Good. 2002. Community-wide effects of nonindigenous species on temperate rocky reefs. Ecology 83:3182–3193.

Lilley, S.A. and D.R. Schiel. 2006. Community effects following the deletion of a habitat-forming alga from rocky marine shores. Oecologia 148:672–681.

Lyons, K.G. and M.W. Schwartz. 2001. Rare species loss alters ecosystem function-invasion resistance. Ecology Letters 4:358–365.

Margalef, R. 1968. Perspectives in Ecological Theory. University of Chicago Press, Chicago.

May, R.M. 1973. Stability and Complexity in Model Ecosystems. Princeton University Press, Princeton.

McCann, K., A. Hastings, and G.R. Huxel. 1998. Weak trophic interactions and the balance of nature. Nature 395:794–798.

McCann, K.S., J.B. Rasmussen, and J. Umbanhowar. 2005. The dynamics of spatially coupled food webs. Ecology Letters 8:513–523.

Menge, B. 1995. Indirect effects in marine rocky intertidal interaction webs: patterns and importance. Ecological Monographs 65:21–74.

Menge, B.A. 1997. Detection of direct versus indirect effects: were experiments long enough? American Naturalist 149:801–823.

Miriti, M.N. 2006. Ontogenetic shift from facilitation to competition in a desert shrub. Journal of Ecology 94:973–979.

Moore, J.C., P.C. de Ruiter, H.W. Hunt, D.C. Coleman, and D.W. Freckman. 1996. Microcosms and soil ecology: critical linkages between field studies and modeling food webs. Ecology 77:694–705.

Neutel, A.M., J.A.P. Heesterbeek, and P.C. de Ruiter. 2002. Stability in real food webs: weak links in long loops. Science 296:1120–1123.

Osenberg, C.W., O. Sarnelle, and S.D. Cooper. 1997. Effect size in ecological experiments: the application of biological models in meta-analysis. American Naturalist 150:798–812.

Paine, R.T. 1992. Food-web analysis through field measurement of per-capita interaction strength. Nature 355:73–75.

Palmer, M.W. and P.S. White. 1994. Scale dependence and the species-area relationship. American Naturalist 144:717–740.

Pennings, S.C., E.R. Selig, L.T. Houser, and M.D. Bertness. 2003. Geographic variation in positive and negative interactions among salt marsh plants. Ecology 84:1527–1538.

Pinheiro, J.C. and D.M. Bates. 2000. Mixed-Effects Models in S and S-PLUS. Springer, New York.

R Development Core Team. 2008. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Raffaelli, D. and S. Hall. 1996. Assessing the relative importance of trophic links in food webs. Pages 185–191 in G.A. Polis and K.O. Winemiller, editors. Food Webs: Integration of Patterns and Dynamics. Chapman and Hall, New York.

Robles, C., R. Sherwood-Stephens, and M. Alvarado. 1995. Responses of a key intertidal predator to varying recruitment of its prey. Ecology 76:565–579.

Roxburgh, S.H. and J.B. Wilson. 2000. Stability and coexistence in a lawn community: mathematical prediction of stability using a community matrix with parameters derived from competition experiments. Oikos 88:395–408.

Santelices, B., J.C. Castilla, J. Cancino, and P. Schmiede. 1980. Comparative ecology of *Lessonia nigrescens* and *Durvillaea antarctica* (Phaeophyta) in Central Chile. Marine Biology 59:119–132.

Schmitz, O.J. 1997. Press perturbations and the predictability of ecological interactions in a food web. Ecology 78:55–69.

Shurin, J.B., E.T. Borer, E.W. Seabloom, K. Anderson, C.A. Blanchette, B. Broitman, S.D. Cooper, and B.S. Halpern. 2002. A cross-ecosystem comparison of the strength of trophic cascades. Ecology Letters 5:785–791.

Soule, M.E., J.A. Estes, B. Miller, and D.L. Honnold. 2005. Strongly interacting species: conservation policy, management, and ethics. Bioscience 55:168–176.

Southwood, T.R.E. 1961. The number of species of insect associated with various trees. Journal of Animal Ecology 30:1–8.

Stachowicz, J.J. 2001. Mutualism, facilitation, and the structure of ecological communities. Bioscience 51:235–246.

Tirado, R. and F.I. Pugnaire. 2005. Community structure and positive interactions in constraining environments. Oikos 111:437–444.

Wilson, W.G., P. Lundberg, D.P. Vazquez, J.B. Shurin, M.D. Smith, W. Langford, K.L. Gross, and G.G. Mittelbach. 2003. Biodiversity and species interactions:

extending Lotka-Volterra community theory. Ecology Letters 6:944–952.

Woodward, G., B. Ebenman, M. Ernmerson, J.M. Montoya, J.M. Olesen, A. Valido, and P.H. Warren. 2005. Body size in ecological networks. Trends in Ecology and Evolution 20:402–409.

Wootton, J.T. 1997. Estimates and tests of per capita interaction strength: diet, abundance, and impact of intertidally foraging birds. Ecological Monographs 67:45–64.

Wootton, J.T. and M. Emmerson. 2005. Measurement of interaction strength in nature. Annual Review of Ecology Evolution and Systematics 36:419–444.

Yodzis, P. 1981. The stability of real ecosystems. Nature 289:674–676.

Yodzis, P. 1988. The indeterminacy of ecological interactions as perceived through perturbation experiments. Ecology 69:508–515.

Zar, J.H. 1984. Biostatistical Analysis. Prentice Hall, Englewood Cliffs.

Chapter 3

The prevalence of nonlinear species interactions and their performance in models of intertidal community dynamics [§]

3.1 Introduction

Models of community dynamics provide predictions of how populations of co-occurring species change over time. The basic building blocks of these models are estimates of species interaction strengths: the per-capita effect of a focal species on the growth of a target population (Laska and Wootton 1998). Most models make a number of simplifying assumptions about the nature of interactions, foremost of which is that a focal species' impact is linear across gradients in its density. This is a contentious assumption however, and numerous empirical examples of nonlinear interactions have been shown (Abrams 2001, Jeschke et al. 2004). Consumers that change their feeding rate as a function of prey density (their functional response) are one common type of nonlinearity. Ruesink (1998) observed, for example, that the per-capita effect of the hermit crab *Pagurus* on its diatom resource increases nonlinearly after surpassing a threshold density of crabs. Similarly, the abundance of phytoplankton is not linearly related to the density of its predator, *Daphnia* (Sarnelle 2003). Given the prevalence of nonlinear species interactions in nature, models using linear interaction coefficients should have limited success predicting community dynamics.

   Models incorporating nonlinear species interactions have limitations however.

Nonlinearities can make models sensitive to small changes in parameter values, which restricts their usefulness in communities with more than a few species (Abrams 2001). Nonlinear interactions can also theoretically produce complex and unpredictable chaotic dynamics, even in simple systems (May 1974, 1976, Ellner and Turchin 1995). One additional limitation of the nonlinear approach is that we lack knowledge about what the functional form ought to be. Numerous studies have used simple linear interaction coefficients to successfully predict the outcomes of experimental perturbations (Pfister 1995, Schmitz 1997, Wootton 1997). Additional studies have found that linear interaction strengths actually perform better than nonlinear estimates even when the form of the nonlinear function is known (Ives 1995, Ives and Jansen 1998, Sala and Graham 2002, Novak 2008). The importance of considering nonlinear species interactions therefore remains questionable.

Why, despite the prevalence of nonlinear species interactions in nature, are linear estimates of interaction strength so effective? There are a number of potential explanations. First, nonlinearities may exist, but will be inconsequential if they lie outside the range of a species' natural focal density (Abrams 1980). In other words, an interaction may be approximately linear around a species' average abundance, even though it has the potential for nonlinear effects at higher or lower levels. Alternatively, it is possible that nonlinear responses of many taxa simply sum together to give overall linear pairwise interactions between species, but as Abrams (1980, 2001) rightfully points out, this is unlikely. It is perhaps more likely that nonlinear interactions are obscured by stochastic effects of the environment (Ives 1995) or indirect biotic effects (Peacor and Werner 1997). A final possibility is that the added precision of the nonlinear estimate is outweighed by the error introduced by its extra model parameters (Ludwig and Walters 1985, Wootton 2002).

The goal of this study is to test the prevalence and performance of linear and nonlinear interaction strength estimates in rocky intertidal communities. In the first set of experiments, we create gradients of focal species abundance to test the hypothesis that interactions are linear across focal species' densities. Then, a second, independent manipulative experiment is used to test the hypothesis that linear interaction strength estimates can predict the responses of species to a perturbation. We find that interactions are typically linear across focal species densities, and that predictions regarding the outcome of short-term perturbations are not significantly

improved by using nonlinear estimates.

3.2   Methods

Interaction coefficient estimates

The experiments were done at Prasiola Point in Barkley Sound, British Columbia (Figure 1.1, 1.2). The high intertidal community of this rocky headland is characterized by algae such as *Fucus gardneri* and *Mastocarpus papillatus* (and its alternate crustose life-history phase '*Petrocelis franciscana*'), barnacles (*Balanus glandula* and *Chthamalus dalli*), mussels (*Mytilus californianus*), limpets (*Lottia digitalis*, *L. paradigitalis*, and *L. pelta*), snails (*Littorina scutulata* [may also include rare *L. plena* or *L. subrotundata*] and *L. sitkana*) and whelks (*Nucella spp.*). This site is representative of the high intertidal of the region (Schoch et al. 2006). For further descriptions of the study site see Kim and DeWreede (1996) and Scrosati (1998). Three abundant species, *B. glandula*, *F. gardneri*, and *L. digitalis* (hereafter referred to by genera), representing different trophic levels, were chosen as focal taxa and press manipulations were used to alter their abundances in the field (Bender et al. 1984). Initial average densities of the focal species, before applying the press treatments, were 257, 51, and 11 individuals $\cdot$ 0.025 m^{-2}, respectively. For each focal species, three randomized blocks of five 0.025 m^2 plots were arrayed on a semi-protected rock face. In the *Balanus* experiment, plots were randomly assigned to one of five density levels: ambient, 25, 75, 130, or 180 individuals per plot. *Fucus* was pressed to 1, 10, 20, or 30 individuals per plot or not manipulated. *Lottia* plots were pressed to 1, 5, 11, or 17 individuals per plot in addition to an untreated control. Numerical densities of *Balanus* and *Fucus* were strongly correlated with their percent coverage in study plots (S. Wood *unpublished data*).

The *Fucus* and *Balanus* experiments were initiated in October 2005 and the *Lottia* manipulations began in May 2006. All three experiments ran for two years. To maintain focal densities, *Balanus* and *Fucus* presses were checked monthly and *Lottia* presses were serviced semiweekly. Focal taxa were added or removed manually. The abundances of the focal and target taxa in the study plots were monitored after 3, 6, 12, 18, and 24 months. Sessile target population abundances were es-

timated as the percent cover of a quadrat. Numeric abundances of mobile target species were enumerated. The number of individuals of *Balanus*, *Fucus*, and *Lottia* was also counted in each plot to use in calculating their per-capita effects. Later, abundances of all target taxa were converted into biomass using an abundance:mass relationship for each species (Appendix B). Throughout the study, biomass and abundance were both quantified in supplementary plots at the study site. Total abundance was then regressed against biomass to estimate biomass of the target populations in each plot (cf. Schmitz 1997).

To estimate interaction strength, we employ the discrete-time version of the generalized Lotka-Volterra multispecies equation (Laska and Wootton 1998). In this formula,

$$N_{i,p} = N_{i,p-1} \cdot e^{\left\{ r_i + \left(\sum_{j=1}^{s} \alpha_{ij} \cdot N_{j,p-1} \right) \right\} \Delta t} \tag{3.1}$$

N_i is the biomass of target species i, and N_j represents the numerical abundance of the focal species j, during monitoring period p. Elapsed time in months is denoted by Δt. The intrinsic rate of growth is r_i, and α_{ij} gives the per-capita interaction coefficient. This equation can be rearranged into a linear regression format (Equation 3.2) where r_i is the y-intercept and α_{ij}, the interaction coefficient, is the slope of the regression, which is linear across all focal densities of N_j. The response is the log ratio of the change in target abundance over time.

$$\frac{ln\left(\frac{N_{i,p}}{N_{i,p-1}} \right)}{\Delta t} = \begin{cases} \sum_{j=1}^{s} \alpha \cdot N_{j,p-1} + r_i & \text{linear} \\ \sum_{j=1}^{s} \beta_{ij1} \cdot N_{j,p-1}^2 + \sum_{j=1}^{s} \beta_{ij2} \cdot N_{j,p-1} + r_i & \text{quadratic} \\ \sum_{j=1}^{s} \frac{V_{max} \cdot N_{j,p-1}}{K_m + N_{j,p-1}} + r_i & \text{Michaelis-Menten} \\ g(N_{j,p-1}) & \text{loess} \end{cases} \tag{3.2}$$

We also test three nonlinear relationships between the response and the interaction coefficient: a quadratic function, saturating Michaelis-Menten model, and local polynomial regression (LOESS) using the same notation as before, with V_{max} giving

the maximum rate of change in target abundance, K_m representing the half saturation constant, and $g(N_{j,p-1})$ denoting a smooth function fit by locally weighted regression (Equation 3.2). The quadratic equation allows us to detect weak nonlinearities, or 'dome-shaped' responses (Jeschke et al. 2004). The Michaelis-Menten is a saturating function that mimics the popular Type II functional response proposed by Holling (1959), but can become approximately linear when V_{max} approaches infinity. These nonlinear responses are observed most frequently, although a variety of more complex equations, such as the sigmoidal Type III response (Holling 1959), could also be fit (Skalski and Gilliam 2001). However, since there is no way to know which model is most appropriate, we compare the linear, quadratic, and Michaelis-Menten models with the more flexible LOESS regression. Regressions were fit for target species that occurred in more than seven of the study plots in a given monitoring period. Parameters were estimated using least-squares regression by the lm (for lines), nls (for quadratic and Michaelis-Menten models), and loess (for LOESS models) functions for R (R Development Core Team 2008). The best form of Equation 3.2 was chosen using Akaike weights of Akaike's information criterion (AIC$_C$; Burnham and Anderson 2002).

Testing model predictions

In February 2008, a second press experiment was done at the same site to assess the capacity of the linear and nonlinear interaction coefficients, measured above, to predict population dynamics. Plots were randomly assigned a treatment level (*Balanus*, *Fucus*, *Lottia*, or Control) in which the focal taxon was pressed to 65% of its natural density in four replicate 0.025 m^2 plots. Mass abundances of target taxa were measured, using the same protocol as above, before initiating the press treatments and again after three months. Then, the linear, quadratic, and Michaelis-Menten parameters estimated in the first experiment at month three were used to predict the experimental outcomes in this second experiment, given each plot's initial biomass. The different forms of Equation 3.2 (excluding the LOESS model) were used to predict the final abundance ($N_{i,p}$) and percent change from initial abundance ($N_{i,p-1}$) for each plot. The mean and standard deviation of the estimates for all plots was computed to compare to the actual outcome.

Target Species	Balanus				Fucus				Lottia			
	Line	Quad	M-M	LOESS	Line	Quad	M-M	LOESS	Line	Quad	M-M	LOESS
Balanus glandula	·	·	·	·	**0.66**	0.16	0.07	0.11	**0.61**	0.17	0.09	0.13
Callithamnion pikeanum	·	·	·	·	**0.43**	0.17	0.03	0.37	·	·	·	·
Chthamalus dalli	**0.52**	0.23	0.09	0.15	**0.59**	0.15	0.04	0.22	**0.46**	0.22	0.08	0.16
Cladophora columbiana	·	·	·	·	**0.48**	0.09	0.05	0.34	·	·	·	·
Endocladia muricata	**0.72**	0.12	0.06	0.10	**0.72**	0.09	0.05	·	·	·	·	·
Fucus gardneri	**0.57**	0.16	0.10	0.17	·	·	·	·	**0.51**	0.22	0.06	0.20
Littorina scutulata	**0.60**	0.18	0.08	0.13	**0.51**	0.23	0.04	0.22	**0.56**	0.15	0.13	0.16
Littorina sitkana	**0.41**	0.16	0.03	0.36	**0.44**	0.06	0.03	0.22	**0.60**	0.15	0.10	0.13
Lottia digitalis	0.33	0.19	0.06	**0.41**	**0.44**	0.25	0.05	0.26	·	·	·	·
Lottia paradigitalis	·	·	·	·	·	·	·	·	**0.49**	0.07	0.04	0.07
Lottia pelta	**0.38**	0.06	0.02	0.04	·	·	·	·	**0.73**	0.11	0.09	0.08
Mastocarpus papillatus	**0.68**	0.10	0.06	0.15	**0.59**	0.16	0.08	0.16	**0.54**	0.22	0.06	0.18
Mytilus californianus	**0.42**	0.19	0.04	0.33	**0.56**	0.15	0.09	0.20	**0.55**	0.08	0.04	0.33
Pelvetiopsis limitata	**0.80**	0.08	0.07	0.05	**0.73**	0.12	0.08	0.08	**0.60**	0.17	0.10	0.12
'*Petrocelis franciscana*'	**0.59**	0.19	0.10	0.12	**0.58**	0.15	0.10	0.09	**0.41**	0.17	0.10	0.29
Scytosiphon dotyi	·	·	·	·	**0.45**	0.10	0.29	0.16	·	·	·	·
Mean	**0.54**	0.15	0.07	0.18	**0.55**	0.14	0.08	0.20	**0.55**	0.16	0.08	0.17

Table 3.1: Akaike weights calculated from Akaike information criterion (AIC_C) values of the linear and nonlinear models for each pairwise interaction, averaged across all times. The quadratic model is abbreviated as Quad, Michaelis-Menten as M-M, and the local polynomial regression as LOESS. The best fit models, with the highest Akaike weights, are in bold type.

Focal Species	Target Species	Linear		Quadratic			Michaelis-Menten		
		α	r_i	β_{ij1}	β_{ij2}	r_i	V_{max}	K_m	r_i
Balanus glandula	*Chthamalus dalli*	0.0001	0.0082	-0.00001	0.0037	-0.2151	0.0965	16.46	-0.044
	Endocladia muricata	-0.0008	-0.0386	-0.00001	0.0007	-0.1166	-2408	$4.676 \cdot 10^6$	-0.1095
	Fucus gardneri	0.0007	-0.0022	-0.00001	0.0050	-0.2678	0.6134	9.533	-0.4449
	Littorina scutulata	0.0011	-0.3994	-0.00001	0.0047	-0.6239	0.6711	74.54	-0.6612
	Littorina sitkana	0.0017	-0.2479	-0.00001	0.0050	-0.4562	1.197	347.7	-0.3409
	Lottia digitalis	0.0016	-0.3303	-0.00002	0.0092	-0.8045	3.456	5.240	-3.378
	Lottia pelta	-0.0006	0.0815	-0.00001	0.0028	-0.1356	-12.56	$1.011 \cdot 10^5$	-0.0076
	Mastocarpus papillatus	0.0000	-0.0016	0.00000	-0.0010	0.0649	-1.724	0.8517	1.728
	Mytilus californianus	-0.0002	-0.0760	-0.00002	0.0054	-0.4440	-3.535	$1.639 \cdot 10^4$	-0.1270
	Pelvetiopsis limitata	0.0000	0.0235	-0.00002	0.0041	-0.1889	0.0208	53.24	0.0186
	'Petrocelis franciscana'	-0.0014	0.4153	0.00000	-0.0026	0.4903	-1.149	26.52	1.150
Fucus gardneri	*Balanus glandula*	0.0012	-0.0578	-0.00005	0.0030	-0.0729	-95.52	$2.534 \cdot 10^6$	-0.0695
	Chthamalus dalli	0.0110	-0.1773	0.00046	-0.0109	0.0461	1042	$5.042 \cdot 10^5$	0.0085
	Cladophora columbiana	-0.0023	-0.0543	0.00063	-0.0270	0.1403	-0.2995	4.120	0.1355
	Littorina scutulata	-0.0110	-0.5050	-0.00089	0.0234	-0.7966	$-6.188 \cdot 10^{10}$	$2.042 \cdot 10^{13}$	-0.8131
	Littorina sitkana	0.0025	-0.1679	0.00011	-0.0018	-0.1329	$2.775 \cdot 10^6$	$5.211 \cdot 10^8$	-0.1390
	Lottia digitalis	-0.0014	0.1775	0.00194	-0.0769	0.8053	3.609	2013	0.2296
	Mastocarpus papillatus	-0.0087	0.2056	-0.00065	0.0075	0.1265	-414.9	$-3.259 \cdot 10^6$	0.0724
	Mytilus californianus	0.0036	-0.0466	-0.00124	0.0514	-0.4469	0.5959	0.1960	-0.5766
	'Petrocelis franciscana'	-0.0027	0.0552	0.00024	-0.0119	0.1331	$1.722 \cdot 10^{10}$	$9.900 \cdot 10^{12}$	0.1153
Lottia digitalis	*Balanus glandula*	0.0055	-0.0791	0.00046	-0.0054	-0.0301	$1.378 \cdot 10^{11}$	$2.631 \cdot 10^{13}$	-0.0318
	Chthamalus dalli	0.0079	-0.1127	0.00275	-0.0568	0.1800	17.00	$1.923 \cdot 10^4$	-0.0225
	Fucus gardneri	-0.0080	-0.2907	0.00221	-0.0600	-0.0556	-2.144	0.3074	1.517
	Littorina scutulata	-0.0266	0.5014	-0.00077	-0.0085	0.4198	$-1.209 \cdot 10^{12}$	$6.072 \cdot 10^{13}$	0.4295
	Littorina sitkana	0.0026	0.2549	-0.00264	0.0649	-0.0266	1.387	0.3452	-1.023
	Mastocarpus papillatus	-0.0022	0.0183	0.00253	-0.0631	0.2685	-0.0628	0.7400	0.0572
	Mytilus californianus	0.0095	-0.2120	0.00021	0.0043	-0.1873	$1.871 \cdot 10^4$	$1.521 \cdot 10^8$	-0.1078
	Pelvetiopsis limitata	-0.0187	0.2358	0.00238	-0.0772	0.5108	-0.7672	0.1525	0.8556
	'Petrocelis franciscana'	-0.0056	-0.1515	-0.00079	0.0131	-0.2359	-157.0	$3.259 \cdot 10^4$	-0.1690

Table 3.2: Parameters estimated by the linear, quadratic, and Michaelis-Menten equations (Equation 3.2) explaining the effect of the focal species on the target species after three months. These parameters were used to predict the final and percent change in abundance of the target populations of the second experiment, the results of which are shown in Figure 3.2.

3.3 Results

Interaction coefficient estimates

During the study we observed 34 species in the experimental plots. Interaction coefficients were computed for 16 target species present in more than seven plots during at least one monitoring period, which amounted to 35 pairwise interaction coefficients for the three focal species. One coefficient was best explained by the LOESS model, while the remainder were best described by a linear equation; none of the relationships were fit best by the quadratic or Michaelis-Menten functions (Table 3.1). On average, the linear function fit 3.7, 7.4, and 3.0 times better than the quadratic, Michaelis-Menten, and LOESS models respectively. As an example, Figure 3.1 shows the effects of the three focal species on *L. scutulata* after three months.

Testing model predictions

In the second experiment, we were able to test the predicted interactions between the three focal taxa and eight target taxa that were present in at least three replicate plots, during the three month trial (Table 3.2, Figure 3.2). In 16 of the 21 pairwise effects, the linear interaction coefficient predicted the mean final abundance of the target organism across all plots within one SD. The quadratic and Michaelis-Menten estimates accurately predicted 17 and 18 outcomes respectively, but in many cases with less precision (Figure 3.2a–c). The average percent change in a target species' abundance, which accounts for differences in its initial abundance, was often not within the range predicted by either the linear or nonlinear interaction coefficients (Figure 3.2d–f). The direction of the change in abundance was generally predicted by the linear estimates, with five notable exceptions (*Fucus* on *L. scutulata*, *Balanus* on *L. scutulata*, *Balanus* on *L. digitalis*, *Balanus* on *M. californianus*, and *Lottia* on *F. gardneri*). Predictions using linear interaction coefficients were best for sessile species, and poorest for the mobile species *L. scutulata* and *L. digitalis*, which showed greater changes in abundance, but were low ranked species in terms of total biomass.
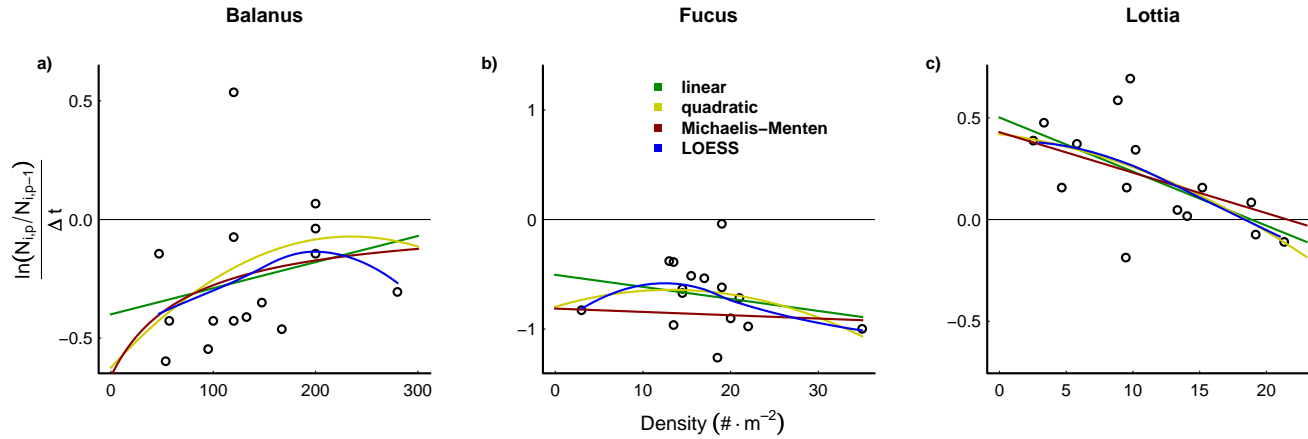
Figure 3.1: The response of one target population (*L. scutulata*) across density gradients of the three manipulated focal taxa (*B. glandula*, *F. gardneri*, and *L. digitalis*). Each point represents the log ratio of the change in abundance of the target population over three months. The lines depict the fit of the linear (green), quadratic (yellow), Michaelis-Menten (red), and local polynomial regression (LOESS; blue) equations. In all cases, the nonlinear fits are only weakly curvilinear.

3.4 Discussion

Pairwise interactions between species in intertidal communities can be approximated using per-capita interaction coefficients that are linear functions of focal species density. This simplifying assumption allows interaction coefficients to be measured more easily in the field, because experiments at one focal density can be used to infer species' per-capita effects at other densities. This result is also encouraging because it suggests that simplified models assuming linear interaction coefficients can make useful predictions. A number of studies (Pfister 1995, Schmitz 1997, Wootton 1997, Berlow 1999, Emmerson and Raffaelli 2004, Novak 2008) have reached similar conclusions, despite the evidence that direct nonlinear effects are common in nature (Ruesink 1998, Abrams 2001, Sarnelle 2003, Jeschke et al. 2004). Here we explore this discrepancy and discuss why linear coefficients often can be used to predict community dynamics.

We find that interaction strength, measured as the response of a target species to the press treatment, is highly variable (Figure 3.1), as observed in other empirical studies (Paine 1992, Raffaelli and Hall 1996). This variation in interaction strength between plots is due in large part to environmental influences such as temperature (Chapter 4) or physical disturbances including drifting logs and large waves (Dayton 1971). This variability makes it difficult to distinguish linear from nonlinear patterns. It should also be noted that the AIC_c method we use to select models favors the simpler linear form (Bolker 2008). However, even if there are undetected nonlinearities in the relationships, they must be slightly curvilinear and thus offer little improvement over the linear fits (Figure 3.1). A similar conclusion was reached by Sala and Graham (2002) who found that the effects of marine herbivores on their prey, *Macrocystis*, were only marginally nonlinear and thus the linear forms served as reasonable estimates of consumption.

The prevalence of weak species interactions, which are often more variable in space and time than strong links (Berlow 1999), may also reduce the potential to detect nonlinearities. Weak interactions may play an important stabilizing role in communities by dampening the impact of strong interactions among populations (Yodzis 1981, McCann et al. 1998). Studies have shown that interactions between species in the intertidal (Paine 1992, Raffaelli and Hall 1996, Wootton 1997, Chap-

ter 2) and other systems (Fagan and Hurd 1994) are disproportionately weak, with only a few strong effects. Therefore, regardless of their functional form, most species interactions have limited direct effects on other populations, especially relative to the environmental variation between plots. Consequently, if our goal is to identify nonlinear interactions between species, we should focus on the few strong interactors, by assessing their impacts across a range of densities. Confirming that their effects are linear, as we have done here, should indicate that the majority of species in a community meet this simplifying assumption.
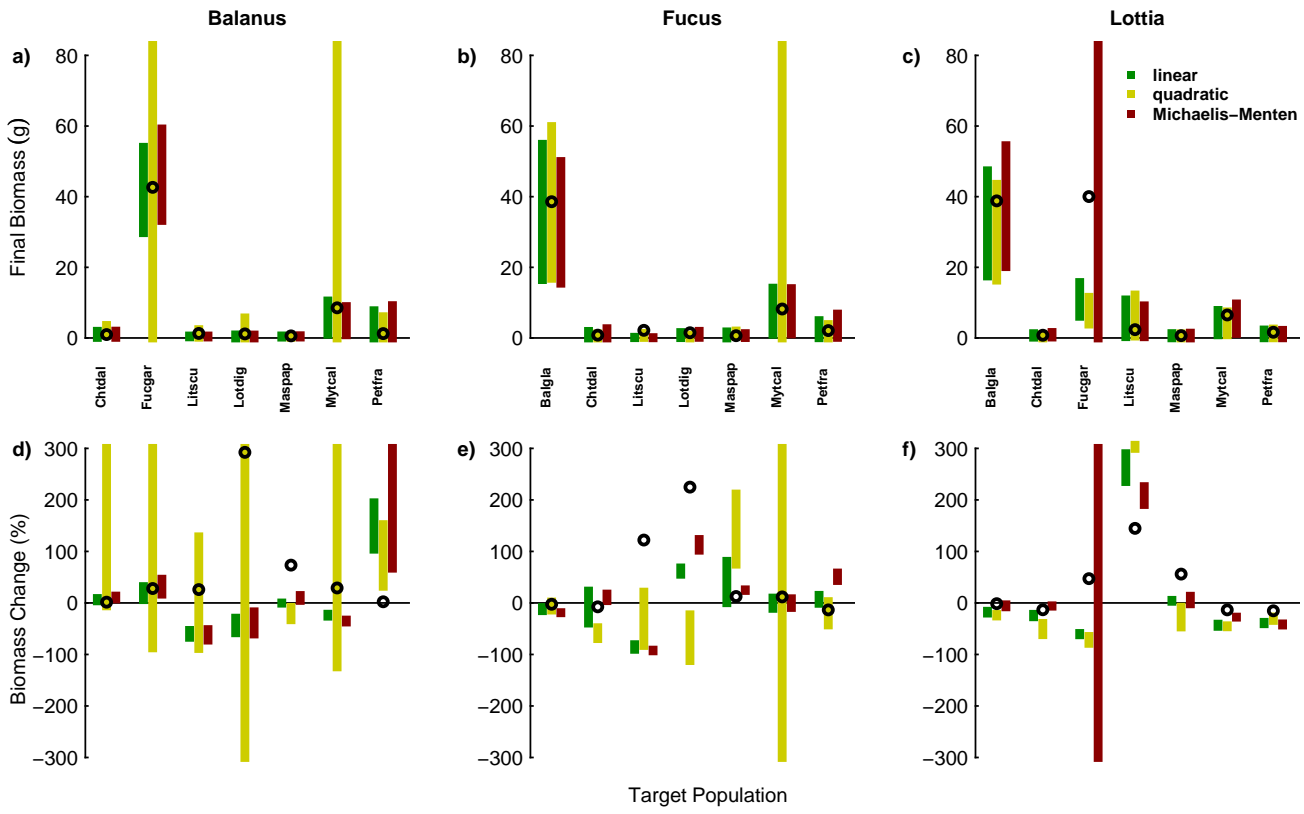
Another possibility is that nonlinear effects were masked by indirect interactions. Since we are measuring the sum of both interaction types, indirect modifications of the environment (Crowder and Cooper 1982, Gilinsky 1984) or the traits of the interacting species (Werner 1992, Peacor and Werner 1997) may have obscured nonlinearities in the direct effects. In temporary ponds in Michigan, for example, the green frog *Rana clamitans* has a nonlinear impact on its vegetative prey, mainly the pondweed *Potamogeton crispus* (Werner 1994). However, in the non-lethal presence of the predatory dragonfly *Anax junius*, frogs reduce their foraging activity (Werner and Anholt 1996). As a result of this behavioral modification, the effect of *R. clamitans* on pondweed is diminished to the point where the interaction is weak and the nonlinearity is undetectable and less consequential. A second possibility is that indirect interactions conceal nonlinearities in direct effects by producing complex and unpredictable dynamics that manifest themselves as increased variability in a target organism's response to the focal species (Yodzis 1988, Berlow 1999). For example, chains of nonlinear indirect effects can result in time lags, cycles, or theoretically

Figure 3.2 *(preceding page)*: Predictions of the final (a–c) and percent change in abundance (d–f) of the target populations using linear (green) and nonlinear (yellow and red) interaction coefficients. Coefficients were estimated in experiment one and used to predict the outcome of a second experiment at the same site. The circle indicates the average observed response of all manipulated plots. The bars show the range (mean ± 1 SD) of predictions made for all plots, given the initial biomass of the target organisms. Abbreviated species names are *Balanus glandula* (Balgla), *Chthamalus dalli* (Chtdal), *Fucus gardneri* (Fucgar), *Littorina scutulata* (Litscu), *Lottia digitalis* (Lotdig), *Mastocarpus papillatus* (Maspap), *Mytilus californianus* (Mytcal), and '*Petrocelis franciscana*' (Petfra).

even chaos (May 1976, Hastings and Powell 1991, Turchin and Taylor 1992). If these sources of variation are greater than the signal produced by the species interactions, the resulting patterns may be too convoluted to be fit by simple nonlinear functions such as the quadratic or Michaelis-Menten used here.

It is possible that extreme nonlinearities or thresholds were not detected because they lie outside the range of focal densities tested for this experiment (Abrams 1980, Jaschke et al. 2004, Novak 2008). In such cases, an unusually large deviation in one species' abundance, due to high recruitment for example, might have unpredictable effects. To address this possibility, our press treatments spanned the widest possible range of focal species abundance. In the *Balanus* and *Fucus* presses, densities ranged from just a few individuals up to the highest abundances observed in the field (12,000 m^{-2} and 2,800 m^{-2} respectively). In the *Lottia* experiment, individuals were added to some treatments to create abundances (680 m^{-2}) higher than those naturally found at the study site, yet we still did not observe strong nonlinearities. So although we cannot rule out the possibility of nonlinear interactions under more extreme conditions, linear approximations describe the interactions and predict the outcomes of manipulations at our study site.

We conclude from our study that linear interaction coefficients are often as effective at predicting short-term dynamics as their nonlinear counterparts. The linear estimates from the first experiment accurately predicted the mean final biomass ($\pm$ 1 SD) of 76% of the target species in the second press experiment. The nonlinear estimates performed slightly better, but with less precision (Figure 3.2a–c). The percent change in abundance was less predictable, with some estimates off by three orders of magnitude, especially for the mobile grazer *L. digitalis*. This discrepancy was most likely due to the seasons when the experiments were conducted and whether they overlapped with the period of high recruitment. *L. digitalis* reproduces in winter and new individuals appear in early spring (Frank 1965). The initial experiments that we used to estimate the interaction coefficients were done before peak recruitment (October–December), while the second set of experiments we used to test the model predictions spanned the recruitment window (February–April). Thus, the unpredicted increase in *L. digitalis* biomass (Figure 3.2d–e) is indicative of high recruitment and not necessarily the product of an unexpected biotic interaction. This species has a low mass abundance and therefore even the large percent

change amounts to a small difference in final biomass. Nonetheless, these results demonstrate that interactions can vary substantially over time, and illustrate that there are limitations to the applicability of this short-term experimental approach (Chapter 2).

Although the target populations exhibited a high degree of variation in their responses to the focal species, none of the patterns were distinctly nonlinear. This suggests that the variation arose primarily out of extrinsic processes such as environmental stochasticity, that are consistent across focal densities. We expect that experiments in more controlled environments such as mesocosms (e.g. Sarnelle 2003) will be more likely to observe nonlinear interactions between species. However, the added precision may be offset by a loss of accuracy in terms of making relevant predictions for real ecosystems. Similarly, studies that control species presence and absence, and thereby reduce the potential for indirect effects, or reduce species pools to just a few strong interactors will also be more powerful for detecting nonlinearities. However, our results demonstrate that interactions between most species are weak, nonlinearities are often subtle, and linear interaction strength estimates can serve as adequate, and more experimentally tractable, approximations.

3.5 Bibliography

Abrams, P. 1980. Are competition coefficients constant? Inductive versus deductive approaches. American Naturalist 116:730–735.

Abrams, P.A. 2001. Describing and quantifying interspecific interactions: a commentary on recent approaches. Oikos 94:209–218.

Bender, E.A., T.J. Case, and M.E. Gilpin. 1984. Perturbation experiments in community ecology: theory and practice. Ecology 65:1–13.

Berlow, E.L. 1999. Strong effects of weak interactions in ecological communities. Nature 398:330–334.

Bolker, B.M. 2008. Ecological Models and Data in R. Princeton University Press, Princeton.

Burnham, K.P. and D.R. Anderson. 2002. Model Selection and Multimodel Inference. Springer, New York.

Crowder, L.B. and W.E. Cooper. 1982. Habitat structural complexity and the interaction between bluegills and their prey. Ecology 63:1802–1813.

Ellner, S. and P. Turchin. 1995. Chaos in a noisy world: new methods and evidence from time-series analysis. American Naturalist 145:343–375.

Emmerson, M.C. and D. Raffaelli. 2004. Predator-prey body size, interaction strength and the stability of a real food web. Journal of Animal Ecology 73:399–409.

Fagan, W.F. and L.E. Hurd. 1994. Hatch density variation of a generalist arthropod predator: population consequences and community impact. Ecology 75:2022–2032.

Frank, P.W. 1965. The biodemography of an intertidal snail population. Ecology 46:831–844.

Gilinsky, E. 1984. The role of fish predation and spatial heterogeneity in determining benthic community structure. Ecology 65:455–468.

Hastings, A. and T. Powell. 1991. Chaos in a three-species food chain. Ecology 72:896–903.

Holling, C.S. 1959. Some characteristics of simple types of predation and parasitism. Canadian Entomologist 91:385–398.

Ives, A.R. 1995. Predicting the response of populations to environmental change.

Ecology 76:926–941.

Ives, A.R. and V.A.A. Jansen. 1998. Complex dynamics in stochastic tritrophic models. Ecology 79:1039–1052.

Jeschke, J.M., M. Kopp, and R. Tollrian. 2004. Consumer-food systems: why type I functional responses are exclusive to filter feeders. Biological Reviews 79:337–349.

Kim, J. and R. DeWreede. 1996. Effects of size and season of disturbance on algal patch recovery in a rocky intertidal community. Marine Ecology Progress Series 133:218–228.

Laska, M.S. and J.T. Wootton. 1998. Theoretical concepts and empirical approaches to measuring interaction strength. Ecology 79:461–476.

Ludwig, D. and C.I. Walters. 1985. Are age-structured models appropriate for catch-effort data? Canadian Journal of Fisheries and Aquatic Sciences 42:1066–1072.

May, R.M. 1974. Biological populations with nonoverlapping generations: stable points, stable cycles, and chaos. Science 186:645–647.

May, R.M. 1976. Simple mathematical models with very complicated dynamics. Nature 261:459–467.

McCann, K., A. Hastings, and G.R. Huxel. 1998. Weak trophic interactions and the balance of nature. Nature 395:794–798.

Novak, M. 2008. Trophic omnivory and the structure, strength, and nonlinear nature of species interactions across a productivity gradient. PhD Thesis. University of Chicago, Chicago.

Paine, R.T. 1992. Food-web analysis through field measurement of per-capita interaction strength. Nature 355:73–75.

Peacor, S.D. and E.E. Werner. 1997. Trait-mediated indirect interactions in a simple aquatic food web. Ecology 78:1146–1156.

Pfister, C.A. 1995. Estimating competition coefficients from census data: a test with field manipulations of tidepool fishes. American Naturalist 146:271–291.

R Development Core Team. 2008. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Raffaelli, D. and S. Hall. 1996. Assessing the relative importance of trophic links in food webs. Pages 185–191 in G.A. Polis and K.O. Winemiller, editors. Food

Webs: Integration of Patterns and Dynamics. Chapman and Hall, New York.

Ruesink, J.L. 1998. Variation in per capita interaction strength: thresholds due to nonlinear dynamics and nonequilibrium conditions. Proceedings of the National Academy of Sciences of the United States of America 95:6843–6847.

Sala, E. and M.H. Graham. 2002. Community-wide distribution of predator-prey interaction strength in kelp forests. Proceedings of the National Academy of Sciences of the United States of America 99:3678–3683.

Sarnelle, O. 2003. Nonlinear effects of an aquatic consumer: causes and consequences. American Naturalist 161:478–496.

Schmitz, O.J. 1997. Press perturbations and the predictability of ecological interactions in a food web. Ecology 78:55–69.

Schoch, G.C., B.A. Menge, G. Allison, M. Kavanaugh, S.A. Thompson, and S.A. Wood. 2006. Fifteen degrees of separation: latitudinal gradients of rocky intertidal biota along the California Current. Limnology and Oceanography 51:2564–2585.

Scrosati, R. 1998. Mechanisms of recolonization of the clonal intertidal alga *Mazzaella cornucopiae* (Rhodophyta, Gigartinaceae) after disturbances. Canadian Journal of Botany 76:1717–1724.

Skalski, G.T. and J.F. Gilliam. 2001. Functional responses with predator interference: viable alternatives to the Holling Type II model. Ecology 82:3083–3092.

Turchin, P. and A.D. Taylor. 1992. Complex dynamics in ecological time series. Ecology 73:289–305.

Werner, E.E. 1992. Individual behavior and higher-order species interactions. American Naturalist 140:S5–S32.

Werner, E.E. 1994. Ontogenic scaling of competitive relations: size-dependent effects and responses in two anuran larvae. Ecology 75:197–213.

Werner, E.E. and B.R. Anholt. 1996. Predator-induced behavioral indirect effects: consequences to competitive interactions in anuran larvae. Ecology 77:157–169.

Wootton, J.T. 1997. Estimates and tests of per capita interaction strength: diet, abundance, and impact of intertidally foraging birds. Ecological Monographs 67:45–64.

Wootton, J.T. 2002. Indirect effects in complex ecosystems: recent progress and future challenges. Journal of Sea Research 48:157–172.

Yodzis, P. 1981. The stability of real ecosystems. Nature 289:674–676.

Yodzis, P. 1988. The indeterminacy of ecological interactions as perceived through perturbation experiments. Ecology 69:508–515.

Chapter 4

The combined influence of biotic and abiotic factors on species diversity and interactivity [§]

4.1 Introduction

One of the oldest questions in ecology concerns the relative importance of biotic interactions and abiotic factors for diversity (Hutchinson 1959, Paine 1966, Connell 1970, Dayton 1971, Dayton et al. 1974, Menge 1976, Menge and Farrell 1989). Ecologists have long sought model frameworks for predicting the influences of ecological and environmental processes on community structure (Hairston et al. 1960, Connell 1975, Dayton and Tegner 1984, Menge and Sutherland 1976, Menge and Olson 1990). Many of these models focus on the harshness of the environment as a source of variation in trophic structure and interaction types. They predict that the balance between facilitative and antagonistic species interactions is altered by environmental stress. As stress increases, antagonistic interactions are expected to weaken (Connell 1972, Grime 1979, Huston 1979, Louda 1986, Welden and Slauson 1986, Menge and Sutherland 1987, but see Tilman 1988), while facilitative interactions strengthen (Hacker and Gaines 1997, Bruno et al. 2003), creating an overall shift in the relative importance of positive versus negative effects (Bertness and Shumway 1993, Bertness and Callaway 1994, Callaway and Walker 1997, Brooker and Callaghan 1998). Some empirical studies have found evidence in support of this theory. For example, in a meta-analysis of alpine plant removal experiments, Callaway et al. (2002) observed a switch from competitive to facilitative plant–plant interactions along a stress gradient. However, the results of my study quantifying the

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community-wide distribution of species interactions across a similar stress gradient in the intertidal did not support the model predictions (Chapter 2). This apparent contrast calls into question the generality of the conclusion that environmental stress affects species interaction in a predictable way.

The combined influence of abiotic and biotic processes can be assessed by studying both factors in combination. Variation in the sign and magnitude of biological interactions can be measured using experimental manipulations such as species presses in the field (Chapter 3). One of the primary abiotic forces structuring high intertidal communities is heat stress (Hutchins 1947, Southward 1958, Tsuchiya 1983, Helmuth et al. 2006). Temperature variation imposes physiological stress on organisms that live near their tolerance limits (Newell 1969, Somero 2002, Tomanek and Helmuth 2002). Rising global temperatures are expected to exacerbate heat stress in the high intertidal (Fields et al. 1993, Harley et al. 2006) and this may restructure communities by reshaping interaction webs. Competition between the barnacles *Chthamalus* and *Semibalanus*, for example, may be reduced by stressful conditions (Wethey 1984). Alternatively, environmental stress may have greater effects on higher trophic levels (Menge and Sutherland 1976, 1987) with cascading effects through the food web (Terborgh et al. 2001, Duffy 2003). In the rocky intertidal, for example, temperature variation reduces the foraging activity of mobile predators that would otherwise exert strong top-down control (Sanford 1999, Harley and Lopez 2003). These studies show that environmental changes can restructure interactions between particular species, however it is unclear how interactions community-wide will be constrained by stressful conditions, and what the consequences of this reorganization will be for diversity.

Empirical tests of the effects of environmental stress on species interactions often only consider subsets of communities. However, the impacts of the environment on the abundance and distribution of species are filtered through a complex network of biotic interactions that can reverse species' autecological responses and produce unexpected outcomes (Davis et al. 1998, Jiang and Morin 2004, Suttle et al. 2007). In one example, drought stress decreased foraging by a predator in a bush lupine community, which weakened its ability to control herbivore outbreaks and the productivity of lupine plants (Preisser and Strong 2004). In the arctic, warmer temperatures have direct positive effects on plant biomass, but these are countered by

biotic interactions, primarily increased grazing by caribou and muskoxen (Post and Pedersen 2008). These examples illustrate how the responses of subsets of species to the environment may not scale up to whole communities (Lehmann-Ziebarth and Ives 2006). They also indicate that interactions between biotic and abiotic processes may further alter diversity. Such counter-balancing effects, however, are not accounted for by most environmental stress models.

Here I describe a study that investigates how biotic interactions, abiotic stress, and interactions between the two processes regulate diversity. I quantify the responses of rocky intertidal communities to a natural temperature stress gradient, artificial warming treatments, and species press perturbations. I measure the impacts of biotic and abiotic processes on species richness, biomass, and interaction strength at the population and community levels. This allows me to test the hypothesis that biotic and abiotic factors, and interactions between the two, impact the measured community properties. The results demonstrate that environmental stress alters the magnitude of certain species interactions, but does not change the overall distribution of weak and strong interactions, nor the even balance of positive and negative effects. In high intertidal communities, biotic processes can mitigate the effects of the abiotic environment and allow the community to retain its biomass and richness under harsh and fluctuating abiotic conditions.

4.2 Methods

Experimental procedure

Experiments were performed in the high intertidal community of Prasiola Point in Barkley Sound, British Columbia (Figure 1.1, 1.2). The shoreline is moderately exposed with a high intertidal dominated by the alga *Fucus gardneri*, barnacles such as *Balanus glandula*, the mussel *Mytilus californianus*, and grazing limpets, primarily *Lottia digitalis* (hereafter referred to by genus; see Chapter 3 for a site description). Study plots of 0.025 m^2 were established on gently sloping rock faces. Plots were arranged in four completely randomized blocks with two multilevel treatments crossed in a fully factorial design. The first treatment factor consisted of three levels of temperature stress: high, low, and ambient conditions. The stress treatment was

crossed with a species press treatment (Bender et al. 1984) in which the abundance of one focal species was continually suppressed to approximately 65% of its initial natural density. Species presses were performed on *Balanus*, *Fucus*, and *Lottia*, and compared to unmanipulated control plots.

The imposed temperature stress treatments were applied using a method similar to Allison (2004). High stress plots were heated to 10° C above ambient temperature for 30 minutes, approximately once every three months (dates shown in Figure 4.3). A 6,000 BTU heater was mounted horizontally in an aluminum box with a heat shield between the heater and substrate (Figure 4.1). Temperature was regulated using an adjustable flap on the front of the box, and monitored using a thermometer at the substrate. A low stress treatment level was applied by pouring $\approx$ 15 L of sea water over the study plot every 10 minutes for 30 minutes. Heat and desiccation stress are inseparable in high intertidal communities and this technique reduced temperature up to 10° C for the duration of the 30 minute treatment period. Treatments were applied in a preselected random order to blocks, and plots within blocks, to account for emersion and immersion times. Two blocks could be treated per low tide; hence, the treatments took place over two subsequent daytime low tides. The high and low stress treatments were intended to be similar in magnitude, but necessarily varied with ambient temperature (see Figure 4.3). Air temperature and radiant heat are expected to increase with global climate change (Harley et al. 2006) which will impact communities episodically during low tides by raising the maximum body temperature of organisms (Gilman et al. 2006, Helmuth et al. 2006). I simulated this effect by raising air temperature for short periods throughout the year. The frequency and duration were chosen to represent one plausible climate change scenario from a variety of possible outcomes.

Since the stress manipulation occurred over relatively short time periods, the angle of incidence (AI) was also calculated as a second measure of temperature stress of plots. The AI is defined as the angle of incoming solar radiation in degrees from perpendicular to the substrate, and is inversely related to the maximum temperature experienced by the intertidal organisms (Harley 2008). For each plot I measured the elevation above sea level, the aspect in degrees from North, and the slope in degrees from horizontal using an inclinometer. The AI was calculated at 15 minute intervals for the duration of the study using the plot angles and azimuths measured
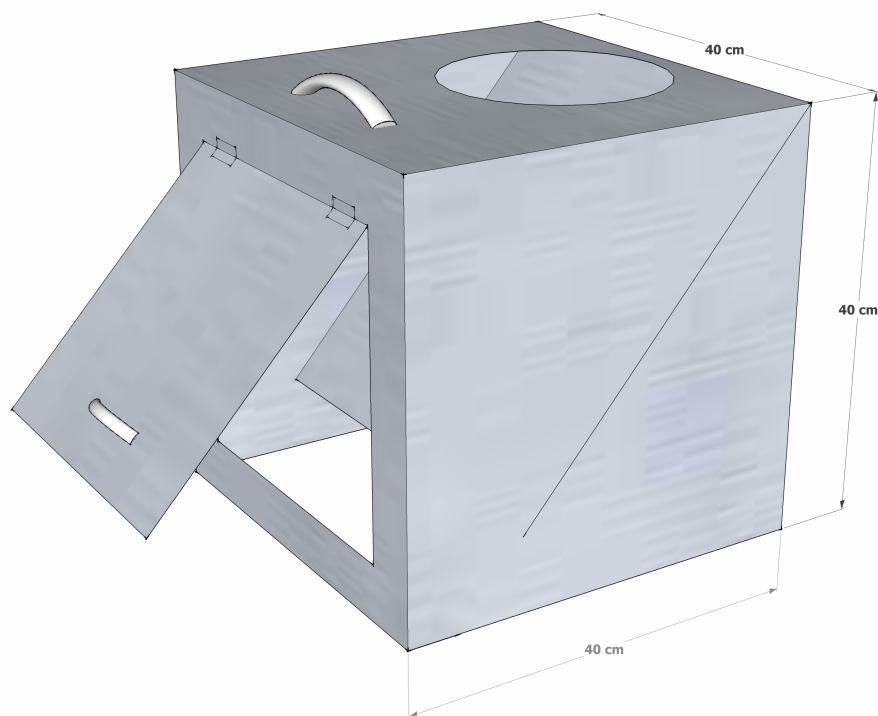
Figure 4.1: A diagram of the aluminum box used to raise the ambient temperature of intact intertidal communities in the field. A heater was mounted in the top opening. The door was opened or closed to regulate the temperature, which was monitored using a thermometer at the substrate.

in the field, and solar positions returned by the tripEstimation package for R (R Development Core Team 2008). I chose this frequency to capture the within-day variation due to the timing of low tides. The average AI of each plot was computed for times when the plot was emersed (tide data from Tides and Currents software, Portland, OR, USA).

Species press treatments were initiated in February 2008, after the plots had been exposed to the stress treatments for 19 months. Press treatments were maintained bi-weekly. Abundances of all organisms were monitored 0, 3, 5, and 7 months after the species press treatments were initiated (dates shown in Figure 4.3). I visually estimated percent cover of sessile taxa and enumerated mobile organisms. In order

to calculate a per-capita interaction coefficient, I also tallied numbers of individuals of the sessile focal species. Target species abundances were converted into biomass in order to capture the energetic and functional importance of links (Bender et al. 1984, Raffaelli and Hall 1996). Separate regressions of mass on abundance were used for each target species at the study site. The equations (Appendix B) were then used to translate measured numerical abundances into population biomass estimates (cf. Schmitz 1997).

Ambient temperature

Ambient temperature at the site was logged continuously throughout the study period using a StowAway Tidbit temperature recorder (Onset Corporation, Pocasset, MA, USA). I used tidal data to determine when the recorder was submerged and distinguish between air and water temperature. Wave action can interfere with air or water measurements taken when the water level is nearest the elevation of the logger. I therefore discarded observations made when the tidal elevation was within 0.5 m of the temperature recorder.

Community composition

To assess the relative influence of biotic and abiotic factors on community composition, I used a nonparametric multivariate analysis of variance (PERMANOVA) for distance matrices (Anderson 2001). Average mass abundance during the final two months was used as the response. Variation in untransformed Bray-Curtis community dissimilarity was partitioned between the two abiotic factors (AI of solar radiation and the temperature stress treatment) and the biotic factor (species press) for each plot. Interactive effects between the factors were also tested. The PERMANOVA was performed using the vegan package for R (R Development Core Team 2008).

Two of the three experimental factors (temperature stress and species press) were manipulated in factorial combinations while the third factor (AI) was treated as a covariate. However, given the result of the PERMANOVA (below) showing that variation in community composition is much more closely related to AI than to the warming treatments (Figure 4.2), I present only results using AI as the

metric of abiotic stress. I explored the possibility of using an aggregate measure of abiotic stress in which the AI was summed with a score for the warming treatments. However, in all analyses, results using the aggregate measure were qualitatively identical to those using the AI alone. Since AI is inversely related to heat stress, for ease of interpretation I subtracted the AI from twice its median value to make it a direct measure. Hereafter, this factor is referred to simply as 'solar stress'.
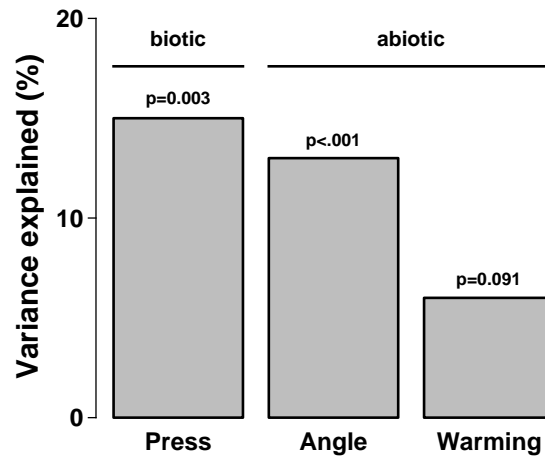
Figure 4.2: The percentage of variance in community Bray-Curtis dissimilarity explained by biotic (press perturbation) and abiotic (angle of incidence and warming treatment) factors. Press perturbations, which were manual reductions of biomass of focal species, explained 15% of the dissimilarity of communities. The abiotic factors together explained 20% of the variability in community dissimilarity.

To determine which species drove the compositional differences due to press treatments and solar stress, I then used a similarity percentages (SIMPER) analysis. As in the PERMANOVA, Bray-Curtis dissimilarity was computed for the average mass abundances of species during the final two months of the experiment. Press treatments were each compared to the untreated control. Solar stress was converted into two equal levels (low and high) for comparisons.

Biomass and richness

The change in total population biomass was computed for each target species in each plot as the slope of the trend in biomass over time. A multilevel model was then used to analyze the effects of the target population trophic type (producer, suspension feeder, or mobile consumer), the identity of the pressed species, and solar stress on the change in population biomass (see Appendix A for basic information on multilevel models). Target trophic type was used to assess whether the biomass of populations within trophic groups followed similar trends over time. Initial biomass was also included as a factor to account for differences in the starting abundance of populations. The multilevel model tested the four fixed effects and their interactions in a hierarchy of random target populations nested in random plots, nested in random blocks. A Box-Cox transformation was used to meet model assumptions. A second multilevel model was used to test whether changes in species richness over time were explained by the same fixed factors (initial richness, target trophic type, the identity of the pressed species, and solar stress). For each trophic group, nested in random plots, in random blocks, the variation in species richness was tested against the main effects and their interactions.

Sign and strength of species interactions

Pairwise interaction coefficients were calculated using the 'dynamic regression' approach (Pfister 1995, Laska and Wootton 1998). This technique uses a Ricker-type equation to estimate the per-capita effect of the focal species on each target population as

$$\frac{ln\left(\frac{N_{i,p}}{N_{i,p-1}}\right)}{\Delta t} = r_i + \sum_{j=1}^{s} \alpha_{ij} \cdot N_{j,p-1} \qquad (4.1)$$

where N_i is the biomass of target population i, and N_j represents the numerical abundance of the focal species j, during monitoring period p. Elapsed time in months is denoted by Δt. This equation fits a regression in which the intercept, r_i, represents the intrinsic rate of growth, and the slope, α_{ij}, gives the per-capita interaction coefficient. Discrete groups of data are required to estimate the interaction coefficients in this equation. Hence, the continuous measure of solar stress was categorized into three equal levels (low: 45–52°, medium: 53–60°, and high: 61–67°).
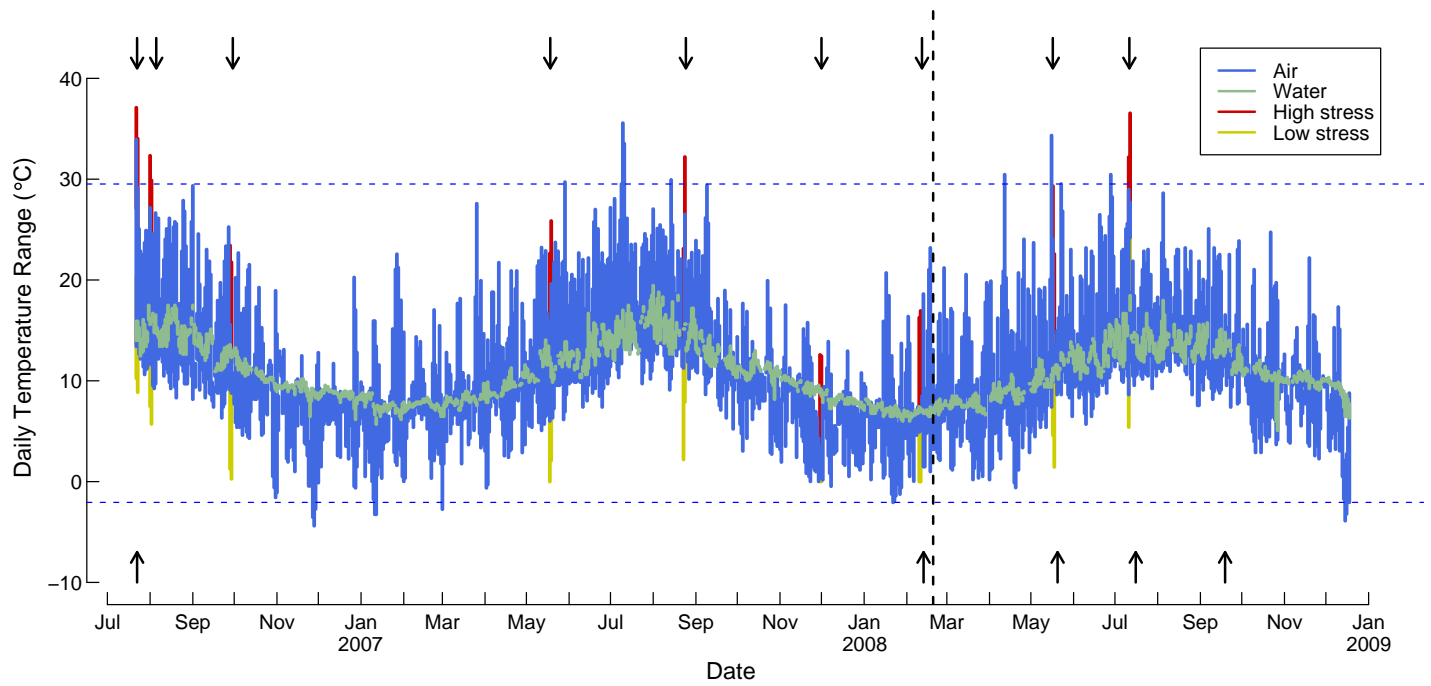
Interaction coefficients were calculated for each of the nine solar stress · species press combinations, pooling the pressed and unpressed control plots. Because interaction coefficients were computed as the slope of the regression line, estimates were made only for target species present in at least four plots of a given stress · press group.

The interaction coefficients (α_{ij} values calculated using Equation 4.1) were then used to test the hypothesis that solar stress and species presses alter species interactions. The sign and strength of the interactions were used as the responses in two separate multilevel models (Appendix A), each with three nested random levels (dates nested in target populations, nested in treatments) and four fixed effects (date, target population trophic type [producer, suspension feeder, or mobile consumer], the identity of the pressed species [*Balanus*, *Fucus*, or *Lottia*], and solar stress [low, medium, or high as an ordered factor]). The full models included tests for all interactive effects. In the first model, testing the effects of the main factors on the sign of the interaction coefficient, I used a logit link function expressing interaction sign as a probability of being positive. In the second model, testing for effects on interaction strength, the response was the absolute value of the interaction coefficient. Strength values were square-root transformed to meet assumptions of normality. An autoregressive variance/covariance matrix, accounting for corre-

Figure 4.3 *(preceding page)*: A plot of daily temperature ranges over the course of the experiment, for air (blue) and water (green). The temperature recorder was affixed near the study plots, thus air temperatures were recorded during emersed periods and water temperatures during immersion. Horizontal dashed lines indicate the 1st and 99th percentile of the daily minimum and maximum air temperatures, respectively. The vertical dashed line denote the date when species press treatments were initiated (February 2008). Upward pointing arrows mark times when abundances of all target species were monitored in the study plots. Downward pointing arrows indicate times when warming treatments were applied.

The warming treatments heated or cooled plots by approximately 10° C. These were applied throughout the year and varied according to the ambient temperature. Yellow and red segments show the estimated temperature range of the low and high stress treatments. These were calculated by subtracting 10° C from the 33% quantile of the daily temperature range or adding 10° C to the 66% quantile, for the low or high stress treatments respectively.

lations between sampling times (Pinhiero and Bates 2002), did not improve the model fit or alter the qualitative results. All multilevel models were fit with the lmer function and p-values were calculated using the Markov Chain Monte Carlo method of the mcmcsamp function in the lme4 package for R (R Development Core Team 2008).

4.3 Results

Ambient temperature

A summary of air and water temperatures is shown in Figure 4.3. Intertidal air temperatures are highly variable and influenced by weather and the timing of the low tides. Daily fluctuations in temperature often span 20° C, which is greater than the difference between the median summer and winter air temperatures. Extreme high temperature stress events, in the the 99th percentile, typically occur in June or July, but can occur as early as April and May, as in 2008. Throughout the summer, low tides occur during the daytime in this region.

Factor	df	SS	MS	F	R^2	p
Warming	2	0.344	0.172	1.836	0.063	0.091
Press	3	0.837	0.279	2.979	0.154	0.003
Angle	1	0.722	0.722	7.704	0.132	<.001
Warming · Press	6	0.521	0.087	0.926	0.096	0.552
Warming · Angle	2	0.064	0.032	0.340	0.012	0.939
Press · Angle	3	0.365	0.122	1.301	0.067	0.237
Warming · Press · Angle	6	0.349	0.058	0.620	0.064	0.902
Residuals	24	2.248	0.094		0.413	

Table 4.1: Community response to biotic and abiotic effects.

Community composition

Fifty-eight taxa were found in the plots over the course of the study. The stress and press perturbation regimes explained 59% of the dissimilarity among plot assemblages (Figure 4.2, Table 4.1). Press treatments explained the most variation in community dissimilarity ($R^2 = 0.154$, p = 0.003). AI explained slightly less variation ($R^2 = 0.132$, p < 0.001), but over twice as much as the warming treatment,

which was not significant ($R^2 = 0.063$, p = 0.091). Interactions between the main terms were also not significant.

a) Control vs *Balanus*	Diss	% Diss	b) Control vs *Fucus*	Diss	% Diss
Fucus gardneri	16.1	35.5	*Fucus gardneri*	17.3	38.0
Balanus glandula	14.7	32.3	*Balanus glandula*	14.2	31.1
Mytilus californianus	4.44	9.77	*Mytilus californianus*	4.21	9.26
Semibalanus cariosus	2.06	4.53	*Petrocelis franciscana*	1.82	4.00

c) Control vs *Lottia*	Diss	% Diss	d) Low vs High Stress	Diss	% Diss
Fucus gardneri	14.5	34.4	*Fucus gardneri*	18.0	36.8
Balanus glandula	13.8	32.8	*Balanus glandula*	15.5	31.7
Mytilus californianus	3.40	8.08	*Mytilus californianus*	4.48	9.15
Semibalanus cariosus	2.09	4.98	*Semibalanus cariosus*	2.02	4.13

Table 4.2: SIMPER results showing the top four species contributions to Bray-Curtis dissimilarity between press treatments (a–c) and levels of solar stress (d).

The SIMPER analysis revealed that dissimilarity between communities was due mainly to differences in *Fucus* and *Balanus* abundance (Table 4.2). Comparisons of the pressed and control plots showed that *Fucus* and *Balanus* together explained between 67–69% of the dissimilarity in all press experiments, regardless of the treatment level. The presses reduced the biomass of *Fucus* by 37%, *Balanus* by 38%, and *Lottia* by 42%, compared to the unpressed control plots. However, *Lottia* removal only explained 1.8% of the dissimilarity in composition between the *Lottia* press and control plots because of its low total biomass relative to *Fucus* and *Balanus*. Compositional differences due to solar stress were also primarily due to differences in *Fucus* and *Balanus* abundance, which together explained 69% of the dissimilarity between high and low solar stress plots. The effect of solar stress on the biomass of these three species is shown in Figure 4.4.

Biomass and richness

The rate of change in biomass of populations over the course of the experiment was explained by initial biomass, the target trophic type, and degree of solar stress (Table 4.3, 4.7a). Larger populations contracted faster than populations with less initial biomass (p < 0.001). However, even after accounting for starting conditions,

a.)

Fucus

b.)

Balanus

c.)

Lottia
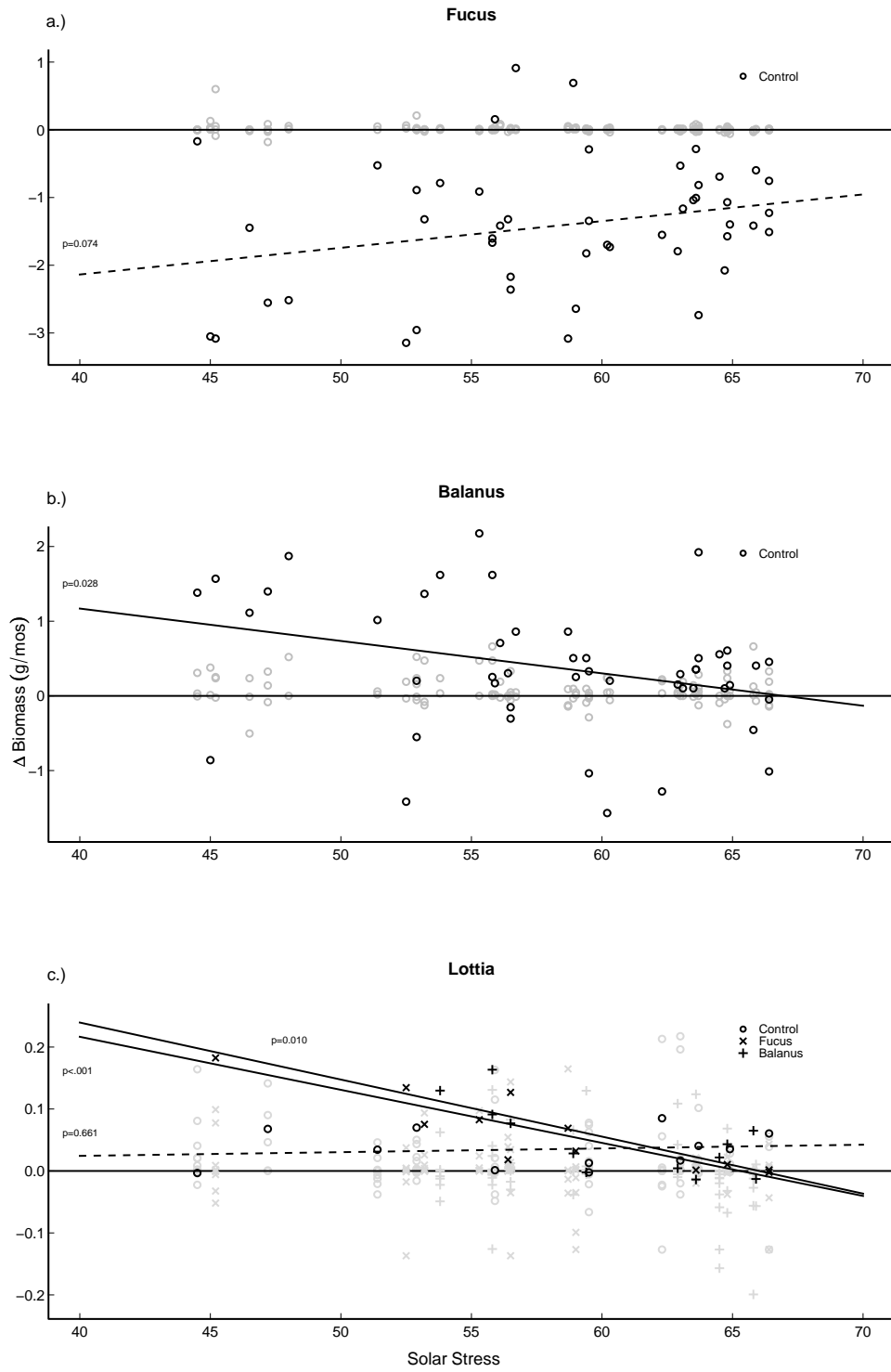
Solar Stress

different trophic groups showed distinct trends in abundance over time ($p < 0.001$). Suspension feeders such as *Balanus* increased in abundance (evident as positive response values in Figure 4.4b). Biomass of the dominant producer, *Fucus*, decreased (negative values in Figure 4.4a) while that of the dominant consumer, *Lottia*, increased over time (positive values in Figure 4.4c), although responses of producers and consumers as a whole varied (Table 4.7a). The effect of solar stress on biomass depended on the organism's trophic group (Trophic · Stress $p = 0.002$). Stress had negative effects on suspension feeders such as *Balanus* (evident as a negative slope in Figure 4.4b), but weak effects on producers and mobile consumers (Figure 4.4a,c, Table 4.7a). In all three cases however, stress reduced fluctuations in abundance of the dominant species (evident as regression lines approaching zero in Figure 4.4). Finally, although the press perturbations effectively reduced the biomass of the focal species, these treatments were not large enough to significantly impact total community biomass ($p = 0.199$), nor the biomass of any one trophic group (Trophic · Press $p = 0.143$). No other interaction terms in the model were significant.

Initial species richness explained much of the variation in richness over time, along with trophic membership, and its interactions with species press and solar stress (Table 4.4, Table 4.7b). Over time, more speciose trophic groups tended to have greater extinction rates than less rich groups ($p < 0.001$). Independent of any

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Figure 4.4 *(preceding page)*: The change in mass abundance over time as a function of solar stress, for primary producers (a), suspension feeders (b), and mobile consumers (c). Black points and lines are given for *Fucus*, *Balanus*, and *Lottia*, while other members of the trophic group are shown in grey. *Fucus* tends to decrease in abundance, seen as negative response values in (a), while *Balanus* and *Lottia* often increase in biomass, showing positive responses in (b–c). For all three species, environmental stress dampens changes in biomass over time. The results show that there is not a significant interaction among target trophic types, press treatments, and levels of solar stress (Table 4.3), however, there is an interesting difference in how *Lottia* responds to press treatments across the stress gradient. Thus, panel (c) compares the change in consumer biomass in the unmanipulated control, *Balanus* press, and *Fucus* press plots (across all times). Data points in panels (a–b) show simply the change in unmanipulated plots (control plots at all times; pressed plots at pre-pressed times). Solid lines show statistically significant relationships, while dashed lines are used for insignificant trends.

Factor	df	SS	MS	p
Initial	1	29.0	29.0	<.001
Trophic	2	8.04	4.02	<.001
Press	3	0.48	0.16	0.199
Stress	1	0.34	0.34	0.715
Trophic · Press	6	1.34	0.22	0.143
Trophic · Stress	2	1.97	0.98	0.002
Press · Stress	3	0.23	0.08	0.455
Trophic · Press · Stress	6	0.62	0.10	0.145

Table 4.3: Effects of initial biomass, environmental stress, press perturbations, and the trophic identity of the target population on the rate of biomass change through time.

Factor	df	SS	MS	p
Initial	1	0.299	0.299	<.001
Trophic	2	0.072	0.036	<.001
Press	3	0.010	0.004	0.343
Stress	1	0.001	0.001	0.880
Trophic · Press	6	0.023	0.004	0.006
Trophic · Stress	2	0.000	0.000	0.046
Press · Stress	3	0.003	0.001	0.687
Trophic · Press · Stress	6	0.011	0.002	0.170

Table 4.4: Effects of initial richness, environmental stress, press perturbations, and the trophic identity of the target population on the rate of species richness change through time.

other factor, mobile consumer richness increased, compared to the producers and suspension feeders ($p < 0.001$). Consumer richness also responded differently than primary producer and suspension feeder richness to the press and stress regimes: it declined slightly in the *Fucus* and *Balanus* removals ($p = 0.006$; see also Harley 2006), and also in the more stressful plots ($p = 0.046$). Remaining interaction terms, as well as the main effects of solar stress and species press, did not explain significant variation in trophic group richness.

Sign and strength of species interactions

None of the main effects (target trophic type, solar stress, or species press), nor their interactions, explained significant variation in the proportion of positive and negative interactions (Table 4.5, 4.8a). The sign of the interactions, calculated using

the response of populations to the press perturbation (Equation 4.1), did not change over the seven months that the interaction coefficients were measured (p = 0.710). As an example, Figure 4.5 shows that positive and negative interactions between *Fucus* and the target populations were equally prevalent.

The community-wide strength of species interactions also did not change predictably over time (p = 0.154, Table 4.6, 4.8b). All target trophic types were engaged in similarly strong interactions (p = 0.439). Community-wide, interaction strength was not affected by the solar stress gradient (p = 0.208), but differed among the species press treatment levels (p = 0.006). That is because *Balanus* had weaker per-capita effects on other community members than *Lottia* or *Fucus* (Table 4.8b), consistent with the results presented in Chapters 2 and 3. Finally, none of the interaction terms in the model explained significant variation in interaction strength.

Factor	df	SS	MS	p
Time	1	0.150	0.150	0.710
Trophic	2	1.556	0.778	0.385
Press	2	3.570	1.785	0.204
Stress	1	0.962	0.962	0.934
Trophic · Press	4	3.394	0.848	0.553
Trophic · Stress	2	3.186	1.593	0.259
Press · Stress	2	0.848	0.424	0.796
Trophic · Press · Stress	4	1.631	0.408	0.807

Table 4.5: Sign of species interactions in response to time, trophic type, stresses and presses.

Factor	df	SS	MS	p
Time	1	0.014	0.014	0.154
Trophic	2	0.001	0.000	0.439
Press	2	0.346	0.173	0.006
Stress	1	0.002	0.002	0.208
Trophic · Press	4	0.011	0.003	0.531
Trophic · Stress	2	0.001	0.000	0.231
Press · Stress	2	0.008	0.004	0.138
Trophic · Press · Stress	4	0.013	0.003	0.426

Table 4.6: Strength of species interactions in response to time, trophic type, stresses and presses.

4.4 Discussion

Effects of stress on diversity and interactivity

My results support the contention that environmental stress alters community composition (Southward 1958, Wethey 1983, Harte and Shaw 1995) and interactions between species (Connell 1972, Menge and Sutherland 1987, Hacker and Gaines 1997). However, in contrast to many of these studies, I do not find consistent patterns in the way that populations, trophic levels, or whole communities respond to abiotic stress. A number of studies have shown that harsher environments favor weaker negative and stronger positive interactions between species (Bertness and Callaway 1994, Callaway and Walker 1997, Brooker and Callaghan 1998). This is based on the argument that stress events limit growth by continually resetting populations to lower abundances, thereby reducing the potential for competition for space or other resources (Hutchinson 1961, Wiens 1977, Huston 1979). Similarly, predation is predicted to weaken because stress has more severe impacts on mobile consumers relative to their sessile prey (Menge and Sutherland 1987, but see Menge and Farrell 1989). Facilitation, however, may strengthen as stress increases if the presence of other species counteracts the negative effects of the environment, for instance by reducing desiccation. None of these patterns were apparent in my results at the level of the whole community, although elements of them can be seen in the responses of particular species. This suggests that heat stress has a more context-dependent effect on community interaction webs.

I find that abiotic stress does not impact the mean community-wide interaction strength, nor the balance of positive and negative effects (Table 4.5–4.6). This is not because stress failed to affect diversity or biotic processes. In fact, solar stress explained a significant amount of the dissimilarity in community composition (Figure 4.2), primarily because it reduced *Balanus* abundance and increased *Fucus* biomass (Table 4.2, Figure 4.4a–b). Previous studies have observed that high temperatures negatively impact *Balanus* by increasing mortality, but have positive effects on *Fucus*, which relies on warm air temperatures for its reproduction (Dunmore 2006, S. Wood *unpublished data*). In addition, solar stress altered these two species' per-capita effects on other populations. Under stressful conditions *Balanus* and *Fucus* had weak effects on *Lottia*, but their effects became strongly negative

as abiotic stress decreased (Figure 4.4c, 4.5). However, as Figure 4.5 shows, other pairwise interactions showed different trends along the stress gradient. As a result, the sign and strength of the distribution of interaction types was unchanged.
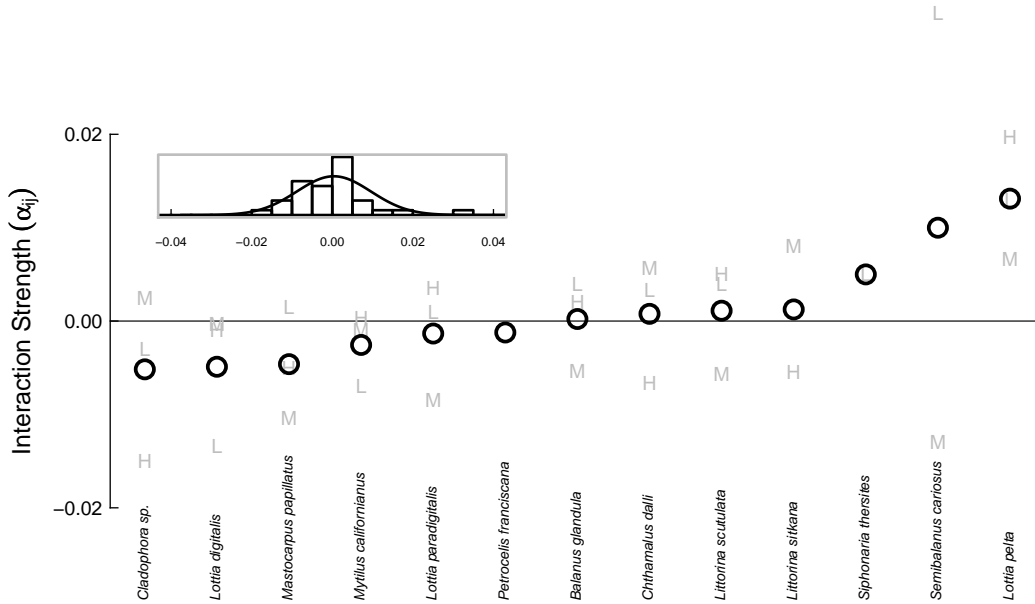
Figure 4.5: The per-capita effect of *Fucus* on target populations, measured in the *Fucus* press manipulations. The average effect of *Fucus* across all times and stress levels is shown as the black circle. The average interaction in each of the low, mid, and high solar stress plots is depicted by the grey letters. The graph includes only target species present in at least four plots during two times. The inset histogram shows the distribution of per-capita effects. Note the central tendency, with many weak and equal proportions of positive and negative effects.

Model limitations — biotic feedbacks

Menge et al. (1986) emphasize that results such as these, that depart from the expectations of environmental stress models, are most effective at revealing their limitations. The first of these limitations is that environmental stress models don't account for interactive effects of the biotic and abiotic processes (Ives 1995, Allison 2004, Wilmers and Post 2006, Suttle et al. 2007, Post and Pedersen 2008). My

results show that environmental processes alter species interactions, which, in turn, modify the effect of the environment in unpredictable ways. In plots where *Balanus* or *Fucus* abundances were pressed to lower levels, abiotic stress had stronger negative impacts on *Lottia* abundance, while in unmanipulated control plots *Lottia* biomass was more constant (Figure 4.4c, 4.5). This is akin to the observation by Suttle et al. (2007) that species interactions can reverse the direct responses of grassland species to warming, and demonstrates how the responses of populations to the environment can be mediated by interactions among species. It's not enough to know the direct effects of warming on populations; how biotic interactions will intensify or counteract such effects must also be considered.

Model limitations — heterogeneity

Second, environmental stress models do not account for spatio-temporal heterogeneity in the stressor or the physical environment that may have important consequences. In this study, spatial variability can explain why stress reduced the biomass of sessile more than higher trophic mobile consumers, in contrast to Menge and Sutherland's (1987) prediction and the results of other studies (e.g. Petchey et al. 1999, Logan et al. 2003). In the high intertidal, environmental heterogeneity at microhabitat scales (< 10 cm; Helmuth and Hofmann 2001) produces a patchy landscape (Denny et al. 2006) where mobile taxa take short-term refuge in cracks and crevices to curb the impacts of temperature during stress events (Garrity 1984). The limpet *Cellana grata*, for example, can reduce its body temperature by 8° C by hiding in crevices or on shaded slopes (Williams and Morritt 1995), but sessile consumers cannot. Other stressors such as ocean acidification are more spatially extensive and thus may produce the predicted decrease in predation. However, this is unlikely since low pH impacts species with traits like calcification that, unlike mobility, are not tied to particular trophic types (Wootton et al. 2008).

Spatio-temporal heterogeneity also may have prevented stress from weakening the competitive interactions among species by creating a 'successional mosaic' (Chesson and Huntly 1997 p. 542). In this scenario, spatial and temporal heterogeneity in the environment can promote coexistence through species sorting (Questad and Foster 2002) and turnover (Sousa 1979), and result in more speciose communities

	a)			b)		
Factor	Estimate	Std. Error	p	Estimate	Std. Error	p
Intercept	1.55	0.034	<.001	0.13	0.014	<.001
Initial	-0.01	0.001	<.001	-0.04	0.002	<.001
Target Trophic Type						
Suspension	0.03	0.051	<.001	0.00	0.014	0.946
Consumer	-0.01	0.041	0.883	0.07	0.014	<.001
Species Press						
Fucus	-0.09	0.460	0.070	0.02	0.015	0.266
Balanus	-0.06	0.050	0.234	-0.01	0.016	0.669
Lottia	-0.01	0.047	0.873	0.02	0.015	0.190
Solar Stress	0.00	0.005	0.739	0.00	0.002	0.731
Target Trophic Type · Species Press						
Suspension · Fucus	0.09	0.072	0.221	-0.02	0.020	0.233
Suspension · Balanus	-0.09	0.078	0.269	0.01	0.021	0.820
Suspension · Lottia	0.05	0.073	0.538	-0.02	0.020	0.222
Consumer · Fucus	0.08	0.570	0.166	-0.06	0.020	0.002
Consumer · Balanus	0.05	0.630	0.421	-0.05	0.021	0.033
Consumer · Lottia	0.01	0.058	0.898	-0.01	0.198	0.674
Target Trophic Type · Solar Stress						
Suspension · Stress	-0.02	0.007	0.003	0.00	0.002	0.779
Consumer · Stress	0.00	0.006	0.847	-0.01	0.002	0.018
Species Press · Solar Stress						
Fucus · Stress	0.00	0.007	0.721	0.00	0.002	0.802
Balanus · Stress	0.01	0.009	0.123	0.00	0.003	0.848
Lottia · Stress	0.00	0.006	0.517	0.00	0.002	0.353
Target Trophic Type · Species Press · Solar Stress						
Suspension · Fucus · Stress	-0.01	0.011	0.381	0.00	0.003	0.728
Suspension · Balanus · Stress	-0.01	0.014	0.391	0.00	0.004	0.964
Suspension · Lottia · Stress	0.01	0.010	0.148	0.00	0.002	0.424
Consumer · Fucus · Stress	0.00	0.008	0.750	0.01	0.003	0.120
Consumer · Balanus · Stress	-0.01	0.011	0.211	0.01	0.004	0.047
Consumer · Lottia · Stress	0.01	0.010	0.148	0.01	0.003	0.016

Table 4.7: Effects of starting biomass or richness, environmental stress, press perturbations, and the trophic identity of the target species on the rate of change in biomass (a) and richness (b). Initial is the the starting biomass or richness of the population or trophic group. Target Trophic Type is a categorical factor and differences between levels are tested using linear contrasts against primary producers. Species Press is also a categorical variable and differences are tested against the unmanipulated control level using linear contrasts. Solar Stress is an ordered factor, centered on the 'medium' level to test for differences from average conditions.

	a)			b)		
Factor	Estimate	Std. Error	p	Estimate	Std. Error	p
Intercept	-0.76	0.458	0.098	0.08	0.014	<.001
Time	0.04	0.077	0.590	0.00	0.002	0.065
Target Trophic Type						
Suspension	0.50	0.608	0.409	0.00	0.018	0.938
Consumer	0.76	0.565	0.180	0.02	0.017	0.273
Species Press						
Balanus	0.69	0.600	0.248	-0.05	0.018	0.071
Lottia	1.16	0.581	0.047	0.07	0.018	0.034
Solar Stress	-0.01	0.574	0.994	0.03	0.017	0.210
Target Trophic Type · Species Press						
Suspension · Balanus	-0.77	0.861	0.370	0.01	0.026	0.826
Suspension · Lottia	-0.64	0.796	0.421	-0.01	0.025	0.589
Consumer · Balanus	-0.02	0.767	0.975	0.00	0.023	0.990
Consumer · Lottia	-0.9	0.750	0.231	-0.03	0.023	0.161
Target Trophic Type · Solar Stress						
Suspension · Stress	-0.57	0.750	0.450	-0.03	0.023	0.254
Consumer · Stress	0.41	0.705	0.558	-0.04	0.021	0.084
Species Press · Solar Stress						
Balanus · Stress	-0.24	0.746	0.748	-0.02	0.022	0.394
Lottia · Stress	0.27	0.726	0.715	-0.05	0.022	0.100
Target Trophic Type · Species Press · Solar Stress						
Suspension · Balanus · Stress	1.26	1.107	0.254	0.03	0.033	0.370
Suspension · Lottia · Stress	0.22	0.987	0.825	0.04	0.031	0.236
Consumer · Balanus · Stress	0.20	0.956	0.836	0.03	0.028	0.327
Consumer · Lottia · Stress	-0.00	0.933	0.999	0.06	0.029	0.051

Table 4.8: Sign (a) and strength (b) of species interactions in response to stresses and presses. Target Trophic Type is a categorical factor and differences between levels are tested using linear contrasts against primary producers. Species Press is also a categorical variable and tested against the Fucus level using linear contrasts. Solar Stress is an ordered factor, centered on the 'medium' level to test for differences from average conditions.

(Paine and Levin 1981, Dethier 1984). At Prasiola Point, stress events often create open spaces in the high intertidal that are colonized by opportunistic ephemeral algae and grazers (Kim 1997). Over time, a succession of species follows, and at each successional stage there are important competitive and facilitative interactions. For example, the early colonizer *Chthamalus dalli* is out-competed by the more dominant barnacle, *Balanus*, which through negative effects on grazing *Lottia* and *Littorina* facilitates the recruitment of *Fucus* (Lubchenco 1983, Farrell 1991, van Tamelen and Stekoll 1996). *Fucus*, in turn, has a positive effect on *Mytilus californianus*, a mussel species that overgrows *Balanus* (Dayton 1971, Paine 1984). There is no point in this sequence that appears to be dominated by negative or positive interactions. Furthermore, because the high intertidal is a diverse mosaic of patches at different successional stages there is no consistent effect of stress on the prevailing interaction type or magnitude of the effects.

Lastly, heterogeneity at the landscape level may also explain the marked differences in magnitude of the effects between the natural stress gradient and experimental warming treatments (Figure 4.2). The high intertidal is subjected to large natural variations in temperature (Figure 4.3) and frequent disturbance (Dayton 1971). As a result, preexisting environmental heterogeneity is large relative to the predicted variations in temperature due to climate change. Thus, the warming treatments, which mimicked intermittent temperature stress events, had considerably less impact on diversity than the natural gradient in heat and desiccation stress at the study site.

Conclusions

The apparent contrast between the results presented here and other studies of stress on interaction webs suggests several possible explanations. First, this study is unique in that I examine the community-wide distribution of interactions, whereas most previous work has focused on interactions between a few key species. I demonstrate that although a few species interactions follow the expected pattern, most are weak, highly variable, and unpredictable. The community-wide approach also incorporates complex ecological relationships and interactive effects of biotic and abiotic processes that are not accounted for by current environmental stress models, but

can influence the strength of species interactions across the stress gradient. Second, this study and the experiments in Chapter 2 integrate results over multiple years, thereby discounting seasonal and annual differences in responses of species to changes in the environment. So although environmental stress has intermittent effects on facilitation (Bertness and Shumway 1993, Greenlee and Callaway 1996, Gasith and Resh 1999), these are offset by equally pronounced negative effects, such that over time the strength and frequency of negative and positive interactions in this high intertidal community is balanced.

4.5 Bibliography

Allison, G. 2004. The influence of species diversity and stress intensity on community resistance and resilience. Ecological Monographs 74:117–134.

Anderson, M.J. 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecology 26:32–46.

Bender, E.A., T.J. Case, and M.E. Gilpin. 1984. Perturbation experiments in community ecology: theory and practice. Ecology 65:1–13.

Bertness, M.D., and R. Callaway. 1994. Positive interactions in communities. Trends in Ecology and Evolution 9:191–193.

Bertness, M.D., and S.W. Shumway. 1993. Competition and facilitation in marsh plants. American Naturalist 142:718–724.

Brooker, R.W., and T.V. Callaghan. 1998. The balance between positive and negative plant interactions and its relationship to environmental gradients: a model. Oikos 81:196–207.

Bruno, J.F., J.J. Stachowicz, and M.D. Bertness. 2003. Inclusion of facilitation into ecological theory. Trends in Ecology and Evolution 18:119–125.

Callaway, R.M., R.W. Brooker, P. Choler, Z. Kikvidze, C.J. Lortie, R. Michalet, L. Paolini, F.I. Pugnaire, B. Newingham, E.T. Aschehoug, C. Armas, D. Kikodze, and B.J. Cook. 2002. Positive interactions among alpine plants increase with stress. Nature 417:844–848.

Callaway, R.M., and L.R. Walker. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. Ecology 78:1958–1965.

Chesson, P., and N. Huntly. 1997. The roles of harsh and fluctuating conditions in the dynamics of ecological communities. American Naturalist 150:519–553.

Connell, J.H. 1970. A predator-prey system in the marine intertidal region. I. *Balanus glandula* and several predatory species of *Thais*. Ecological Monographs 40:49–78.

Connell, J.H. 1972. Community interactions on marine rocky intertidal shores. Annual Review of Ecology and Systematics 3:169–192.

Connell, J.H. 1975. Some mechanisms producing structure in natural communities: a model and evidence from field experiments. Pages 460–490 in M.L. Cody and J. Diamond, editors. Ecology and Evolution of Communities. Belknap Press,

Cambridge.

Davis, A.J., L.S. Jenkinson, J.H. Lawton, B. Shorrocks, and S. Wood. 1998. Making mistakes when predicting shifts in species range in response to global warming. Nature 391:783–786.

Dayton, P. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecological Monographs 41:351–387.

Dayton, P., and M. Tegner. 1984. Catastrophic storms, El Niño, and patch stability in a Southern California kelp community. Science 224:283–285.

Dayton, P.K., R.G. A., R.T. Paine, and L.B. Dayton. 1974. Biological accommodation in benthic community at McMurdo Sound, Antarctica. Ecological Monographs 44:105–128.

Denny, M.W., L.P. Miller, and C.D.G. Harley. 2006. Thermal stress on intertidal limpets: long-term hindcasts and lethal limits. Journal of Experimental Biology 209:2420–2431.

Dethier, M.N. 1984. Disturbance and recovery in intertidal pools: maintenance of mosaic patterns. Ecological Monographs 54:99–118.

Duffy, J.E. 2003. Biodiversity loss, trophic skew and ecosystem functioning. Ecology Letters 6:680–687.

Dunmore, R.A. 2006. Demography of early life stages of habitat-forming intertidal fucoid algae. PhD Thesis. University of Canterbury, Christchurch.

Farrell, T. 1991. Models and mechanisms of succession: an example from a rocky intertidal community. Ecological Monographs 61:95–113.

Fields, P.A., J.B. Graham, R.H. Rosenblatt, and G.N. Somero. 1993. Effects of expected global climate change on marine faunas. Trends in Ecology and Evolution 8:361–367.

Garrity, S.D. 1984. Some adaptations of gastropods to physical stress on a tropical rocky shore. Ecology 65:559–574.

Gasith, A., and V.H. Resh. 1999. Streams in Mediterranean climate regions: abiotic influences and biotic responses to predictable seasonal events. Annual Review of Ecology and Systematics 30:51–81.

Gilman, S.E., D.S. Wethey, and B. Helmuth. 2006. Variation in the sensitivity of organismal body temperature to climate change over local and geographic

scales. Proceedings of the National Academy of Sciences of the United States of America 103:9560–9565.

Greenlee, J.T., and R.M. Callaway. 1996. Abiotic stress and the relative importance of interference and facilitation in montane bunchgrass communities in Western Montana. American Naturalist 148:386–396.

Grime, J.P. 1979. Plant Strategies and Vegetation Processes. Wiley, Chichester.

Hacker, S.D., and S.D. Gaines. 1997. Some implications of direct positive interactions for community species diversity. Ecology 78:1990–2003.

Hairston, N.G., F.E. Smith, and L.B. Slobodkin. 1960. Community structure, population control, and competition. American Naturalist 94:421–425.

Harley, C.D.G. 2006. Effects of physical ecosystem engineering and herbivory on intertidal community structure. Marine Ecology Progress Series 317:29–39.

Harley, C.D.G. 2008. Tidal dynamics, topographic orientation, and temperature-mediated mass mortalities on rocky shores. Marine Ecology Progress Series 371:37–46.

Harley, C.D.G., A.R. Hughes, K.M. Hultgren, B.G. Miner, C.J.B. Sorte, C.S. Thornber, L.F. Rodriguez, L. Tomanek, and S.L. Williams. 2006. The impacts of climate change in coastal marine systems. Ecology Letters 9:228–241.

Harley, C.D.G., and J.P. Lopez. 2003. The natural history, thermal physiology, and ecological impacts of intertidal mesopredators, *Oedoparena* spp. (Diptera : Dryomyzidae). Invertebrate Biology 122:61–73.

Harte, J., and R. Shaw. 1995. Shifting dominance within a montane vegetation community: results of a climate-warming experiment. Science 267:876–880.

Helmuth, B., B.R. Broitman, C.A. Blanchette, S. Gilman, P. Halpin, C.D.G. Harley, M.J. O'Donnell, G.E. Hofmann, B. Menge, and D. Strickland. 2006. Mosaic patterns of thermal stress in the rocky intertidal zone: implications for climate change. Ecological Monographs 76:461–479.

Helmuth, B.S.T., and G.E. Hoffmann. 2001. Microhabitats, thermal heterogeneity, and patterns of physiological stress in the rocky intertidal zone. Biological Bulletin 201:374–384.

Huston, M. 1979. A general hypothesis of species diversity. American Naturalist 113:81–101.

Hutchins, L. 1947. The bases for temperature zonation in geographical distribution. Ecological Monographs 17:325–335.

Hutchinson, G. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? American Naturalist 93:145–159.

Hutchinson, G.E. 1961. The paradox of the plankton. American Naturalist 95:137–145.

Ives, A.R. 1995. Predicting the response of populations to environmental change. Ecology 76:926–941.

Jiang, L., and P.J. Morin. 2004. Temperature-dependent interactions explain unexpected responses to environmental warming in communities of competitors. Journal of Animal Ecology 73:569–576.

Kim, J. 1997. The role of herbivory, and direct and indirect interactions, in algal succession. Journal of Experimental Marine Biology and Ecology 217:119–135.

Laska, M.S., and J.T. Wootton. 1998. Theoretical concepts and empirical approaches to measuring interaction strength. Ecology 79:461–476.

Lehmann-Ziebarth, N., and A.R. Ives. 2006. The structure and stability of model ecosystems assembled in a variable environment. Oikos 114:451–464.

Logan, J.A., J. Regniere, and J.A. Powell. 2003. Assessing the impacts of global warming on forest pest dynamics. Frontiers in Ecology and the Environment 1:130–137.

Louda, S.M. 1986. Insect herbivory in response to root cutting and flooding stress on a native crucifer under field conditions. Acta Oecologica 7:37–53.

Lubchenco, J. 1983. *Littorina* and *Fucus*: effects of herbivores substratum heterogeneity, and plant escapes during succession. Ecology 6:1116–1123.

Menge, B.A. 1976. Organization of the New England rocky intertidal community: role of predation, competition, and environmental heterogeneity. Ecological Monographs 46:355–393.

Menge, B.A., and T.M. Farrell. 1989. Community structure and interaction webs in shallow marine hard bottom communities: tests of an environmental stress model. Advances in Ecological Research 19:189–262.

Menge, B.A., J. Lubchenco, S.D. Gaines, and L.R. Ashkenas. 1986. A test of the Menge-Sutherland model of community organization in a tropical rocky intertidal food web. Oecologia 71:75–89.

Menge, B.A., and A.M. Olson. 1990. Role of scale and environmental factors in regulation of community structure. Trends in Ecology and Evolution 5:52–57.

Menge, B.A., and J.P. Sutherland. 1976. Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. American Naturalist 110:351–369.

Menge, B.A., and J.P. Sutherland. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. American Naturalist 130:730–757.

Newell, R.C. 1969. Effect of fluctuations in temperature on metabolism of intertidal invertebrates. American Zoologist 9:293–307.

Paine, R.T. 1966. Food web complexity and species diversity. American Naturalist 100:65–75.

Paine, R.T. 1984. Ecological determinism in the competition for space. Ecology 65:1339–1348.

Paine, R.T., and S.A. Levin. 1981. Intertidal landscapes: disturbance and the dynamics of pattern. Ecological Monographs 51:145–178.

Petchey, O., P. McPhearson, R. Casey, and P. Morin. 1999. Environmental warming alters food-web structure and ecosystem function. Nature 402:67–72.

Pfister, C.A. 1995. Estimating competition coefficients from census data: a test with field manipulations of tidepool fishes. American Naturalist 146:271–291.

Pinheiro, J.C., and D.M. Bates. 2000. Mixed-Effects Models in S and S-PLUS. Springer, New York, NY.

Post, E., and C. Pedersen. 2008. Opposing plant community responses to warming with and without herbivores. Proceedings of the National Academy of Sciences of the United States of America 105:12353–12358.

Preisser, E.L., and D.R. Strong. 2004. Climate affects predator control of an herbivore outbreak. American Naturalist 163:754–762.

Questad, E.J., and B.L. Foster. 2008. Coexistence through spatio-temporal heterogeneity and species sorting in grassland plant communities. Ecology Letters 11:717–726.

R Development Core Team. 2008. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Raffaelli, D., and S. Hall. 1996. Assessing the relative importance of trophic links in food webs. Pages 185–191 in G.A. Polis and K.O. Winemiller, editors. Food Webs: Integration of Patterns and Dynamics. Chapman and Hall, New York.

Sanford, E. 1999. Regulation of keystone predation by small changes in ocean temperature. Science 283:2095–2097.

Schmitz, O.J. 1997. Press perturbations and the predictability of ecological interactions in a food web. Ecology 78:55–69.

Somero, G.N. 2002. Thermal physiology and vertical zonation of intertidal animals: optima, limits, and costs of living. Integrative and Comparative Biology 42:780–789.

Sousa, W. 1979. Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. Ecology 60:1225–1239.

Southward, A.J. 1958. Note on the temperature tolerances of some intertidal animals in relation to environmental temperatures and geographical distribution. Journal of the Marine Biological Association of the United Kingdom 37:49–66.

Suttle, K.B., M.A. Thomsen, and M.E. Power. 2007. Species interactions reverse grassland responses to changing climate. Science 315:640–642.

Terborgh, J., L. Lopez, P. Nunez, M. Rao, G. Shahabuddin, G. Orihuela, M. Riveros, R. Ascanio, G.H. Adler, T.D. Lambert, and L. Balbas. 2001. Ecological meltdown in predator-free forest fragments. Science 294:1923–1926.

Tilman, D. 1988. Plant Strategies and the Dynamics and Structure of Plant Communities. Princeton University Press, Princeton.

Tomanek, L., and B. Helmuth. 2002. Physiological ecology of rocky intertidal organisms: a synergy of concepts. Integrative and Comparative Biology 42:771–775.

Tsuchiya, M. 1983. Mass mortality in a population of the mussel *Mytilus edulis* L. caused by high temperature on rocky shores. Journal of Experimental Marine Biology and Ecology 66:101–111.

van Tamelen, P., and M. Stekoll. 1996. The role of barnacles in the recruitment and subsequent survival of the brown alga, *Fucus gardneri* (Silva). Journal of Experimental Marine Biology and Ecology 208:227–238.

Welden, C.W., and W.L. Slauson. 1986. The intensity of competition versus its importance: an overlooked distinction and some implications. The Quarterly

Review of Biology 61:23–44.

Wethey, D.S. 1983. Geographic limits and local zonation: the barnacles *Semibalanus* (*Balanus*) and *Chthamalus* in New England. Biological Bulletin 165:330–341.

Wethey, D.S. 1984. Sun and shade mediate competition in the barnacles *Chthamalus* and *Semibalanus*: a field experiment. Biological Bulletin 167:176–185.

Wiens, J.A. 1977. Competition and variable environments. American Scientist 65:590–597.

Williams, G.A., and D. Morritt. 1995. Habitat partitioning and thermal tolerance in a tropical limpet, *Cellana grata*. Marine Ecology Progress Series 124:89–103.

Wilmers, C.C., and E. Post. 2006. Predicting the influence of wolf-provided carrion on scavenger community dynamics under climate change scenarios. Global Change Biology 12:403–409.

Wootton, J.T., C.A. Pfister, and J.D. Forester. 2008. Dynamic patterns and ecological impacts of declining ocean pH in a high-resolution multi-year dataset. Proceedings of the National Academy of Sciences of the United States of America 105:18848–18853.

Chapter 5

Concluding remarks

5.1 A synopsis

A variety of environmental, organismal, and scale-dependent variables dictate the nature of species interactions in communities (Elton 1927, Paine 1966, Grime 1973, Menge 1976). Predicting the relative importance of these factors has been a primary goal of theoretical and empirical research for decades (Hutchinson 1959, Hairston et al. 1960, Dayton and Tegner 1984, Menge and Sutherland 1976). However, due to the logistical challenge of quantifying species interactions in diverse communities, most studies focus on only one explanatory variable, in a single location, for short periods of time (Polis 1994). Few studies assess multiple factors influencing species interactions in combination, and consequently we do not know the degree to which interactions are contingent on biotic and abiotic context. Research that examines this context-dependency and how it evolves over space and time is critical for developing effective conservation and management plans (Berlow et al. 2004, Soule et al. 2005, Wootton and Emmerson 2005, Agrawal et al. 2007).

A primary goal of this dissertation was to grapple with the challenge of assessing the relative importance of the multiple biotic and abiotic factors that influence the sign and strength of species interactions. In Chapter 2 I presented a synthetic test of six variables suggested to influence species interactivity (diversity, environmental stress, spatial and temporal scale, body size, and trophic status) using field experiments at sites in the Northern and Southern Pacific. In Chapter 4 I took a more detailed look at how one abiotic factor, heat stress, affected species interactions, and how feedbacks between the biotic and abiotic processes secondarily altered community structure. In Chapter 3 I tested the validity of one assumption of the methods used to quantify species interaction coefficients, that interactions are linear across a broad range of densities of the focal species. The main conclusions of the research

are outlined below.

Organismal traits, not environment, predict interactivity

Interaction strengths are related to traits of species, such as body size and trophic level, but are insensitive to environmental conditions such as tidal height or the level of abiotic stress (Chapter 2, 4). These results are encouraging because they indicate that the shape of interaction webs can be predicted without detailed information on particular species. Although larger organisms with higher trophic positions have stronger per-capita effects, their populations have equivalent impacts to lower trophic groups. Population densities decline with increasing body size and trophic status, and together these changes yield a comparable population-level impact on other community members across a range of sizes (Chapter 2). This suggests that interaction intensity is based on requirements for resources, such as for food or space, that show similar allometric relationships. These conclusions are supported by previous research showing that body size is correlated with several allometric properties including metabolism, home range, abundance, and trophic status (Brown et al. 2004, Woodward et al. 2005), and scaled to interaction strength in food webs (Jonsson and Ebenman 1998, Emmerson and Raffaelli 2004).

Interactions follow a predictable community-wide distribution

My experiments confirm that rocky intertidal communities are characterized by many weak and few strong species interactions (Chapter 2–4). Previous studies in the rocky intertidal (Paine 1992, Wootton 1997) and other ecosystems (Raffaelli and Hall 1996, de Ruiter et al. 1995) have found similar patterns in interaction strength, typically between predators and their prey. According to theory, this configuration stabilizes ecosystems because weak interactions balance oscillatory dynamics caused by strong links (McCann et al. 1998). I provide additional empirical evidence that weak links are important stabilizing elements of communities by showing that greater proportions of weak interactors are associated with more diverse assemblages (Chapter 2). I also observe that there are balanced proportions of positive and negative interactions in communities (Chapter 2–4). This is an interesting result because prior research on subsets of species has concluded that the environment

affects interactions in a consistent fashion. For example, studies have shown that positive interactions are more important in harsher environments (e.g. Callaway and Walker 1997). However, I find that while the environment alters certain pairwise interactions, it does not favor positive or negative effects (Chapter 2, 4).

Effects of species are linear across a range of densities

The per-capita effects of intertidal species are approximately linear across their range of natural densities. This was verified using short-term perturbation experiments which showed that the impact of one species on another increased as a linear function of its density, and that nonlinear interaction strength estimates did not improve our ability to predict the response of populations to perturbations (Chapter 3). This result is interesting for a number of reasons. First, it allows interaction coefficients to be measured more easily in the field, because experiments at one focal density can be used to estimate focal species' per-capita effects at other densities. Second, although nonlinear effects are common in nature (Abrams 2001, Jeschke et al. 2004), it appears that they do not result in more unpredictable dynamics. Nonlinearities in interactions may be obscured by variation in the environment. Nonetheless, it appears that linear interaction coefficients can serve as more pragmatic estimates of interaction intensity (Pfister 1995, Schmitz 1997, Wootton 1997).

5.2 Looking forward

Species interactions have provided a foundation for many of the earliest ecological and evolutionary theories, dating back over 100 years (Haeckel 1866, Warming 1896, Lotka 1925, Elton 1927). In 1887, Stephen Forbes observed that competition and predation were particularly important interactions between species in lakes and stated:

> If one wishes to become acquainted with the black bass, for example, ...he must evidently study also the species upon which it depends for its existence, and the various conditions upon which these depend. He must likewise study the species with which it comes in competition, and the entire system of conditions affecting their prosperity (p. 77).

In the intervening century, considerable research has examined the causes and consequences of species interactions, yet the field is, in many ways, in its infancy. We still have a limited ability to predict the outcomes of perturbations to ecosystems, particularly the impacts of species introductions and extinctions. Here I discuss some of the barriers to progress and prospects for future research on species interactions.

Choosing an interaction metric

Vagaries in the definition of an 'interaction strength' have historically created confusion. The per-capita metrics that I use throughout this dissertation are useful because they are related to the Lotka-Volterra interaction coefficient that forms the basis of many dynamical models of communities (Laska and Wootton 1998, Abrams 2001). However, there are a number of other useful metrics that quantify interactions differently and offer unique advantages (Berlow et al. 2004). As I showed in Chapter 2, for example, there can be disparities between species' per-capita and per-population effects. While per-capita interaction strengths are often useful, they are at other times problematic, like when comparing populations containing disparate numbers of individuals (e.g. across trophic levels). Studies addressing the loss of whole populations may find a per-population interaction metric more prudent (Duffy 2003). Ultimately it is up to empiricists to select the measure that is most appropriate to their research question. Since it is unlikely that any one metric of interaction strength will ever meet everyone's needs, clearly defining the chosen measure will be critical.

Direct and indirect interactions

The per-capita interaction strengths I use are an amalgamated measure of an organism's direct and indirect effects on a population. When indirect effects are minimal, this measure is related to the Lotka-Volterra interaction coefficient, α_{ij} (Laska and Wootton 1998). Theoretically, indirect effects take longer to manifest since they are transmitted along chains of direct interactions (Davidson et al. 1984, Yodzis 1988). Therefore, short term perturbation experiments measure predominantly direct effects (the definition of 'short term' depends on the numerical responses of the species, their generation times, and population grown rates). However, results presented in

this thesis (Chapter 2), and in other intertidal research (Menge 1997), indicate that direct and indirect interactions occur in concert over all time scales from one day to 10 years. It would be sensible, therefore, to consider my studies, and others using the same technique (e.g. Paine 1992, Fagan and Hurd 1994, Raffaelli and Hall 1996), as preliminary tests of the theoretical predictions, until further studies can explore the associations between the separate and combined measures. This may be accomplished using experiments that estimate direct effects independently of the indirect ones (e.g. Wootton 1994, Schmitz 1997). For example, it might be possible to measure direct effects using factorial combinations of species pairs in the field and then compare the results to those from more complex communities in which indirect effects also operate, as Neill (1974) did with small aquatic crustaceans and algae in laboratory microcosms.

Ontogenetic shifts

In the field, I quantified responses of entire populations, and this may have masked important ontogenic differences in their interactivity (Werner and Gilliam 1984). As organisms develop they frequently change habitats (Werner et al. 1983), resource use (Sebens 1981, Hines 1982), and environmental tolerance (Kellman and Kading 1992, Sans et al. 1998). Often these shifts correspond with differences in diet (Clady 1974, Grossman 1980) and predation risk (Paine 1976, Foster et al. 1988, Markel and DeWreede 1998) due to increased body size. As a result, interactions between populations can fluctuate between positive and negative depending on the ontogeny of the focal and target organisms (Berkowitz et al. 1995, Rousset and Lepart 2000, Miriti 2006). For example, on intertidal mud flats, burrows created by adult *Neohelice granulata* crabs facilitate recruitment by the mud crab *Cyrtograpsus angulatus*. However, *N. granulata* adults also predate large juvenile *C. angulatus* and this results in a shift from positive to negative effects of burrowing crabs as mud crabs develop (Casariego et al. 2009). Analytically, ontogeny could be incorporated into the multilevel framework I used throughout this dissertation by including it as an additional random level (see Appendix A). For example, to test for differences between interactivity of juveniles and adults, life stage could be nested within population, and its effects could be compared to factors at the population level or at

higher random levels such as whole communities.

Trophic and nontrophic interactions

A parallel line of research on food webs measures interaction strength as the contribution of species to the diets of others. Studies have shown that interaction strength, α_{ij}, can be estimated using predator:prey body size, W, as $\alpha_{ij} = \phi \cdot W^{\theta}$, where ϕ and θ are constants (Emmerson et al. 2005). Nontrophic effects are minimal and therefore interactions between other pairs of species are near zero. Emmerson and Raffaelli (2004) tested this technique with intertidal crabs and shrimp from the Ythan Estuary and successfully predicted interaction strengths when $\phi = 0.007$ and $\theta \approx 0.75$. It is unclear, however, whether the model can be applied at other sites, such as Prasiola Point (Figure 1.1).

Factor	df	SS	MS	F	p
Size Ratio	1	0.049	0.049	0.112	0.743
Trophic	1	1.135	1.135	2.606	0.129
Sign	1	0.165	0.165	0.378	0.549
Size Ratio · Trophic	1	0.878	0.878	2.014	0.178
Size Ratio · Sign	1	0.553	0.553	1.268	0.279
Trophic · Sign	1	0.019	0.019	0.043	0.839
Size Ratio · Trophic · Sign	1	1.334	1.334	3.061	0.102
Residuals	14	6.101	0.436		

Table 5.1: Results from an analysis of variance used to determine whether variation in interaction strength is explained by the focal:target body size ratio, the type of interaction (trophic or nontrophic), and the interaction sign (negative or positive).

I contrasted interaction strengths measured in a *Lottia digitalis* press experiment in the field (Chapter 3) with the focal:target body sizes of the species and found no relationship (Table 5.1). Interactions were much stronger than predicted for both predator-prey pairs and nontrophic links (Figure 5.1). The body size ratio was also unable to explain variation in the strength of negative versus positive interactions. Body sizes were measured as the average mass of an individual of a population. I chose the *L. digitalis* press because it was the only experiment in which I quantified both focal and target body sizes, and the focal species was a consumer. Target prey of *L. digitalis* were identified using a food web assembled for a site elsewhere in the region (Maschner et al. 2009).
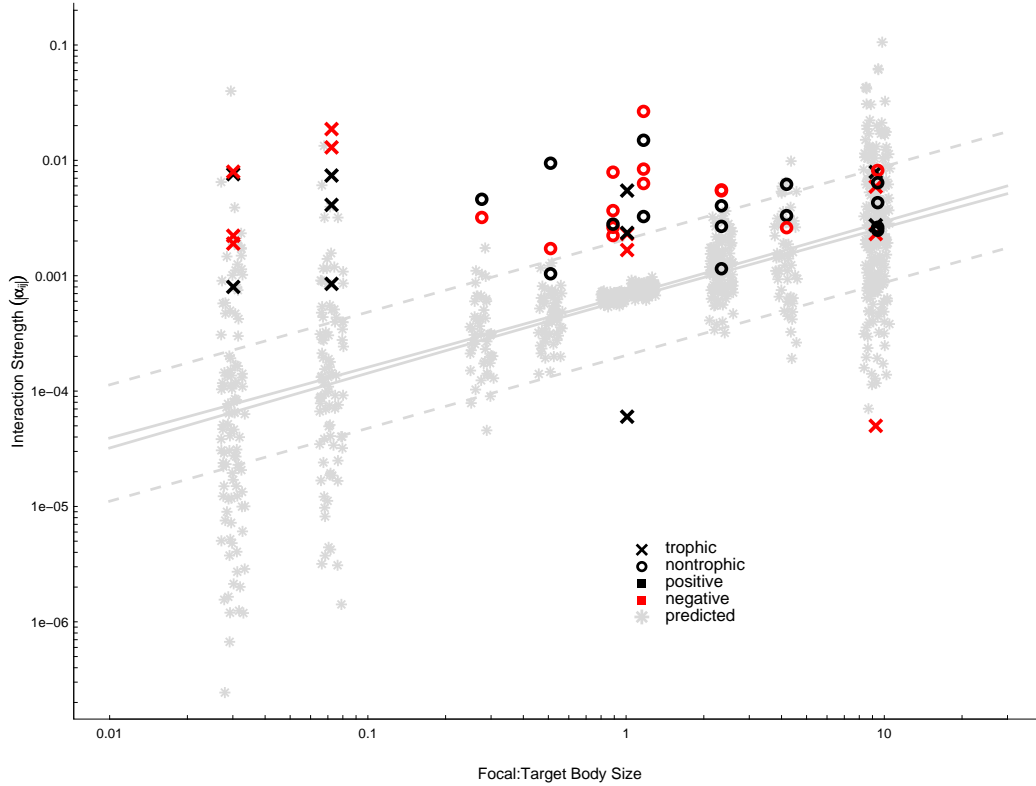
Figure 5.1: The relationship between interaction strength and focal:target body size. Black and red symbols represent the absolute effect of *L. digitalis* on a target population over one time period, with black symbols showing the strength of positive effects on target populations and red symbols showing negative interactions. Potential prey of *L. digitalis* are represented by an x, and nonprey populations are shown as an o. The grey points display the relationship between predator:prey body size, W, and interaction strength, α_{ij}, predicted by Emmerson and Raffaelli (2004) to be $\alpha_{ij} = 0.007 * W^{0.60\pm0.14 \ (1SE)}$. The focal:target body sizes measured in the field were used in this equation to generate 1000 simulated interaction coefficients. The dotted grey lines show two standard errors of the estimates, and the solid grey lines show two standard errors of the predicted response values.

The results (Table 5.1, Figure 5.1) can be explained by the presence of strong nontrophic effects. This is supported by the observation that *L. digitalis* has equally strong effects on prey and nonprey taxa. In one study on trophic and nontrophic effects of *L. digitalis* on the barnacle *Balanus glandula*, Miller and Carefoot (1989) observed that 26% of juvenile *B. glandula* mortality was due to predation by *L. digitalis*, while 74% was the result of the barnacles being physically 'bulldozed' off the substrate by the limpets. *L. digitalis* also grazes young *Fucus gardneri*, however, it prefers to eat the ephemeral algae and epiphytes that compete with *F. gardneri* for light and nutrients (Lubchenco 1983, Kim 1997, Blanchette 1997). These indirect effects may be concealing a relationship between body size and direct interaction strength, however, it is unlikely that they account for the entire discrepancy of the results. One last possibility is that the model is site specific, and simply needs to be parameterized for Prasiola Point. However, the slope of the relationship between body size and interaction strength at Prasiola Point is not significantly different from zero, meaning that other factors, such as the strength of nontrophic and indirect effects, are probably more deserved of attention.

5.3 Conclusion

In a recent review, Agrawal et al. (2007) stated that progress in community ecology is limited by a lack of knowledge in four primary areas:

> 1) how biotic and abiotic contexts shape the strength of species interactions, 2) the degree to which the distribution and abundance of a given species are influenced by interspecific interactions, 3) how biotic and abiotic factors interact and vary in magnitude over time or space, and 4) how variation in the abundance of particular species influences variation in the abundance of the species with which they interact (p. 2).

My thesis research provides answers to these four questions, while also reconciling discrepancies in the conclusions of prior studies. Ultimately, I anticipate this dissertation will advance our understanding of the processes that generate patterns of species distribution and abundance in communities, and improve our capacity to predict how ecosystems will respond to future change.

5.4 Bibliography

Abrams, P.A. 2001. Describing and quantifying interspecific interactions: a commentary on recent approaches. Oikos 94:209–218.

Agrawal, A.A., D.D. Ackerly, F. Adler, A.E. Arnold, C. Caceres, D.F. Doak, E. Post, P.J. Hudson, J. Maron, K.A. Mooney, M. Power, D. Schemske, J. Stachowicz, S. Strauss, M.G. Turner, and E. Werner. 2007. Filling key gaps in population and community ecology. Frontiers in Ecology and the Environment 5:145–152.

Berkowitz, A.R., C.D. Canham, and V.R. Kelly. 1995. Competition vs. facilitation of tree seedling growth and survival in early successional communities. Ecology 76:1156–1168.

Berlow, E.L., A.M. Neutel, J.E. Cohen, P.C. de Ruiter, B. Ebenman, M. Emmerson, J.W. Fox, V.A.A. Jansen, J.I. Jones, G.D. Kokkoris, D.O. Logofet, A.J. McKane, J.M. Montoya, and O. Petchey. 2004. Interaction strengths in food webs: issues and opportunities. Journal of Animal Ecology 73:585–598.

Blanchette, C. 1997. Size and survival of intertidal plants in response to wave action: a case study with *Fucus gardneri*. Ecology 78:1563–1578.

Brown, J.H., J.F. Gillooly, A.P. Allen, V.M. Savage, and G.B. West. 2004. Toward a metabolic theory of ecology. Ecology 85:1771–1789.

Callaway, R.M. and L.R. Walker. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. Ecology 78:1958–1965.

Casariego, A.M., J. Alberti, T. Luppi, and O. Iribarne. 2009. Stage-dependent interactions between intertidal crabs: from facilitation to predation. Journal of the Marine Biological Association of the United Kingdom 89:781-788.

Clady, M.D. 1974. Food habits of yellow perch, smallmouth bass and largemouth bass in two unproductive lakes in northern Michigan. American Midland Naturalist 91:453–459.

Davidson, D.W., R.S. Inouye, and J.H. Brown. 1984. Granivory in a desert ecosystem: experimental evidence for indirect facilitation of ants by rodents. Ecology 65:1780–1786.

Dayton, P. and M. Tegner. 1984. Catastrophic storms, El Niño, and patch stability in a Southern California kelp community. Science 224:283–285.

de Ruiter, P.C., A.M. Neutel, and J.C. Moore. 1995. Energetics, patterns of interaction strengths, and stability in real ecosystems. Science 269:1257–1260.

Duffy, J.E. 2003. Biodiversity loss, trophic skew and ecosystem functioning. Ecology Letters 6:680–687.

Elton, C. 1927. Animal Ecology. Sidgwick and Jackson, London.

Emmerson, M.C., J.M. Montoya, and G. Woodward. 2005. Body size, interaction strength, and food web dynamics. Pages 167–178 in P.C. de Ruiter, V. Wolters, and J.C. Moore, editors. Dynamic Food Webs: Multispecies Assemblages, Ecosystem Development, and Environmental Change. Academic Press, Amsterdam.

Emmerson, M.C. and D. Raffaelli. 2004. Predator-prey body size, interaction strength and the stability of a real food web. Journal of Animal Ecology 73:399–409.

Fagan, W.F. and L.E. Hurd. 1994. Hatch density variation of a generalist arthropod predator: population consequences and community impact. Ecology 75:2022–2032.

Forbes, S.A. 1887. The lake as a microcosm. Bulletin of the Peoria Scientific Association 1887:77–87.

Foster, S.A., V.B. Garcia, and M.Y. Town. 1988. Cannibalism as the cause of an ontogenetic shift in habitat use by fry of the threespine stickleback. Oecologia 74:577–585.

Grime, J.P. 1973. Competitive exclusion in herbaceous vegetation. Nature 242:344–347.

Grossman, G.D. 1980. Ecological aspects of ontogenetic shifts in prey size utilization in the bay goby (Pisces, Gobiidae). Oecologia 47:233–238.

Haeckel, E. 1866. Generelle Morphologie der Organismen. Druck und Verlag von Georg Reimer, Berlin.

Hairston, N.G., F.E. Smith, and L.B. Slobodkin. 1960. Community structure, population control, and competition. American Naturalist 94:421–425.

Hines, A.H. 1982. Coexistence in a kelp forest: size, population dynamics, and resource partitioning in a guild of spider crabs (Brachyura, Majidae). Ecological Monographs 52:179–198.

Hutchinson, G.E. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? American Naturalist 93:145–159.

Jeschke, J.M., M. Kopp, and R. Tollrian. 2004. Consumer-food systems: why type I functional responses are exclusive to filter feeders. Biological Reviews 79:337–349.

Jonsson, T. and B. Ebenman. 1998. Effects of predator-prey body size ratios on the stability of food chains. Journal of Theoretical Biology 193:407–417.

Kellman, M. and M. Kading. 1992. Facilitation of tree seedling establishment in a sand dune succession. Journal of Vegetation Science 3:679–688.

Kim, J. 1997. The role of herbivory, and direct and indirect interactions, in algal succession. Journal of Experimental Marine Biology and Ecology 217:119–135.

Laska, M.S. and J.T. Wootton. 1998. Theoretical concepts and empirical approaches to measuring interaction strength. Ecology 79:461–476.

Lotka, A.J. 1925. Elements of Physical Biology. Williams and Wilkins, Baltimore.

Lubchenco, J. 1983. *Littorina* and *Fucus*: effects of herbivores substratum heterogeneity, and plant escapes during succession. Ecology 6:1116–1123.

Markel, R.W. and R.E. DeWreede. 1998. Mechanisms underlying the effect of the chiton *Katharina tunicata* on the kelp *Hedophyllum sessile*: size escapes and indirect effects. Marine Ecology Progress Series 166:151–161.

Maschner, H.D.G., M.W. Betts, J. Cornell, J.A. Dunne, B. Finney, N. Huntly, J.W. Jordan, A.A. King, N. Misarti, K.L. Reedy-Maschner, R. Russell, A. Tews, S.A. Wood, and B. Benson. 2009. An introduction to the biocomplexity of Sanak Island, Western Gulf of Alaska. Pacific Science 63:673–709.

McCann, K., A. Hastings, and G.R. Huxel. 1998. Weak trophic interactions and the balance of nature. Nature 395:794–798.

Menge, B.A. 1976. Organization of the New England rocky intertidal community: role of predation, competition, and environmental heterogeneity. Ecological Monographs 46:355–393.

Menge, B.A. 1997. Detection of direct versus indirect effects: were experiments long enough? American Naturalist 149:801–823.

Menge, B.A. and J.P. Sutherland. 1976. Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. American Naturalist 110:351–369.

Miller, K.M. and T.H. Carefoot. 1989. The role of spatial and size refuges in the interaction between juvenile barnacles and grazing limpets. Journal of Experimental Marine Biology and Ecology 134:157–174.

Miriti, M.N. 2006. Ontogenetic shift from facilitation to competition in a desert shrub. Journal of Ecology 94:973–979.

Neill, W.E. 1974. The community matrix and interdependence of the competition coefficients. American Naturalist 108:399–408.

Paine, R.T. 1966. Food web complexity and species diversity. American Naturalist 100:65–75.

Paine, R.T. 1976. Size-limited predation: an observational and experimental approach with the *Mytilus-Pisaster* interaction. Ecology 57:858–873.

Paine, R.T. 1992. Food-web analysis through field measurement of per-capita interaction strength. Nature 355:73–75.

Pfister, C.A. 1995. Estimating competition coefficients from census data: a test with field manipulations of tidepool fishes. American Naturalist 146:271–291.

Polis, G.A. 1994. Food webs, trophic cascades and community structure. Australian Journal of Ecology 19:121–136.

Raffaelli, D. and S. Hall. 1996. Assessing the relative importance of trophic links in food webs. Pages 185–191 in G.A. Polis and K.O. Winemiller, editors. Food Webs: Integration of Patterns and Dynamics. Chapman and Hall, New York.

Rousset, O. and J. Lepart. 2000. Positive and negative interactions at different life stages of a colonizing species (*Quercus humilis*). Journal of Ecology 88:401–412.

Sans, F.X., J. Escarre, V. Gorse, and J. Lepart. 1998. Persistence of *Picris hieracioides* populations in old fields: an example of facilitation. Oikos 83:283–292.

Schmitz, O.J. 1997. Press perturbations and the predictability of ecological interactions in a food web. Ecology 78:55–69.

Sebens, K.P. 1981. The allometry of feeding, energetics, and body size in three sea anemone species. Biological Bulletin 161:152–171.

Soule, M.E., J.A. Estes, B. Miller, and D.L. Honnold. 2005. Strongly interacting species: conservation policy, management, and ethics. Bioscience 55:168–176.

Warming, E. and M. Vahl. 1909. Oecology of Plants: an Introduction to the Study of Plant-communities. Clarendon Press, Oxford.

Werner, E.E. and J.F. Gilliam. 1984. The ontogenetic niche and species interactions in size structured populations. Annual Review of Ecology and Systematics 15:393–425.

Werner, E.E., G.G. Mittelbach, D.J. Hall, and J.F. Gilliam. 1983. Experimental tests of optimal habitat use in fish: the role of relative habitat profitability. Ecology 64:1525–1539.

Woodward, G., B. Ebenman, M. Ernmerson, J.M. Montoya, J.M. Olesen, A. Valido, and P.H. Warren. 2005. Body size in ecological networks. Trends in Ecology and Evolution 20:402–409.

Wootton, J.T. 1994. Predicting direct and indirect effects: an integrated approach using experiments and path analysis. Ecology 75:151–165.

Wootton, J.T. 1997. Estimates and tests of per capita interaction strength: diet, abundance, and impact of intertidally foraging birds. Ecological Monographs 67:45–64.

Wootton, J.T. and M. Emmerson. 2005. Measurement of interaction strength in nature. Annual Review of Ecology Evolution and Systematics 36:419–444.

Yodzis, P. 1988. The indeterminacy of ecological interactions as perceived through perturbation experiments. Ecology 69:508–515.

Appendix A

Multilevel models

A.1 Overview

The following provides a brief introduction to the multilevel modeling techniques used throughout this dissertation. It is not intended to be a comprehensive review, rather a summary of the basic procedure, with references to more in-depth information. This primer is aimed at readers who have a working understanding of linear regression and mixed-effects models. For more complete information on multilevel models see Kreft and de Leeuw (1998), Pinheiro and Bates (2000), or Raudenbush and Bryk (2002).

Sometimes referred to as a hierarchical model, a multilevel model is a generalization of a mixed-effects model. Nested regression equations are used to explain variation in the response variable at each level of a hierarchy. Explanatory variables can be incorporated into the model at the level at which they were measured (or aggregated and included at higher levels). As I will show in the example below, these models are adept at accounting for the statistical non-independence of observations within levels, and, like other general linear models, they are suitable for unbalanced data.

A.2 An example

McMahon and Diez (2007) provide a simple ecological example which I will summarize here. Imagine a hypothetical assemblage of plants being grazed by a herbivore. Suppose the variation in leaf damage due to herbivory can be explained by attributes of the individual plant (e.g. its initial height) as well as factors at the level of an entire 'patch' (e.g. its species richness). For individual plants, a simple linear regression can be used to represent leaf damage, Y, as a function of initial plant height,

X, as

$$Y_{ij} = \beta_{0j} + \beta_{1j}X_{ij} + r_{ij} \tag{A.1}$$

in which an individual plant i belongs to patch j. Note that the slope, β_{0j}, and intercept, β_{1j}, as well as the residual errors, r_{ij}, refer to patch-level estimates that include all individuals nested within a given patch.

In the second level of the analysis, species richness is used to explain within-patch variation in the β coefficients of Equation A.1. This is done using two higher-level regressions that separate the within-patch coefficients into group means and deviations from the means as

$$\beta_{0j} = \gamma_{00} + \gamma_{01}W_j + \mu_{0j} \tag{A.2}$$

$$\beta_{1j} = \gamma_{10} + \gamma_{11}W_j + \mu_{1j} \tag{A.3}$$

In these equations, W is the patch-level predictor, species richness. μ_{0j} and μ_{1j} are the random deviations of each patch from the overall mean. The intercepts and slopes predicted at level one (β_{0j} and β_{1j}) are treated as responses in level two, with their own intercepts (γ_{00} and γ_{10}) and slopes (γ_{01} and γ_{11}). The level-two equations (Equation A.2–A.3) can be substituted into Equation A.1 to give the full model,

$$Y_{ij} = \gamma_{00} + \gamma_{01}W_j + \gamma_{10}X_{ij} + \gamma_{11}W_jX_{ij} + \mu_{0j} + \mu_{1j}X_{ij} + r_{ij} \tag{A.4}$$

which partitions the within- and between-patch variation in leaf damage between the two predictors and their error terms.

A.3 Additional details

Linear regression requires the assumptions that residual errors are independent and normally distributed with a mean of zero and variance σ^2. The level-one residuals (r_{ij} in Equation A.1) may initially appear non-independent since they describe the deviance in the responses of correlated individuals (i) within patches (j). However, as Equations A.2 and A.3 show, the level-one errors are modeled around the intercept and slope of each of the j independent groups, which accounts for the correlation among samples from a given level. This is also advantageous for an-

alyzing repeated measurements on an individual over time. Correlations and un-equal variances among repeated measures typically violate the central assumptions of traditional techniques like repeated-measures analysis of variance, but can be accounted for by the multilevel model. In practice, sampling time is used as the level-one predictor (X_{ij} in Equation A.1) to model the change in the response of an individual over time (Blackwell et al. 2006). This technique is sometimes referred to as 'response curve analysis' (e.g. Peek et al. 2002).

More complex models can also be designed (Atkins 2005). Models can incorporate multiple predictors at each hierarchical level. Additional hierarchical levels, and corresponding predictors, can also be included. In the previous example, patches could be nested within a third 'site' level, with associated explanatory variables. Theoretically, there is no limit to the number of levels that can be analyzed. However, since each new level requires two additional nested regressions to model the lower-level intercepts and slopes, equations can easily end up having more parameters than is possible to estimate given the data. Lastly, as in traditional linear models, generalized multilevel regressions can be used to analyze non-normal response data (Bolker et al. 2008). The sign of a species interaction (positive or negative) is an example of a non-normal (binary) response. In such cases, the response variable can be related to the predictors by a link function, such as the logit function that expresses the result as a probability of observing a particular outcome.

A.4 Bibliography

Atkins, D.C. 2005. Using multilevel models to analyze couple and family treatment data: basic and advanced issues. Journal of Family Psychology 19:98-110.

Blackwell, E., C.F.M. de Leon, and G.E. Miller. 2006. Applying mixed regression models to the analysis of repeated-measures data in psychosomatic medicine. Psychosomatic Medicine 68:870–878.

Bolker, B.M., M.E. Brooks, C.J. Clark, S.W. Geange, J.R. Poulsen, M.H.H. Stevens, and J.S. White. 2008. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology and Evolution 24:127–135.

Kreft, I. and J. de Leeuw. 1998. Introducing Multilevel Modeling. Sage Publications, Thousand Oaks.

McMahon, S.M. and J.M. Diez. 2007. Scales of association: hierarchical linear models and the measurement of ecological systems. Ecology Letters 10:437–452.

Peek, M.S., E. Russek-Cohen, D.A. Wait, and I.N. Forseth. 2002. Physiological response curve analysis using nonlinear mixed models. Oecologia 132:175–180.

Pinheiro, J.C. and D.M. Bates. 2000. Mixed-Effects Models in S and S-PLUS. Springer, New York.

Raudenbush, S.W. and A.S. Bryk. 2002. Hierarchical Linear Models: Applications and Data Analysis Methods. Sage Publications, Thousand Oaks.

Appendix B

Abundance to mass conversions

Table B.1: Abundance to mass relationships for all taxa in the high intertidal at Prasiola Point, British Columbia. Mass represents the average mass of one individual (mobile taxa) or one percent cover of a 0.025 m^2 quadrat (sessile taxa). For taxa with three or more replicate abundance:mass measurements (shown as N), linear regressions were performed on untransformed mass versus abundance data. Some relationships appeared exponential and so regressions were also fit to log–log transformed mass versus abundance data. The best model was chosen using Akaike's information criterion (AIC$_c$) and shown in the table.

Taxon	Type	N	Mass (g)	Best fit equation	R^2
Amphipoda	#	10	0.017	y = 0.03266x - 0.0178	0.90
Analipus japonicus	%	1	0.150		
Anthopleura elegantissima	%	10	0.727	y = 1.5482x - 2.0198	0.93
Balanus glandula	%	7	0.962	y = 1.1623x - 0.4801	0.77
Callithamnion pikeanum	%	4	0.350	y = 0.8524x - 3.9397	0.70
Chlorostoma funebralis	#	10	3.070	y = 5.4916x - 3.1827	0.98
Chthamalus dalli	%	5	0.215	y = 0.2291x - 0.0163	0.92
Cladophora	%	21	0.308	ln(y) = 1.9464 · ln(x) - 2.8431	0.90
Crepidula adunca	#	1	0.032		
Cumagloia andersonii	%	7	0.172	y = 0.2154x - 0.1980	0.85
Diaulota densissima	#	5	0.002	y = 0.00225x - 0.0001	0.98
Endocladia muricata	%	12	0.161	y = 0.4184x - 0.4979	0.86
Enteromorpha	%	5	0.053	y = 0.02559x + 0.0859	0.19
Fucus gardneri	%	40	0.598	ln(y) = 1.4291 · ln(x) - 2.0659	0.96
Halobisium occidentale	#	6	0.004	y = 0.006038x - 0.0025	0.80
Halosaccion glandiforme	%	10	0.545	y = 0.5569x + 0.0004	0.93
Hemigrapsus nudus	#	4	3.050		
Idotea	#	17	0.422	y = 0.3900x + 0.1122	0.48
Leathesia difformis	%	1	0.300		
Lepidochiton	#	2	0.082		
Ligia	#	6	0.128	y = 0.02783x + 0.2506	0.09
Littorina scutulata	#	36	0.141	y = 0.08482x + 0.3049	0.54
Littorina sitkana	#	11	0.018	y = 0.0110x + 0.0463	0.58
Lottia digitalis	#	24	0.165	y = 0.1249x + 0.1383	0.80

Table B.1 continued . . .

Table B.1 (continued)

Taxon	Type	N	Mass (g)	Best fit equation	R^2
Lottia paradigitalis	#	7	0.040	y = 0.02294x + 0.0283	0.58
Lottia pelta	#	19	0.598	y = 0.3312x + 0.3169	0.17
Mastocarpus papillatus	%	16	0.145	y = 0.2292x - 0.2440	0.85
Mazzaella flaccida	%	5	0.143	y = 0.1347x + 0.0206	0.98
Microcladia borealis	%	4	0.330	y = 0.7659x - 2.7279	0.93
Mytilus californianus	%	29	0.899	ln(y) = 1.7176 · ln(x) - 1.2705	0.89
Nemertea	#	8	0.101	y = 0.1042x - 0.0039	0.17
Neomolgus littoralis	#	8	0.001	y = 0.0008x - 0.0007	0.92
Nereidae	#	2	1.190		
Nucella canaliculata	#	1	0.200		
Nucella lamellosa	#	1	0.500		
Nucella ostrina	#	7	0.657	y = 1.6601x - 1.1935	0.91
Oedoparena	#	9	0.008	y = 0.01221x - 0.0071	0.91
Onchidella borealis	#	4	0.013	y = 0.01549x - 0.0039	0.92
Pagarus beringanus	#	1	0.007		
Pagurus hirsutiusculus	#	19	0.132	y = 0.1471x - 0.0330	0.67
Pagurus samuelis	#	1	0.300		
Pelvetiopsis limitata	%	7	0.974	y = 1.7644x - 22.704	0.89
Petrocelis franciscana	%	8	0.071	y = 0.03754x + 0.0773	0.25
Petrolisthes cinctipes	#	6	0.542	y = 0.5600x - 0.0200	0.26
Platyhelminthes	#	4	0.042	y = 0.03147x + 0.0238	0.73
Polysiphonia hendryii	%	2	0.175		
Porphyra	%	4	0.050	y = 0.1891x - 0.1672	0.99
Saldidae	#	1	0.001		
Scytosiphon dotyi	%	6	0.099	y = 0.1877x - 0.6302	0.83
Semibalanus cariosus	%	5	2.390	y = 4.5143x - 4.4429	0.89
Siphonaria thersites	#	8	0.268	y = 0.1797x + 0.1492	0.27
Tectura persona	#	3	0.917	y = 0.5000x + 0.5000	0.68
Tectura scutum	#	11	0.481	y = 1.0063x - 0.7562	0.87
Ulva	%	3	0.097	y = 0.0900x + 0.0100	0.18

Appendix C

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