THE UNIVERSITY OF CHICAGO

TROPHIC OMNIVORY AND THE STRUCTURE, STRENGTH, AND NONLINEAR NATURE OF SPECIES INTERACTIONS ACROSS A PRODUCTIVITY GRADIENT

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BY
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DEDICATION

Für meinem Vater,
Helmut Novak,
der mich in die Natur genommen hat,
über sowohl auch unter dem Wasserspiegel.

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MN – Nov. 15th, 2008

CHAPTER I

INTRODUCTION

Efforts to understand the regulation and functioning of ecological communities naturally focus on the interactions that exist between species (Agrawal et al. 2007). Empirical observations and manipulative experiments have shown repeatedly that species extinctions can lead to dramatic cascading changes in the structure and dynamics of communities (Duffy 2002), as can the invasion of foreign species (Grosholz 2002). Changes in the presence or abundance of many other species, on the other hand, often appear to have little effect, or do have effects in counterintuitive ways (Polis and Strong 1996, Doak et al. 2008). The challenge for community ecology is to understand and predict which interactions and community components are most important in causing, preventing, or ameliorating community-wide effects. What limits the spread of direct and indirect effects, and controls the stability of nature's large and complex systems? How and when will the over-harvesting of top-predators result in community-reorganizing top-down effects? How do bottom-up factors such as eutrophication modulate the effects of disturbances and extrinsic change? Answers to these questions are needed to inform and facilitate difficult restoration, conservation, and resource-use policy-making decisions.

Our understanding of food webs has seen tremendous advances in this regard. As depictions of who-eats-who in a community, food webs have provided a starting point for understanding the full network complexity of all interaction types that exist between species in nature. There still exist large gaps between food web theory and our empirical knowledge of community dynamics, however; our forecasting powers are still in their infancy. The primary focus of my dissertation work has been to lessen this gap by addressing two fundamental elements of food webs which add significantly to their complexity: the presence of trophic omnivores and the nonlinear nature of predator-prey interactions.

TROPHIC OMNIVORY

Trophic omnivores are species that feed on prey or resources from more than one trophic level (Fig. 1.1). Omnivores are central to seminal conceptual models of ecology (e.g., Hairston et al. 1960, Menge and Sutherland 1987) and have been inherent to the discussion of food webs since the early days of modern ecology (Elton 1927). Their presence in food webs complicates the predictive power of trophic cascades and undermine the utility of the trophic level concept itself (Cousins 1987, Polis and Strong 1996), particularly when they engage in intraguild predation (Fig. 1.1b).

Though once deemed rare and unimportant in natural food webs (Pimm and Lawton 1977, Pimm and Lawton 1978), more recent and complete reconstructions of food web topologies have recognized omnivores as being pervasive components of their communities (Polis et al. 1989, Rosenheim et al. 1995, Coll and Guershon 2002, Arim and Marquet 2004, Williams and Martinez 2004, Bascompte and Melian 2005, Stouffer et al. 2007, Thompson et al. 2007). Early mathematical theory suggesting an inherent instability to omnivorous food webs (Pimm and Lawton 1977, Pimm and Lawton 1978) has been dispelled (McCann and Hastings 1997, McCann et al. 1998, Neutel et al. 2002, Diehl 2003, Kuijper et al. 2003, Emmerson and Yearsley 2004, Teng and McCann 2004, Křivan and Diehl 2005). The empirical importance of omnivores nevertheless remains a contentious issue (e.g., Williams and Martinez 2004).

In large part, this is because only two approaches – the mathematical modeling of small food web modules and the qualitative reconstruction of species-rich food web topologies based on the documentation of feeding relationships – have predominated research on the role that omnivores play. The predictions of food web theory for how omnivores should affect communities remain little-addressed empirically (Morin and Lawler 1995, Agrawal 2003). While advances have been made primarily in microbial (e.g. Holyoak and Sachdev 1998, Diehl and Feißel 2000) and arthropod (e.g. Borer et al. 2003, Amarasekare 2007b) systems, and the size ratio of predators and their prey can be important in determining the net effects of omnivory (Diehl 1993), the difficulty of finding tractable systems in which to assess the role of omnivores has held back empirical work. The behavioral basis of omnivory remains particularly poorly explored (Singer and Bernays 2003) and we know little about how omnivores adjust their diets and prey preferences to changes in the presence or abundance of potential prey. A predictive and empirical understanding of how trophic omnivory affects the structure and dynamics of communities thus remains largely unrealized.

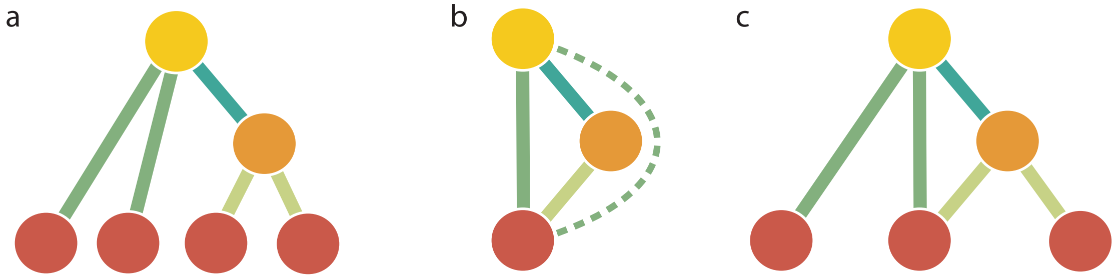

Figure 1.1. Simple food web modules of trophic omnivory representing examples (a) feeding at multiple trophic levels, (b) the indeterminacy of intraguild predation (a.k.a. closed-loop omnivory, Polis et al. 1989) where the direct effect between the omnivore and the basal prey may be masked by the indirect effect (dashed link) mediated by the intermediate predator, and (c) intraguild predation with alternative prey exclusive to each predator.

NONLINEAR SPECIES INTERACTIONS

The behavioral details of species interactions in general are a second pervasive feature of ecological communities that complicate our efforts to understand their complexity. The study of predator foraging behaviors such as prey choice, relative prey preferences, and the manner in which predator feeding rates respond to changes in prey abundance (i.e. their functional responses) has also long been a mainstay of modern ecology (Fig. 1.2, Solomon 1949, Holling 1959, Emlen 1966, MacArthur and Pianka 1966, Pyke et al. 1977). The nonlinear nature of trophic interactions that such behaviors introduce has important implications for the dynamics of populations and the structure and stability of food webs (Murdoch and Oaten 1975, McCann 2000). Populations of specialist predators, for example, fluctuate more than do those of generalist predators (MacArthur 1955, Romanuk et al. 2006), but the mechanisms promoting the stability of generalist predator-prey dynamics have rarely been investigated (Murdoch et al. 2002). The saturating functional responses which most predators exhibit on individual prey species (Jeschke et al. 2004) may likewise destabilize predator-prey dynamics in theory (Hassell and May 1973, Oaten and Murdoch 1975), begging the question of how whole food webs persist in nature.

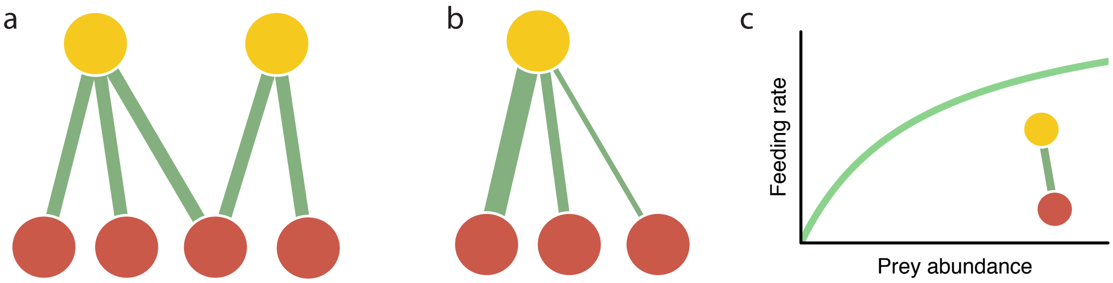

Figure 1.2. Details of predator foraging behavior affecting the structure and dynamics of food webs: (a) predator-specific differences in diet choice, (b) relative prey-preferences, and (c) the dependence of a predator's feeding rate on the abundance of its prey.

Unfortunately, studies of the nonlinear nature of predator-prey interactions have largely focused on isolated species pairs (Murdoch and Oaten 1975, Jeschke et al. 2002), or have been limited to arenas of low species diversity (i.e. trophic modules, Holt 1997). Much current effort in ecology is therefore directed towards placing our understanding of isolated interactions and modules into the larger context of species-rich networks

(Wootton 2002, Werner and Peacor 2003, Peckarsky et al. 2008, Petchey et al. 2008). The goal, of course, is to understand communities in natural field settings, where all species interact concurrently and a predator's feeding on one prey species may be directly and indirectly affected by the presence of other species and its feeding on alternate prey (Murdoch and Oaten 1975, Peacor and Werner 2004). How much of the theory of pairwise and module-based predator-prey interactions is relevant to understanding and predicting the structure and dynamics of whole communities remains an open question in community ecology with important applied implications.

DISSERTATION OVERVIEW

Efforts to gain insight into the empirical importance of both omnivores and the nonlinearity of trophic interactions have been hampered by an inability to measure the species-specific strengths of trophic interactions in species-rich systems. We do not have logistically feasible methods that account for the reticulate indeterminacy of omnivorous food webs (Fig. 1.1b, Yodzis 1988, Dambacher et al. 2002) and the saturating functional responses that predators exhibit (Fig. 1.2c, Abrams and Ginzburg 2000, Abrams 2001, see also Berlow et al. 2004, Wootton and Emmerson 2005). In *Chapter II*, *Estimating nonlinear interaction strengths: an observation-based method for species-rich food webs*, I introduce a new observational method for estimating the direct, species-specific strengths of trophic interactions in multispecies field settings that overcomes these food web complexities. The per capita interaction strength estimates that this method produces scale out species-specific differences in population size (Laska and Wootton 1998). The method thereby standardizes comparisons of interaction strengths (= prey preferences, Chesson 1983) across all taxa of a food web and provides the very estimates we need to empirically parameterize our mechanistic models of theoretical food web ecology. This chapter also uses simulations to determine the amount of logistical effort that is needed to achieve accurate interaction strength estimates given predator-specific differences in diet diversity and feeding rates, and offers a simple technique for assessing one's accuracy given the data at hand.

In *Chapter III*, *Estimating interaction strengths in nature: experimental support for an observational approach*, I present an empirical test of this new method's accuracy. By applying the observational method to two populations of the predatory whelk, *Haustrum* (= *Lepsiella*) *scobina*, that is common to the rocky intertidal shores of New Zealand, I estimated the per capita strengths of its interactions with all nine of the prey species on which these populations of *H. scobina* feed. Intertidal whelks like *H. scobina* (and a second, omnivorous species, *H. haustorium*, which I consider in *Chapters IV* and *V*) are classic Type II functional response foragers (*sensu* Holling 1959); their feeding rates becoming increasingly saturated with experimental increases in their prey's abundance (Fig. 1.2c, Murdoch 1969, Katz 1985, Moran 1985, Rodrigues 1986). By concurrently performing year-long manipulations of *H. scobina*'s two populations in caging experiments, I obtained time-series data for the response of a focal mussel prey species. I used these time series to independently estimate per capita interaction strengths between *H. scobina* and this mussel using maximum-likelihood model-fitting techniques. I then compare estimates from the observational method with those obtained by model-fitting directly and document remarkable concordance between the two methods. This high agreement supports the empirical use of the observational method to investigate the roles that omnivory and the nonlinear nature of trophic interactions play within more species-rich and reticulate food webs.

In *Chapter IV*, *Trophic omnivory across a productivity gradient: intraguild predation theory and the structure and strength of species interactions*, I employ the observational method in a large-scale test of intraguild predation theory. This well-developed subdivision of general food web theory offers two key predictions regarding the mechanisms governing species coexistence in omnivorous food webs and how species abundance patterns should change across gradients of system productivity (Polis and Holt 1992, Holt and Polis 1997). However, although the intraguild predation module (Fig. 1.1c) is perhaps the best studied of all food web modules, the applicability of our theory to real, species-rich food webs remains largely unknown (Rosenheim et al. 1995, Kondoh 2008). In *Chapter IV*, I test the two key predictions of intraguild predation theory by investigating species abundance patterns and the structure and interactions strengths of a series of six species-rich omnivorous food webs situated along a strong gradient of productivity present around New Zealand's coastline. I find that the intermediate predator is the superior competitor for shared prey species, as predicted by intraguild predation theory. Counter to theory, however, I show that it is the omnivore that is the superior competitor when both shared and unshared prey are considered. In further contrast to theory, I document an increase in the abundance of the intermediate predator with increasing productivity. My data nevertheless reveal clear and remarkably regular cross-gradient shifts in the food web structure and strengths of species interactions. This chapter thereby offers empirical insight into the manner by which the predators of omnivorous food webs vary their prey choice and relative prey preferences in response to cross-gradient changes in prey abundance for future modeling efforts to incorporate.

Finally, in *Chapter V*, *The empirical nonlinearity of multispecies functional responses and the stability of generalist predator-prey interactions*, I address the nonlinear nature of trophic interactions in species-rich food webs directly. Using data from all six food webs studied in *Chapter IV*, I ask to what degree the feeding rates of *H. scobina* and *H. haustorium* are saturated with respect to the density of their prey within the empirical context of their multispecies interactions. I also determine the extent to which prey-attributes can be used to predict prey-specific contributions to the nonlinearity of a predator's functional response, and investigate how a predator's diet richness affects the degree to which it's overall feeding rate is saturated. Then, by extending and empirically parameterizing the classic Rosenzweig-MacArthur model of predator-prey interactions (Rosenzweig and MacArthur 1963), I ask whether the degree of saturation observed within New Zealand's whelk populations is nonlinear enough to affect the stability of their predator-prey interactions, and how their dynamics are affected by predator specialization. My results indicate that whelk feeding rates are generally not strongly saturated, that most prey species contribute only very little to their predator's saturation, and that increasing diet richness has a non-additive effect on a predator's saturation such that the addition of alternative prey has a stabilizing effect on predator-prey dynamics. I thereby offer a new mechanism by which generalist predators stabilize the dynamics of their species-rich food webs which does not rely on density-dependent prey-switching (*sensu* Murdoch 1969), as is commonly assumed (Murdoch et al. 2002, Romanuk et al. 2006), and an explanation for why predator-removal experiments (e.g., *Chapter III*) typically result in linear prey responses despite the inherent nonlinearity of trophic interactions.

Overall my dissertation contributes to our growing understanding of the processes regulating the structure and dynamics of ecological communities. Trophic omnivory and the nonlinear nature of predator-prey interactions lie at the core of nature's complexity. By focusing on empirical food webs of intermediate size and complexity – between the scales of trophic modules and the complete network of all the interactions occurring between species in nature – my dissertation brings empirical data to bear at the juncture of theories of focal predator-prey interactions and food webs as a whole. Furthering our understanding of these food web features has the potential to contribute much to both the conceptual and applied goals of ecology.

CHAPTER II

ESTIMATING NONLINEAR INTERACTION STRENGTHS: AN OBSERVATION-BASED METHOD FOR SPECIES-RICH FOOD WEBS[1]

ABSTRACT

Efforts to estimate the strength of species interactions in species-rich, reticulate food webs have been hampered by the multitude of direct and indirect interactions such systems exhibit and have been limited by an assumption that pairwise interactions display linear functional forms. Here we present a new method for directly measuring, on a per capita basis, the nonlinear strength of trophic species interactions within such food webs. This is an observation-based method, requiring three pieces of information: (1) species abundances, (2) predator and prey-specific handling times, and (3) data from predator-specific feeding surveys in which the number of individuals observed feeding on each of the predator's prey species has been tallied. The method offers a straightforward way to assess the completeness of one's sampling effort in accurately estimating interaction strengths through the construction of predator-specific prey accumulation curves. The

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[1] This manuscript previously appeared in Ecology, 2008, volume 89, pages 2083-2089. Included with permission from the Ecological Society of America.

method should be applicable to a variety of systems in which empirical estimates of direct interaction strengths have thus far remained elusive.

Keywords: consumption rates; functional response; handling time; indirect effects; omnivory; parameter estimation; predator–prey interactions; species interaction strengths.

INTRODUCTION

Food webs are fundamental components of ecological communities, characterizing who eats whom within the complex network of species interactions. Natural communities often exhibit species-rich, reticulate food webs that make measuring species interaction strengths difficult. Nevertheless, empirical estimates of interaction strengths represent an important step toward parameterizing mechanistic models of species interactions, understanding the forces that regulate community structure, and making quantitative predictions to inform conservation and resource-use strategies (Berlow et al. 2004, Ebenman and Jonsson 2005, Agrawal et al. 2007).

Many approaches have been employed to quantify the strength of trophic species interactions (reviewed in Berlow et al. 2004, Wootton and Emmerson 2005). Approaches producing estimates on a per capita (or per biomass) basis have the advantage of allowing straight-forward comparisons to be made across populations and taxa because they scale out species-effect differences caused by differences in abundance (i.e., species-impacts; Wootton 1997). Per capita interaction strengths underlay all other metrics of species interaction strengths (Laska and Wootton 1998). Approaches capable of producing per capita estimates have used manipulative field experiments (e.g., Bender et al. 1984, Paine 1992), short-term laboratory experiments (e.g., Levitan 1987), time-series dynamics (e.g., Seifert and Seifert 1976, Ives et al. 2003), energetic perspectives (e.g., Moore et al. 1993, Hall et al. 2000, Libralato et al. 2006), allometric relationships (e.g., Emmerson and Raffaelli 2004), and direct observation-based methods (e.g., Wootton 1997, Woodward et al. 2005). Inherent problems associated with many of these approaches, however, include logistically impractical time, treatment, or replication requirements, or the loss of species-specific properties by the application of generalized relationships (Berlow et al. 2004). Manipulative field experiments also suffer in particular from the indeterminacy of direct and indirect effects of reticulate food webs and cannot, for example, be applied easily to systems exhibiting trophic omnivory (Yodzis 1988, Menge 1997).

A further shortcoming associated with most current approaches is their assumption that predator–prey interactions exhibit a linear functional form (Abrams 2001). Thus they assume that a predator's feeding rate exhibits an unbounded Type I functional response to changes in its prey's abundance. There are some theoretical arguments and empirical evidence to support this assumption (Wootton and Emmerson 2005), but there is also ample indication from laboratory experiments, survey data, and theory that predator–prey interactions can be strongly nonlinear (Ruesink 1998, Abrams 2001, Sarnelle 2003). In fact, at high enough prey densities, predators with nontrivial handling times must exhibit the saturated feeding rate exemplified by the Type II functional response, which is the most often observed response, especially in single-prey studies (Murdoch and Oaten 1975, Jeschke et al. 2002, 2004). Obtaining adequate empirical information on the nonlinear form of interactions in natural multispecies communities therefore represents a major challenge to food web ecologists (Abrams and Ginzburg 2000).

We propose a step toward rectifying these issues by introducing a new method for estimating the per capita strength of trophic species interactions. The observation-based approach of our method enables it to be applied in species-rich systems while avoiding the obscurity of indirect trophic effects. With knowledge of prey abundances, prey-specific handling times, and feeding surveys of focal predator populations, the method estimates species-specific attack rates of predators expected to exhibit Type II functional responses. We present the derivation of our method, assess its success using simulations, and show how the information used in calculating attack rates may be used to gauge the accuracy of one's estimates through the construction of predator-specific prey accumulation curves. We conclude by noting the method's own assumptions and suggest systems in which it is likely to be most suitably applied.

METHODS

Derivation of Type II observation-based method

Our goal was an equation that uses data of an observational type to estimate the attack rate constant *c* of a Holling Type II functional response, written as

$$f(N) = \frac{cN}{1 + chN} \tag{2.1}$$

where *f*(*N*) is a function describing an individual predator's feeding rate in response to changes in the abundance of its prey, *N*, and *h* is the prey's handling time (Holling 1959). This equation remains the most frequently employed representation of saturating feeding rates by both empiricists and theoreticians alike. We define a prey's handling time as the time required for a predator individual to consume a single prey individual, ignoring chase and post-ingestion digestion times (*cf.* Jeschke et al. 2002). Thus handling time denotes the time that a predator could be observed in contact with its prey, as it is commonly used in empirical studies (e.g., Menge 1972, Fairweather and Underwood 1983, Yamamoto 2004). The attack rate constant (also known as the instantaneous rate of discovery [Holling 1959]) describes the rate at which a predator approaches the saturation point of its functional response (1/*h*) as the abundance of its prey increases. Parameter *c*, therefore, has units of feeding events per predator per prey per unit time. When evaluated at a given prey abundance, *f*(*N*)/*N* is equivalent to the per capita interaction strength of most previous approaches.

Eq. 2.1 can be extended to the multispecies functional response with *S* prey species as

$$f(N_i) = \frac{c_i N_i}{1 + \sum_{k=1}^{S} c_i h_i N_i} \tag{2.2}$$

(e.g., Murdoch 1973). This equation assumes no prey switching (i.e., constant c_i). In Appendix 2.A we show that with empirical knowledge of (1) prey abundances, N_i, (2) prey-specific handling times, h_i, and (3) data from surveys of a given predator population that tally the number of individuals observed feeding on different prey species, prey-specific c_i can be calculated as

$$c_i = \frac{F_i A_x}{(F_x - A_x) h_i N_i} \tag{2.3}$$

In Eq. 2.3, F_i is the fraction of feeding individuals that were observed in the process of feeding on prey species i, and A_x denotes the fraction of all predator individuals surveyed (feeding and not feeding) that were observed in the process of feeding on prey species x. Species x is an arbitrarily chosen species used throughout the calculation of all prey-specific attack rates (see Appendix 2.A).

Assessment of observation-based method using simulations

We used stochastic nonspatial individual-based simulations of feeding predator populations to assess the observation error of our method in estimating prey-specific attack rates. Specifically, we were interested in determining how sampling effort (the number of predator individuals that are surveyed), prey richness (the number of prey species in the predator's diet), and a predator population's level of feeding activity (the proportion of the population observed actively feeding) affected the method's accuracy.

To do so we simulated populations of 50 to 7500 predator individuals feeding on a prey pool of four to 40 species at a range of feeding activity levels where between 3% and 60% of the population, on average, was feeding at any given time (see Appendix 2.B for simulation algorithm). All combinations of sampling effort (= simulated population size) and diet richness, and all combinations of sampling effort and feeding activity level, were simulated independently, with species-specific prey attributes of abundance, handling times, and attack rates selected anew each time. Simulations used to assess the influence of sampling effort and diet richness were run at a feeding activity level such that, on average, ~10% of individuals were feeding at any given time. Simulations used to assess how sampling effort and feeding activity affected the method's accuracy were run with predators having a diet richness of 10 prey species.

We parameterized our simulations to capture several general empirical properties of communities (Appendix 2.B: Table 2.B.1). We drew prey abundances from lognormal distributions to reproduce abundance structures commonly observed in nature (Halley and Inchausti 2002). We then made the handling time of each prey species inversely proportional to its abundance, modified with a random term that introduced abundance-dependent amounts of variation. Our rationale was that handling time is probably proportional to prey body size, coupled with the empirically well-documented inverse relationship of both the mean and range of body sizes with abundance (Blackburn and Lawton 1994). Thus, prey species with high abundance were presumed to be small and to require short handling times, while prey species with low abundance could be small or

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  of DANGER OF ETECTRIC SHOCK.

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Plate 2.1. Only the highest quality laboratory equipment should be used when estimating handling times experimentally. For example, I avoided the danger of etectrically shocking my study organisms by aerating their aguaria with pretty air pumps placed ablove water level (see *Chapter III*).

large with correspondingly small or large handling times. Parameter values were chosen to produce prey abundances (per m^2) typical of intertidal invertebrates and handling times (hours) typical of whelks feeding upon them (M. Novak, *unpublished data*; see Plate 2.2). We drew species-specific attack rates from uniform distributions to avoid bias in this parameter across prey attributes. To obtain a target fraction of feeding predators in a given simulation, the distribution from which attack rates were drawn was limited to a maximum value that was inversely related to the richness of the predator's diet. This resulted in prey-specific feeding rates that ranged from being unsaturated when predators fed at low levels, to relatively saturated when a large proportion of the population was feeding at any given time (Appendix 2.B: Fig. 2.B.2).

After sampling effort, prey richness, and feeding level had been set, and the attributes and attack rates of each prey species had been drawn, a simulation proceeded through time with the expected probability that an individual predator encountered a specific prey species in a given time step being equal to the product of the prey's abundance and its attack rate. If an encounter occurred, the predator fed upon that prey species for a number of time steps equal to the handling time of the species. When this time period was over, the predator individual returned to the original status of not feeding and could encounter additional prey. To explore the effects of specific parameters on the method's performance, encounter probabilities between nonfeeding individuals and each prey species were set to remain constant through time; prey abundance was not affected by feeding events. It is straightforward to apply the method to situations with changing

Plate 2.2. *Haustrum* (=*Lepsiella*) *scobina* feeding on *Chamaesipho columna* and *Ch. brunnea* barnacles near Kaikoura, New Zealand. Photo credit: M. Novak.

prey populations by measuring abundance at the same time a feeding survey is performed.

For each simulation we tabulated the number of predators in the process of consuming each prey species after a burn-in time of 500 time steps. This survey was then combined with prey-specific abundances and handling times to calculate estimated prey-specific attack rates using Eq. 2.3. We then correlated these estimates (including estimates of zero for prey species not actually observed being fed upon in the survey) with the “true” attack rates initially drawn for the simulation using Pearson product-moment coefficients to calculate the proportion of variation explained. All simulations were performed in R (R Development Core Team 2006).

RESULTS

Our ability to accurately recover true input attack rates given prey abundances, handling times, and feeding surveys of the simulated predator populations increased asymptotically as the number of predators surveyed was increased (Fig. 2.1a). With a diet of four prey species and 10% of the predator population feeding at any given time, R^2 values >0.85 (0.89 with nonobserved prey removed) were achieved when as few as 80 feeding individuals were observed. R^2 values >0.98 were achieved for six of the seven surveys that observed >300 predators feeding on a diet of four prey species. An increased diet richness led to less accurate estimates at a given sampling effort. When the diet consisted of 40 prey species, observing 600 feeding individuals was sufficient to produce

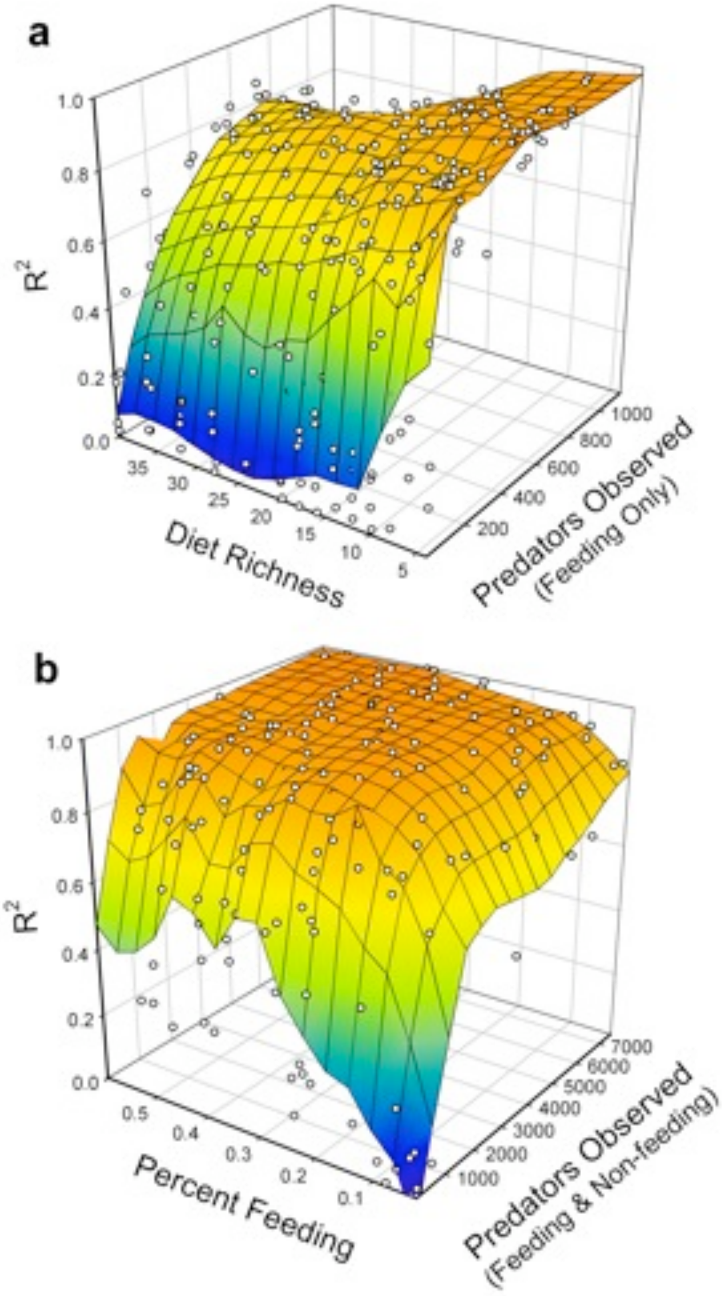

Figure 2.1. Correspondence between estimated and true attack rates assessed as the proportion of variation in true attack rates explained by the estimates (with unobserved prey included). The plots show simulated predator populations varying in (a) diet richness, with ~10% of the individuals feeding at any given time, and (b) feeding activity level, with populations feeding on a potential diet of 10 prey species. Surfaces were produced by Loess smoothing (locally weighted polynomial regression with degree 1 and sampling proportion 0.1) in SigmaPlot (SPSS 2002). Colors reflect the interpolated R^2 values, from low (violet) to high (red-orange).

estimated attack rates that explained >75% of the variation in true attack rates (76% with non-observed prey removed). Such survey sizes are regularly obtained in detailed studies of predator diets (e.g., Paine 1966, 1969, Menge 1972, Estes et al. 1982, Irons et al. 1986, West 1986, 1988, Wootton 1997), though are perhaps unlikely to be necessary for most predators given that the most fully resolved food webs suggest that the average number of trophic interactions per species is typically <10 (Dunne et al. 2002).

Increasing the predator population's level of feeding activity increased the accuracy of attack rate estimates for a given sampling effort (Fig. 2.1b). Thus an increase in the predator population's feeding level from 7% to 15% increased R^2 values from 0.75 to 0.9 for a total population of 1750 individuals feeding on 10 prey species. Equivalently, situations with higher proportions of feeding predators required fewer predator observations to achieve the same level of accuracy. Species-specific estimation accuracies were not affected by prey handling time or abundance, but tended to be higher for larger attack rates (see Appendix 2.C).

DISCUSSION

The results of the simulations suggest that our new observation-based method can perform remarkably well at estimating the attack rate constants needed to assess the per capita strength and functional form of species-specific top-down trophic interactions. Of course, the accuracy of applying the method to empirical data will also depend on the variation measured in prey handling times and abundances, which will differ among studies. Nevertheless, given a sufficient amount of survey effort our method can be successfully applied to predators with a diet richness high enough to otherwise make them empirically intractable. Our conclusions were unchanged by using the mean absolute deviation of estimated and true attack rates as a measure of the method's success. Furthermore, no systematic biases were observed when plotting prey-specific deviations between estimated and true attack rates against prey abundances, handling times, or the true strength of the attack rates themselves (Appendix 2.C).

Moreover, the mean absolute deviation of estimated and true attack rates was related negatively to the proportion of the diet richness that sampled predators were actually observed feeding upon; estimation accuracy increases with the completeness of one's sampling of a predator's diet (Fig. 2.2). This suggests that one's accuracy, or conversely, the remaining sampling effort needed for generating estimates of attack rates at a specified level of accuracy, can be gauged with knowledge of the complete prey pool available to a given predator. Such information can often be obtained directly by comparison of literature compilations of a predator's diet to site-specific prey lists (resulting, for example, from the species abundance surveys performed for the purpose of applying our method). It may also be obtained by constructing species accumulation curves of a predator' s observed diet to make extrapolated estimates of the predator's total diet (methods reviewed by Colwell and Coddington [1994]). Such estimates will also be informative for assessing the number of rarely occurring, though not necessarily weak, interactions that remain unobserved and, therefore, unestimated.

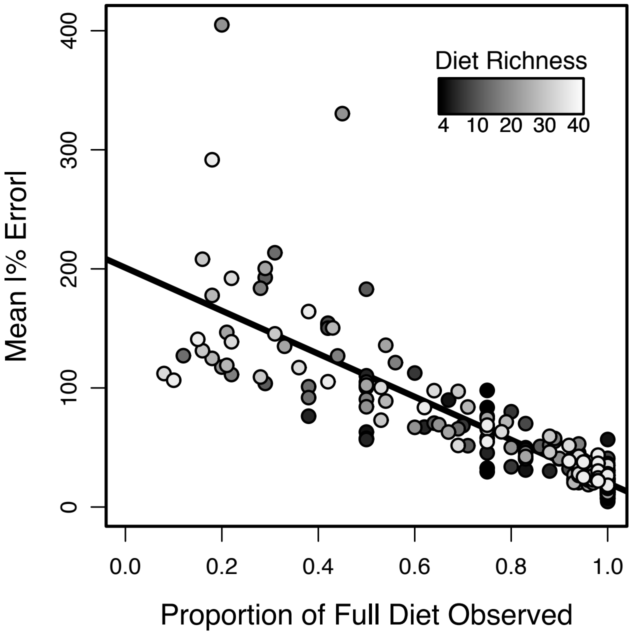

Figure 2.2. Relationship between estimation accuracy of predator attack rates and the proportion of the diet observed. Points represent mean absolute percentage differences between “true” and estimated attack rates of all prey (including unobserved species) in each simulated combination of sampling effort and diet richness. The linear regression line is plotted across all sampling efforts for all independently simulated combinations together.

Our method is not, of course, without its own assumptions. These include: (1) that an individual predator's feeding rate is adequately described by a multispecies Type II functional response (Eq. 2.2); (2) that predator individuals feed upon only one prey item at a time; (3) that predators have sufficiently large handling times that the probability of observing feeding events is nonzero; (4) that post-handling digestion times do not preclude a predator's ability to search for further prey; (5) that there is no bias toward observing either feeding or nonfeeding predator individuals; (6) that patchy prey abundances are measured at a spatial scale appropriate to the feeding biology of the predator and are not significantly reduced by feeding over the time period of a survey; and finally (7) that surveys are performed at a temporal scale appropriate to the scale at which inferences of interaction strengths are to be made. Thus, if predators feed in a periodic fashion at the temporal scale at which feeding surveys are performed (e.g., day/night), extrapolating attack rates to larger temporal scales (e.g., seasonal rates) is unwarranted unless repeated surveys are performed across this temporal scale or nonfeeding times are accounted for (e.g., Wootton 1997). Additionally, if handling times are measured in hourly units, these must be rescaled appropriately if inferences about the strength of interactions are to be made at a different temporal scale. Given these assumptions, our method may be suitably applied to a wide range of species, including invertebrates (e.g., whelks and seastars; Menge 1972, Yamamoto 2004), arthropods (e.g., wolf spiders; Samu 1993), birds (e.g., gulls; Wootton 1997), and mammals (e.g., sea otters, Estes et al. 1982), for many of which a sufficient amount of the necessary pieces of information can already be found in the literature.

The observation-based nature of the approach provides a broadly applicable method that circumvents many of the logistical problems associated with other approaches. The method may easily be applied to size-structured interactions by treating predator or prey cohorts as separate species. Feeding surveys may entail repeated samples of a predator population or of focal individuals, as long as observations are separated by time intervals sufficiently large to ensure independence. Handling times may be derived from several sources that include: (1) detailed observations of focal individuals (e.g., Laidre and Jameson 2006); (2) direct observation in laboratory studies (handling times being both less sensitive than attack rates to differences between laboratory and field conditions, and logistically more feasible to obtain than the treatment permutations needed to characterize all multispecies functional responses experimentally); and (3) application of Eq. 2.3 to empirical situations with differing prey abundances to solve for c_i and h_i simultaneously.

The method's strength lies in its applicability to predators that feed on diverse suites of prey species. The ubiquity of such generalist predators has made the estimation of direct interaction strengths in natural food webs especially difficult, particularly when they engage in omnivorous interactions. Nevertheless, our method may also be applied to the relatively simple systems typically used in experimental approaches and may, in fact, be preferably employed given the confounding factors often involved in manipulating species abundances (Chalcraft et al. 2005, Skelly 2005, Miller and Gaylord 2007, Yoshida et al. 2007). Its suitability to natural field settings, furthermore, allows this observation-based method to estimate the realized strength of trophic species interactions within the empirical context of the multispecies web of density-mediated effects and interaction modifications (Wootton 1994, Peacor and Werner 2004). Species interactions with functional forms more complicated than Holling Type II responses are clearly present in nature (Skalski and Gilliam 2001). By employing derivation techniques similar to those used here or, for example, by repeated application of our method across gradients of community structure, it may nevertheless be possible to assess and quantify the form by which even these modifications affect the strength of trophic species interactions.

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APPENDIX 2.A: DERIVATION OF TYPE II OBSERVATION-BASED METHOD

The derivation of Eq. 2.3 is analogous to the derivation of the Type II functional response itself (Holling 1959, Case 2000). Let an arbitrary amount of time *T* be divided into the total time an individual predator spends searching (T_S) and the total time it spends handling all consumed prey individuals of its prey species (T_H). $T_{H(i)}$ is thus the total time spent handling all individuals of prey *i*, which is the product of the handling time of prey *i* (h_i) and the number of prey *i* individuals eaten in time *T* (E_i). E_i is the product of the attack rate constant (c_i), the abundance of prey *i* (N_i), and T_S. Given a survey of a predator population, the fraction of feeding individuals observed in the act of handling prey species *i* will be

$$F_i = \frac{\#\, observed\, feeding\, on\, prey\, i}{total\, \#\, observed\, feeding} = \frac{T_{H(i)}}{T_H} = \frac{c_i h_i N_i T_S}{\sum_{k=1}^{S} c_k h_k N_k T_S} = \frac{c_i h_i N_i}{\sum_{k=1}^{S} c_k h_k N_k} \qquad (2.A.1)$$

and the fraction of all sampled individuals observed in the act of handling prey species *i* will be

$$A_i = \frac{\#\, observed\, feeding\, on\, prey\, i}{total\, \#\, sampled} = \frac{T_{H(i)}}{T} = \frac{c_i h_i N_i T_S}{T_S + \sum_{k=1}^{S} c_k h_k N_k T_S} = \frac{c_i h_i N_i}{1 + \sum_{k=1}^{S} c_k h_k N_k} \qquad (2.A.2)$$

Using the two prey species case as an example, solve Eq. 2.A.1 to get c_2 as a function of F_1 and c_1,

$$c_2 = \frac{c_1 h_1 N_1 + c_1 h_1 N_1 F_1}{h_2 N_2 F_1} \qquad (2.A.3)$$

Substitute Eq. 2.A.3 into Eq. 2.A.2, set T to unity (since the scale to which time is set is arbitrary), and solve for c_1 to obtain

$$c_1 = \frac{F_1 A_1}{(F_1 - A_1) h_1 N_1} \tag{2.A.4}$$

Substitute Eq. 2.A.4 into the Eq. 2.A.3 to obtain

$$c_2 = \frac{(1 - F_1) A_1}{(F_1 - A_1) h_2 N_2} \tag{2.A.5}$$

Thus, by iteratively solving and substituting, and because in a system of S prey species

$F_i = 1 - \sum_{k \neq i}^{S} F_k$, it can be shown by induction that Eq. 2.3 is true for any prey i.

Eq. 2.3 works for predators with a diet of a single prey species as well (unless all individuals of the population are observed feeding (i.e., $F_i = A_i = 1$)). Thus the choice of prey species x is arbitrary. However, x is preferably the species with the highest A_i since its proportion is likely to be estimated most accurately.

APPENDIX 2.B: SIMULATION ALGORITHM, PARAMETERS, AND RESULTANT FEEDING RATES

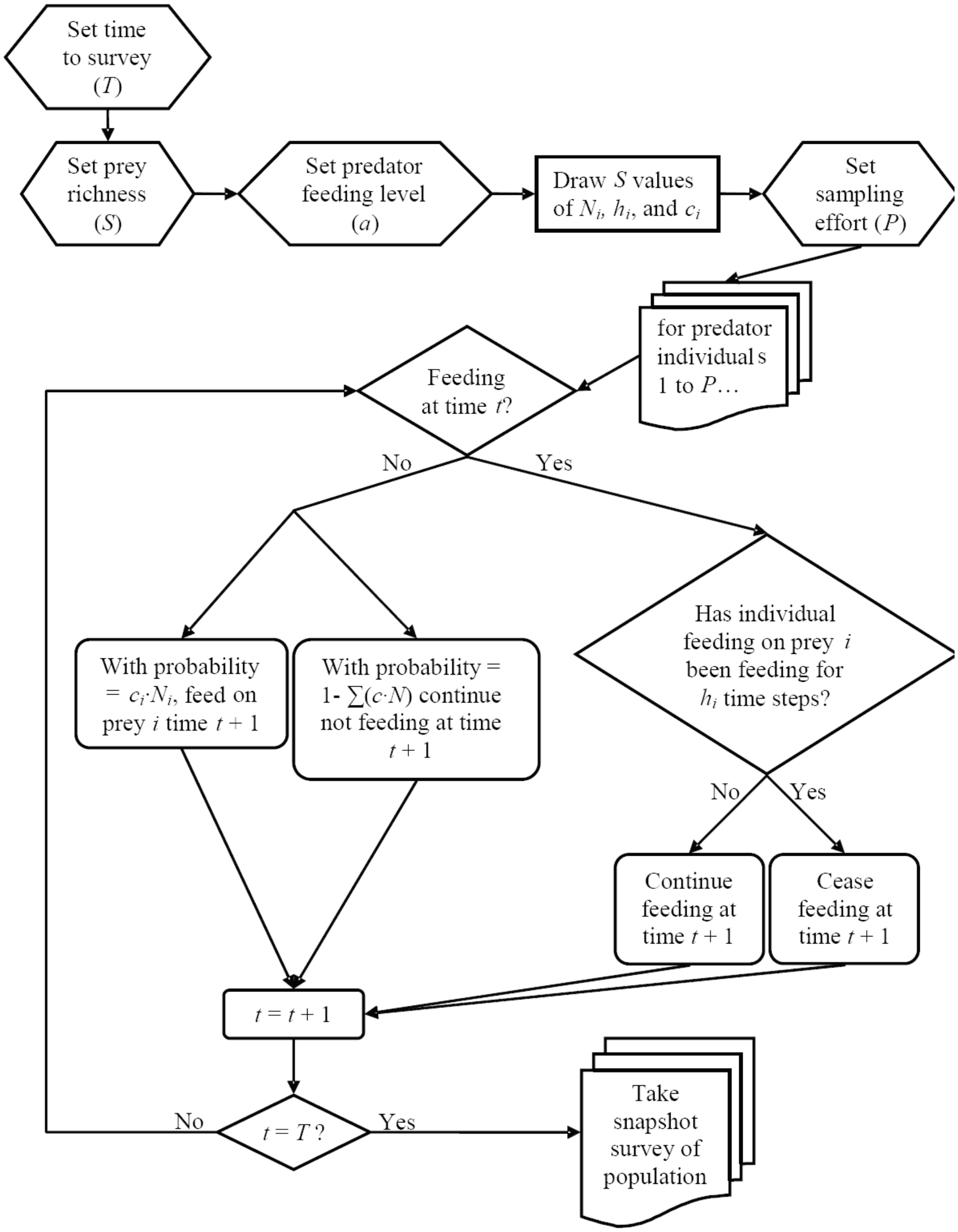

Figure 2.B.1. Flowchart describing the sequence of events simulated to assess the utility of the method in estimating species-specific Type II functional response attack rate constants. See Table 2.B.1 for parameter definitions, values and distributions drawn from.

Table 2.B.1. Simulation parameter values and distributions used in assessing the method.

Parameter	Symbol	Values
Predator population size (= sampling effort)	P	$P \in$ [50, 150, 250, 500, 750, and 1000 to 7500 in steps of 500]
Prey richness	S	$S \in$ [4 to 20 in steps of 2, and 24 to 40 in steps of 4]
Feeding activity level	a	$a \in$ [1, 3, and 6 to 24 in steps of 3] †
Prey *i* abundance	N_i	$N_i \sim \text{logNorm.}(\mu_N,\sigma_N)$, $\mu_N = 2$, $\sigma_N = 1$ ‡
Prey *i* handling time	h_i	$h_i \sim h_{max}/N_i + \varepsilon_i$, $h_{max} = 80$, $\varepsilon_i \sim 2 + \text{Unif.}(-70,0)/N_i$ ‡
Prey *i* 'true' attack rate	c_i	$c_i \sim \text{Unif.}(c_{min}, c_{max})$, $c_{min} = 5\times10^{-6}$
Max. potential attack rate	c_{max}	$c_{max} = a\cdot\mu_N/(S\cdot2000)$ §

† Corresponding to a range of 3 to 60% of the individuals in the predator population feeding, on average, at any given time. This minimum is typical of winter feeding levels of temperate intertidal whelks (MN, *unpublished data*).

‡ Parameters chosen to produce values typical of intertidal invertebrate densities (m^{-2}) and whelk prey handling times (hours) (MN, *unpublished data*).

§ Since the probability of feeding on a particular prey species during a given time-step is equal to $c_i\cdot N_i$, setting c_{max} in this manner guarantees that feeding on any prey (i.e., $\Sigma c\cdot N$) does not exceed a probability of 1.

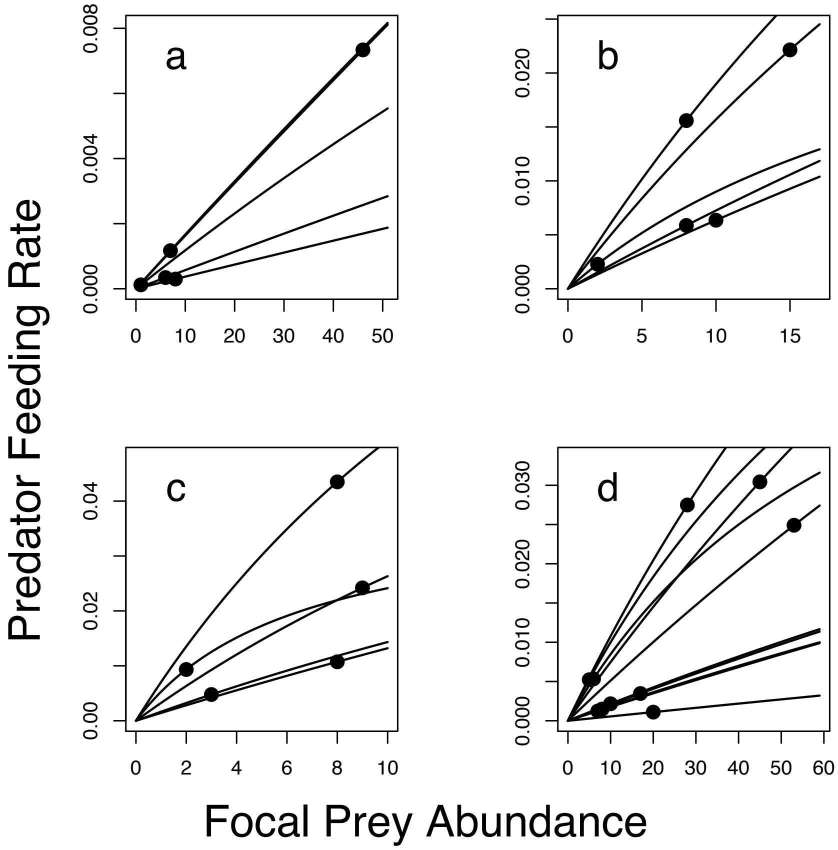

Figure 2.B.2. Multispecies functional response curves resulting from prey parameter values (c_i and h_i) drawn during simulations in which (a) 4%, (b) 33%, and (c) 80% of the individuals in the given predator population are observed feeding with a diet richness of 5 prey species, and (d) for predators in which 55% of individuals are feeding with a diet of 10 species (i.e., the diet richness used to produce Fig. 2.1b). Points represent expected feeding rates actually experienced during the given simulation.

APPENDIX 2.C: THE BIAS AND ACCURACY OF THE OBSERVATION-BASED METHOD

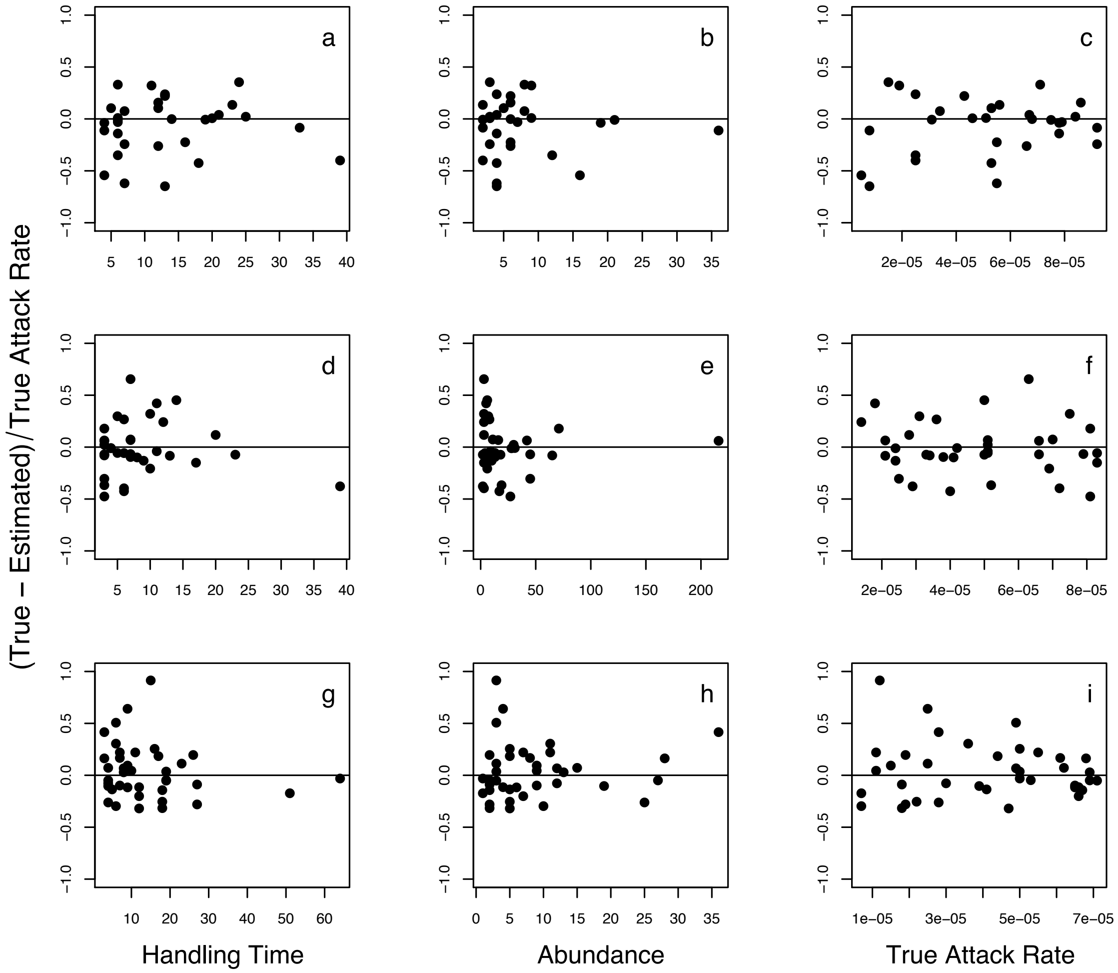

Figure 2.C.1. The proportional deviation of estimated species-specific attack rates from 'true' attack rates as a function of prey handling times (h_i), abundances (N_i), and true attack rates (c_i). Results shown for predator populations of 7500 individuals feeding on diets of (a-c) 32, (d-f) 36, and (g-i) 40 prey species surveyed when 9, 15, and 10%, respectively, of individuals were feeding with unobserved prey species removed. No significant biases were observed as assessed by regressing proportional deviations on h_i, c_i, or log(N_i) in the simulations using 7500 predators ($P > 0.05$ in all cases excepting the simulation of 4 prey species). No changes in accuracy (assessed by regressing absolute proportional deviations on h_i, c_i, or log(N_i)) were observed as a function of handling time or abundance. (While a significant effect of handling time was observed for 4 prey species, and a significant effect of abundance was observed for 36 prey species, slope signs were inconsistent across all the simulated prey richness levels.) Accuracy did, however, consistently increase with the magnitude of true attack rates ($P < 0.10$ for 7 of the 14 prey richness levels, but after Bonferroni correction remained significant for only the 12 prey richness level).

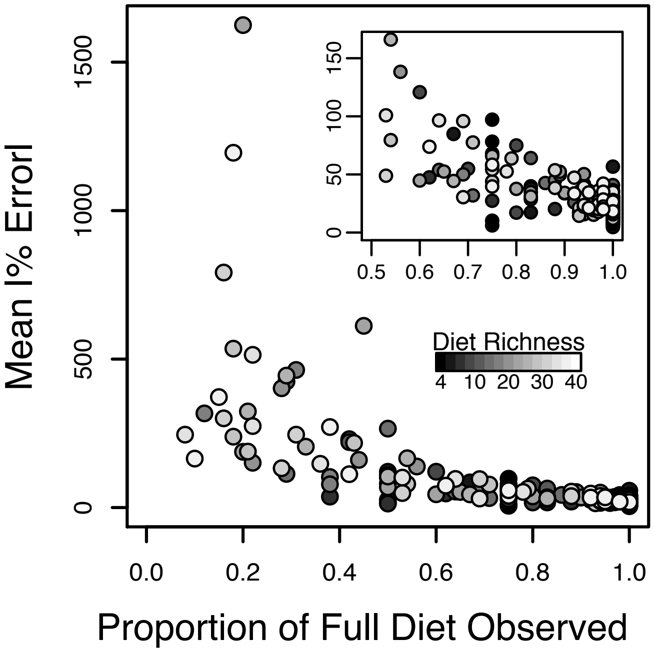

Figure 2.C.2. Relationship between estimation accuracy of predator attack rates and the proportion of the diet observed. Points represent the mean absolute percentage differences between “true” and estimated attack rates of all observed prey (i.e., unobserved prey removed) in each simulated combination of sampling effort and diet richness.

CHAPTER III

ESTIMATING INTERACTION STRENGTHS IN NATURE: EXPERIMENTAL SUPPORT FOR AN OBSERVATIONAL APPROACH

ABSTRACT

The complexity of food webs poses a significant hurdle for our growing understanding of the structure and dynamics of ecological communities. Empirical methods that measure the per capita strength of trophic interactions offer a means to bridge our understanding of feeding behavior and species population dynamics. Many such methods have been proposed, but only few have seen independent validation of their estimates or underlying assumptions. Here I describe an empirical test of a recently proposed observational method for estimating the nonlinear strength of predator-prey interactions in the field. By applying the method to two populations of a classic Type II functional response predator, I estimated its interactions with nine prey species spanning two orders of magnitude of per capita strength. Concurrent experimental manipulations of the two predator populations provided population time-series for the response of a focal prey species. I obtained independent interaction strength estimates for this focal interaction by fitting a series of hypothesized predator-prey models to these time-series. A direct comparison of the estimates from the observational method with those of the best performing models revealed remarkable concordance between the two methods. The results of this study therefore support the use of the observational method in more complex food web applications.

Keywords: species interactions, food webs, attack rate, parameter estimation, functional response.

INTRODUCTION

Efforts to estimate the strengths of species interactions lie at the heart of community and ecosystem ecology, particularly in the context of predator-prey interactions (Paine 1980, Power et al. 1996, Agrawal et al. 2007). Trophic interaction strengths offer insights into how communities are structured by describing the channels by which energy and elements move through food webs (Baird and Ulanowicz 1989), have played a central role in our growing understanding of the ecological processes governing diversity, coexistence, and stability (McCann 2000, Duffy 2002), and are often offered as a means to more accurately predict the community consequences of changing species abundances and extinctions (Ebenman and Jonsson 2005, Agrawal et al. 2007).

Many methods have been proposed to estimate the strengths of species interactions in nature (reviewed in Berlow et al. 2004, Wootton and Emmerson 2005). Of particular interest are methods that estimate interaction strengths on a per capita (or per biomass) basis. Per capita estimates measure the effect of one predator individual on one prey individual, or vice versa. They thereby underlie all other metrics of interaction strength (Laska and Wootton 1998), are directly comparable between all the species of a food web because they scale out differences in population size (Paine 1992, Wootton 1997), and provide a direct means of parameterizing mathematical models to bridge the gap between theoretical ecology and the realities of nature (Berlow et al. 2004, Wootton and Emmerson 2005, Agrawal et al. 2007).

Despite their importance, few of the methods offered to estimate per capita interaction strengths have received independent validation of their estimates or underlying assumptions (Pfister 1995, Schmitz 1997, Wootton 1997, Laska and Wootton 1998, Berlow et al. 1999, Schmitz and Sokol-Hessner 2002). This is surprising given that all methods must make a variety of simplifying but potentially important assumptions regarding the properties of species interactions in nature. Shared among most methods, for example, are assumptions that (i) population abundances are near equilibrium or a mass-balanced state (Bender et al. 1984, Paine 1992, Moore et al. 1993, Hall et al. 2000, Bascompte et al. 2005, Libralato et al. 2006), (ii) that predators and predator-prey size-ratios used in experiments exhibit feeding rates consistent with those experienced by populations in nature (Levitan 1987, Sala and Graham 2002, Emmerson and Raffaelli 2004), (iii) that pairwise interactions are unchanged in multispecies contexts (Levitan 1987, Sala and Graham 2002, Emmerson and Raffaelli 2004), and (iv) that predators display unbounded linear Type I functional responses (Holling 1959) such that their feeding rates remain unsaturated as prey abundances increase (Bender et al. 1984, Levitan 1987, Paine 1992, Moore et al. 1993, Wootton 1997, Hall et al. 2000, Sala and Graham 2002, Emmerson and Raffaelli 2004, Bascompte et al. 2005, Woodward et al. 2005, Libralato et al. 2006). Given that (i) the existence of equilibrium conditions is practically difficult to ascertain, if not contentious (Connell and Sousa 1983), (ii) that predator-prey interactions typically exhibit dynamics that are different in multispecies situations than when species pairs are studied in isolation (Peacor and Werner 2004), (iii) that feeding rates are often sensitive to experimental design and conditions (Ruesink 2000, Chalcraft et al. 2005), and (iv) that the most frequently observed functional responses are of a nonlinear saturating Type II form, even in single-prey studies (Murdoch and Oaten 1975, Jeschke et al. 2002, 2004), such assumptions may be unjustified (Abrams 2001).

Here I describe an empirical test of a new method for estimating the per capita strength of trophic species interactions recently proposed by Novak and Wootton (2008). The observational nature of this method reduces the logistical limitations and circumvents the problems of indirect trophic effects common to many module-based methods for estimating interaction strengths in the field (see also Wootton 1997, Woodward et al. 2005). Requiring only data on prey abundances, handling times, and information from predator-specific feeding surveys (see below), the method also relaxes some of the assumptions of these and other, whole food web-based methods, including assumptions regarding the dynamics of prey populations and the linearity of predator functional responses in multispecies situations. More specifically, it assumes that predators (P) exhibit nonlinear multispecies Type II functional responses to changes in all their prey's abundances (N_i), such that

$$\frac{dN_i}{dt} = g(N_i) - \frac{c_i N_i P}{1 + \sum\limits_{j \forall prey} c_j h_j N_j} \tag{3.1}$$

(e.g., Murdoch 1973), where $g(N)$ is an unspecified function describing the prey population's growth in the absence of predation (which may include self-limitation or competition with other species), and parameters c (the nonlinear per capita attack rates) and h (the handling times) describe the density-dependent form of the predator's feeding rate on prey i (Novak and Wootton 2008).

I tested this method by applying it to two populations of a New Zealand intertidal whelk, *Haustrum scobina*, to estimate the attack rates of this predator on all of its prey. The relatively simple nature of this system allowed me to concurrently estimate *Haustrum*'s attack rates experimentally. I did so by assessing the performance of a series of hypothesized predator-prey models fit to the population dynamics of one of *Haustrum*'s focal prey species in year-long replicated manipulations of the predator. A direct comparison of the observational estimates with those of the best performing models describing the experiments reveals excellent concordance. This study therefore supports the use of the observational method in more complex food webs.

METHODS

Study system

I conducted this study at two rocky intertidal sites located on the northwest coast of New Zealand's South Island: Tauranga Head (41°46′26″ S, 171°27′20″ E) and Cape Foulwind (41°45′09″ S, 171°27′31″ E). These sites are typical of the region's exposed rocky shores (Morton and Miller 1968, Menge et al. 2003), being characterized by an invertebrate-dominated community. The high zone of each site's midlittoral is dominated by *Chamaesipho columna* and *Epopella plicata* barnacles and the mussel *Xenostrobus pulex*. The mid zone is dominated by *Mytilus galloprovincialis* mussels, and the low zone variably consists of *Perna canaliculus* mussels and a *Gigartina*-dominated algal community.

The focal predator of this study, *Haustrum* (=*Lepsiella*) *scobina* (Beu 2004), is a muricid whelk not unlike the *Nucella* species of the northern hemisphere. *Haustrum*'s diet consists primarily of acorn barnacles and mussels (Fearon 1962, Morton and Miller 1968, Luckens 1975b, Menge et al. 1999) but may also include oysters, limpets, snails, and tubeworms (Luckens 1975b, Gardner 1978, McKillup 1982). Muricid whelks like *Haustrum* are classic Type II functional response predators (sensu Holling 1959), typically needing to drill through the shells of their prey to feed. Handling times – the time needed to drill and ingest a prey item – may vary on the order of hours to days, and can limit feeding rates at experimentally manipulated high prey densities (Murdoch 1969, Katz 1985, Moran 1985, Rodrigues 1986). Most digestion of prey tissue occurs during prey ingestion (Boggs et al. 1984), thus digestion times do not limit feeding rates as they do for many vertebrate species (M. Novak, *unpubl. data*; Jeschke et al. 2002). *Haustrum* is abundant at both study sites where it attains a maximum size of ~ 22 *mm* shell height (M. Novak, *unpubl. data*) and lays benthic eggs that hatch to crawl-away larvae.

The focal prey of this study's field experiments was the mytilid mussel *Xenostrobus pulex*, a species that also occurs throughout most of New Zealand's rocky shores. *Xenostrobus* form dense monospecific mats within the high zone, often accumulating significant amounts of sand between their byssal threads. *Xenostrobus* reproduce by broadcast spawning, with larvae recruiting to settle on barnacles, in cracks, or between conspecifics (M. Novak, *pers. obs*.; Luckens 1975a). Individuals attain a maximum of ~ 28 *mm* at the study sites which is not large enough to escape predation by *Haustrum* whelks (M. Novak, *pers. obs.*).

Observational attack rate estimation

The observational method for estimating the per capita attack rates of a predator exhibiting a multispecies Type II functional response requires information on (i) prey-specific handling times (h_i), (ii) prey-specific abundances (N_i), and (iii) data from snapshot feeding surveys used to estimate two additional variables: First, the proportion of individuals in a predator population (feeding and non-feeding) that are observed to be feeding on each of its prey species (A_i), and second, the proportion of the population's feeding individuals that are observed to be feeding on each of its prey species (F_i). With these data, nonlinear capita attack rates (c_i) for each i^{th} species are calculated as

$$c_i = \frac{F_i A_x}{(F_x - A_x) h_i N_i}\,, \tag{3.2}$$

where x denotes an arbitrarily chosen prey species used throughout the calculation of all attack rates. I obtained this information to estimate the attack rates of *Haustrum scobina* on all of its prey at both study sites as follows:

Feeding surveys

I estimated A_i and F_i for both populations by conducting repeated cross-sectional feeding surveys in several predetermined areas at each site over the course of two years (May 2005 – July 2007). These surveys consisted of systematic, ~ ½ hr. long low-tide searches of the high zone during which each found whelk was counted and carefully examined (picked up) to determine whether or not it was feeding. I recorded the identity and size of prey items, and the size of all feeding and non-feeding whelks (± 1 *mm*). Surveys were conducted during both the day and at night, and were not repeated in the same area for at least four high-tides. Preliminary surveys repeated more frequently suggested that four high-tides was ample time for whelks to commence normal feeding activity between surveys.

Abundance surveys

I estimated the population density of all invertebrate species at each site using ten to fifteen 0.25 m^2 quadrats distributed randomly among three 20 *m* transects. Transects were haphazardly located within the same high zone areas in which feeding surveys were conducted. At least one-third of the quadrats were surveyed at night. I accounted for cross-quadrat variation in bedrock topography by dividing each mobile species' quadrat count by the ratio of the minimum distance between opposing quadrat corners (√0.5 m) and the average distance between quadrat corners measured by following the topography of the substrate surface with a flexible line. Sessile species percent-cover estimates were converted to densities using species-specific cover-count conversion relationships determined for each site (M. Novak, *unpubl. data*). Surveys were repeated three times at each site (May-July 2005, January-February 2006, May 2006).

Handling time experiments

Handling times could be measured in a variety of ways (Novak and Wootton 2008). I measured the time needed for a whelk to drill and ingest prey in the laboratory. For example, whelks (7 to 18 *mm*) and *Xenostrobus* mussels (3 to 22 *mm*) were collected at Tauranga Head and transported to the Edward Percival Field Station, Kaikoura. There, mussels were maintained with flowing sea water (~9-11°C) filtered to 40 *m*, while whelks were sorted into aerated aquaria in three temperature-controlled rooms maintained at ~10, 14, and 18°C (monitored using iButton® temperature loggers, Maxim Integrated

Products, CA) and a 12:12*hr* day:night cycle. After an acclimation period of at least 3 days and starvation period of at least 5 days, individual whelks were measured (± 0.1 *mm*), placed into aerated 4 *l* semi-translucent plastic aquaria filled with ~3 *l* of sea-water situated in each temperature room, and provided with six mussels of similar size. Whelks were subsequently checked on an hourly basis and classified as either feeding or not feeding. A trial ended when both the start and end of a whelk's feeding had been well-constrained (each within a 2*hr* 24*min* window or a maximum possible start to end time difference being ≤ 80% of the midpoint time) or if the whelk had not commenced feeding within two weeks. I measured the prey of all successful predation events (± 0.1 *mm*) and visually estimated the proportion of unconsumed tissue remaining.

I estimated handling times for *Haustrum*'s remaining prey species in the same manner but obtained whelks and prey from either Tauranga Head or east coast locations nearer the laboratory. The only prey species for which the above method was not employed were barnacles. Instead, whelks and barnacles were brought to the laboratory from an east coast site (42°27′07″ S, 173°34′08″ E) where barnacles had naturally recruited onto cement tiles over the course of three years. Barnacle tiles and one or two whelks were placed into ~1 *l* plastic aquaria with independent and continually flowing filtered sea-water, the temperature of which varied over the course of the year. Whelk feeding events were monitored using low-light video cameras under natural day:night lighting conditions supplemented by a red light at night. The size of barnacle prey was measured under a dissecting microscope (± 0.1 *mm*).

For each prey species I regressed the duration midpoint of all feeding events on whelk size, prey size, and temperature using log-transformed data weighted by the inverse of the difference between the maximum and minimum possible duration of each feeding event. Thus a handling time that had been constrained to within one hour received less weight than a handling time constrained to 10 minutes. Feeding events in which < 80% of prey tissue had been consumed were excluded.

Attack rate estimation

I used a Stowaway® TidbiT™ temperature logger (Onset Computer, Pocasset, MA) positioned in the low midlittoral of each site to record low-tide air and high-tide water temperatures at ½ hr. intervals over the two year period of feeding surveys. Handling time regression coefficients, whelk and prey sizes, and field temperatures (mean of air and water) observed during the month of a feeding survey were used to back-calculate the expected handling time of each feeding event observed in the field. I then used Eq. 3.2 to estimate attack rate means and calculated conservative 90% confidence intervals by a nonparametric bootstrapping procedure (Efron and Tibshirani 1994), sampling with replacement from the observed feeding events, handling times, and species densities, and using the most frequently observed prey as species x. I estimated attack rates for two time periods: across all feeding surveys combined, and on a seasonal basis with surveys partitioned into austral summer (January – February) and fall-winter (May – July). As species abundances varied little over the course of the study, I estimated both annual and seasonal attack rates by sampling from all the abundance surveys of a site combined.

Experimental attack rate estimation

Caging experiments

I used manipulative caging experiments to estimate the per capita attack rate of *Haustrum scobina* on the focal prey species, *Xenostrobus* mussels, at both Tauranga Head and Cape Foulwind. Each experiment consisted of three treatments – a *Haustrum*-enclosure cage, a predator-exclusion cage, and a cage-free reference plot consisting of four marked corners – replicated six times and haphazardly located in the high zone using a randomized block design. Mussel densities within cages therefore reflected the natural variation in densities observed along the shore. Two additional enclosure/exclusion treatments were implemented at Cape Foulwind in which I reduced the starting number of *Xenostrobus* mussels in each cage to roughly half their pre-manipulation density.

Each cage consisted of a 22 x 20 x 5 *cm* stainless steel mesh perimeter (2.5 *mm* opening diameter, 0.075 *mm* mesh size) with a removable polyethylene Vexar® lid (5.1 *mm* opening diameter, 1.3 *mm* mesh size), and was secured to the bedrock with 8 stainless steel screws (Plate 3.1). At the start of the experiment (August, 2006), each whelk-enclosure cage was stocked with enough whelks to match ambient high zone densities (Cape Foulwind: 4 whelks cage^{-1} vs. the target of 4.1 whelks cage^{-1} based on

Plate 3.1. Predator-exclusion and *Haustrum*-enclosure cages positioned in the high tide zone at Cape Foulwind.

92.9 m^{-2} ± 8.4 SE ambient density; Tauranga Head: 3 whelks cage^{-1} vs. 2.6 whelks cage^{-1} based on 60.4 m^{-2} ± 7.2 ambient density). Whelks were stocked at an initial size of 12-14 *mm* (mean ambient size = 12.6 *mm* ± 2.7 SD at both sites) but grew to 14.7 *mm* ± 4.9 SD by the end of the year-long experiment.

At the start and during each of three subsequent censuses of the experiment (conducted after 178, 280, and 338 elapsed days, Fig. 3.1) I counted and removed all non-stocked *Haustrum* individuals that had either invaded or hatched within the cages, counted all dead *Xenostrobus* individuals, and photographed each plot in a standardized high-resolution manner using a quadrapod. Live *Xenostrobus* counts were obtained by subtracting the observed number of dead individuals from the total number counted in these photographs. Two cages were lost or damaged at each site by storms and were not included in subsequent analysis.

Attack rate estimation

I first used linear mixed effects models to test for the effects of caging and *Haustrum* predation on *Xenostrobus* counts at each site, using treatment and time as fixed effects and blocks and plots as nested random effects. I then fit the experimental time-series from the *Haustrum*-enclosure and predator-exclusion treatments to a nested set of competing models hypothesized to describe the dynamics of *Xenostrobus* in the presence and absence of predation by *Haustrum*. Alternative experimental index methods (e.g., Paine 1992, Wootton 1997) were either inappropriate given the open-recruitment biology

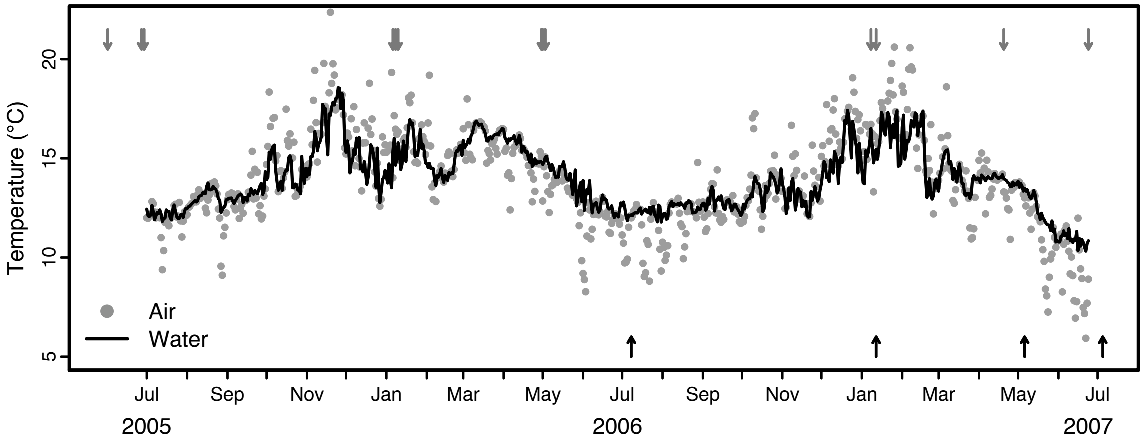

Figure 3.1. Mean daily air and water temperatures observed at Cape Foulwind. Arrows indicate the days when feeding surveys (top arrows) and censuses of the experiment (bottom arrows) were performed.

of *Xenostrobus* mussels, or produce biased attack rate estimates not comparable to those of the observational method (Appendix 3.B). All competing models included a density-independent immigration term (*I*) to reflect the open-recruitment of mussels, but varied in the way they described the whelk-independent and whelk-dependent contributions to mussel population growth. The general model was

$$\frac{dN}{dt} = I - g(N) - f(N, P). \tag{3.3a}$$

Whelk-independent contributions to mussel population growth were described as

$$g(N) = \begin{cases} mN \\ nNN \\ mN + nNN, \end{cases} \tag{3.3b}$$

where *m* modeled the density-independent mortality (or growth) rate of the *Xenostrobus* population *N*, and *n* modeled a density-dependent self-limitation effect of the population on itself. Whelk-dependent contributions to mussel population growth (i.e. feeding rates) were described as

$$f(N) = \begin{cases} 0 \\ \alpha NP \\ cNP/(1 + chN), \end{cases} \tag{3.3c}$$

with whelks (*P*) having no effect, or preying on mussels with either a linear Type I or a nonlinear Type II functional response. (Variable and parameter definitions are summarized in Table 3.1.)

Table 3.1. Model variables and parameter definitions.

Parameter	Description
N	Mussel density
P	Whelk density
I	Mussel immigration rate
m	Mussel mortality rate
n	Mussel per capita self-limitation rate
α	Linear per capita attack rate
c	Nonlinear per capita attack rate
h	Handling time

Assuming log-normally distributed process noise, I used a one-step-ahead prediction procedure and obtained maximum likelihood parameter estimates for each model formulation (Bolker 2008). Repeated counts of 30 randomly chosen photographs representing the range of observed *Xenostrobus* densities suggested that observation error was small enough (5.8%) to avoid bias in parameter estimates (Carpenter et al. 1994). I fit all models with both site-specific and non-site-specific parameters to produce a total of 18 competing models and used AIC_c to compare their performance. AIC_c is the most appropriate criterion with which to compare models at low sample sizes (Burnham and Anderson 2002) and converges on AIC with sufficient sample size (Ward 2008).

To compare the attack rate estimates of the model-fitting to those of the observational method I rescaled them from the area of a cage to a per meter basis. Because the high co-linearity between the attack rate and handling time parameters may have influenced parameter estimation, I (i) refit the best performing nonlinear model after replacing $c\ h$ with a single parameter, and (ii) refit the model with handling times constrained to the mean back-calculated handling times of feeding events observed in the field. I performed this latter procedure to assess the feasibility of reducing parameter uncertainty in attack rates by incorporating this more easily-measured parameter independently (see also Novak and Wootton 2008). I also refit the model to the Cape Foulwind time-series including only cages in which *Xenostrobus* densities had not been manipulated. Confidence intervals were obtained by nonparametric bootstrapping (Efron and Tibshirani 1994) and were conservatively estimated at 90%. All analyses were performed in R (R Development Core Team 2007) using the general-purpose optimization functions *nlminb* and *optim* for model-fitting, and the *bbmle* package (Bolker 2007) for model comparisons.

RESULTS

Observational attack rate estimation

I conducted a total of 33 high zone feeding surveys of the two *Haustrum scobina* populations, examining a total of 4093 whelks in the process. The mean proportion of individuals found feeding in a given survey was 23 ± 2% (SE) at Tauranga Head and 22 ± 2% at Cape Foulwind. I observed *Haustrum* feeding on 8 species at Tauranga Head and 6 species at Cape Foulwind (Fig. 3.A.1). These prey were the snails *Austrolittorina antipodum*, *A. cincta*, and *Risellopsis varia*, the barnacles *Chamaesipho brunnea*, *Ch. columna*, and *Epopella plicata*, the mussels *Mytilus galloprovincialis* and *Xenostrobus pulex*, and a *Notoacmea* sp. limpet from a poorly resolved genus (Nakano and Spencer

2007). *Haustrum*'s diet was dominated by only two species, however. *Ch. columna* and *Xenostrobus* together represented 98% and 97% of the feeding observations made at Tauranga Head and Cape Foulwind, respectively (Table 3.A.1). *Xenostrobus* by itself represented 40% of the observations made at Tauranga Head, and 29% of the observations made at Cape Foulwind.

The proportion of feeding individuals was higher at both sites during summers (27 ± 2% SE) than in the fall-winter seasons (18 ± 1%), commensurate with increased summer temperatures (Fig. 3.1). Mean species abundance ranged across five orders of magnitude within a site (9 to 11 x 10^{-4} individuals m^{-2} for *Mytilus* and *Ch. columna*, respectively; Table 3.A.2). *Xenostrobus* densities averaged 3.5 x 10^{-3} m^{-2} (± 6.4 x 10^{-3} SE) at TH and 3.5 x 10^{-3} m^{-2} (± 6.7 x 10^{-3}) at CF, and *H. scobina* densities averaged 60.4 m^{-2} (± 7.2) at TH and 92.9 m^{-2} (± 8.4) at CF. No species densities exhibited strong or consistent seasonal patterns.

The time required for *Haustrum* individuals to handle prey items in the laboratory also varied greatly among prey species, ranging from a species mean of 15 hours for *Risellopsis* snails to 2.5 days for *Mytilus* mussels. An even larger range of handling times was observed across individuals within prey species however. Handling times for *Xenostrobus* individuals, for example, ranged from 13 hours to 3.6 days. Much of this within-species variation was explained by whelk and prey size, and temperature (Fig. 3.2).

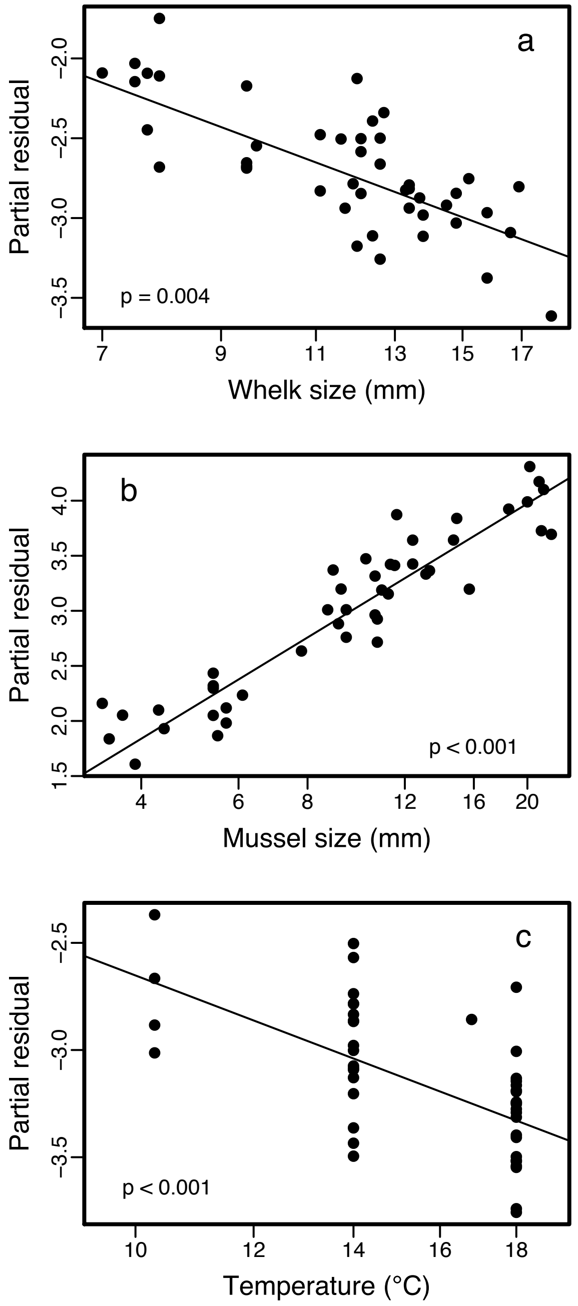

Figure 3.2. Partial residual plots demonstrating the contributions of (a) whelk size (r^2 = 0.07), (b) prey size (r^2 = 0.34), and (c) temperature (r^2 = 0.12) in explaining the handling times required by *Haustrum* whelks to drill and consume *Xenostrobus* mussels in the laboratory (overall R^2 = 0.70). Axes are log-scaled.

Table 3.2. Mean attack rates, *c*, of *Haustrum* whelks on *Xenostrobus* mussels as estimated by the observational method. Units: mussels eaten whelk^{-1} mussel^{-1} m^{-2} day^{-1}.

Site	**Year/Season**	**Estimate**	**90 % Confidence Interval**	
			Lower	**Upper**
Tauranga Head	All year	2.588×10^{-5}	1.911×10^{-5}	3.692×10^{-5}
	Fall-Winter	1.437×10^{-5}	9.870×10^{-6}	2.157×10^{-5}
	Summer	4.203×10^{-5}	3.035×10^{-5}	6.115×10^{-5}
Cape Foulwind	All year	1.342×10^{-5}	9.646×10^{-6}	1.963×10^{-5}
	Fall-Winter	7.763×10^{-6}	5.164×10^{-6}	1.183×10^{-5}
	Summer	2.320×10^{-5}	1.604×10^{-5}	3.469×10^{-5}

Estimates of *Haustrum*'s per capita attack rates varied over two orders of magnitude between prey species when averaged across the two years of the study (Fig. 3.3). Attack rates on *Xenostrobus* mussels were estimated to be higher at Tauranga Head than at Cape Foulwind, and were three times higher during the summer than during the fall-winter seasons (Table 3.2). With the mean back-calculated *Xenostrobus* handling times being 1.24 ± 0.05 (SE) days at Tauranga Head and 1.63 ± 0.08 days at Cape Foulwind, average estimated feeding rates on *Xenostrobus* were also higher at Tauranga Head (0.071 mussels whelk^{-1} m^{-2} day^{-1}) than at Cape Foulwind (0.037 mussels whelk^{-1} m^{-2} day^{-1}).

Experimental attack rate estimation

Mussel population sizes exhibited more growth in the predator-exclusion treatments than in the *Haustrum*-enclosure treatments (Fig. 3.4). This was true at both

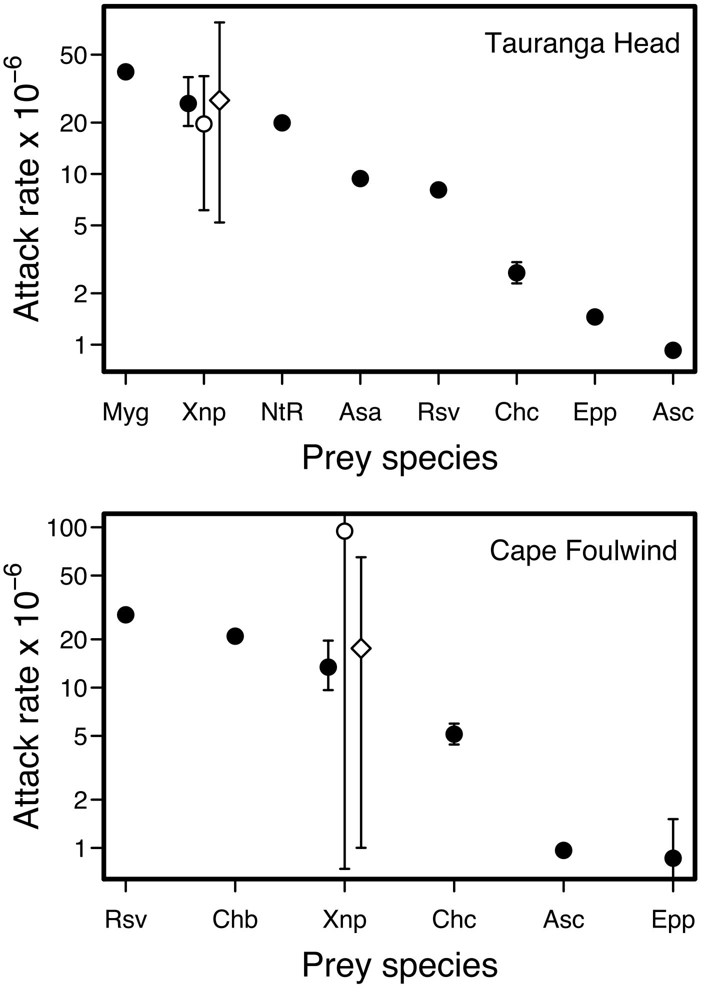

Figure 3.3. Per capita attack rates of *Haustrum* on each of its prey as estimated by the observational approach (closed symbols), with 90% confidence intervals shown only for prey observed > 5 times. Open symbols indicate maximum likelihood estimates from best performing nonlinear model, fit with handling times unconstrained (circle) or constrained (diamond). Species abbreviations: Asa - *Austrolittorina antipodum*, Asc - *A. cincta*, Chb - *Chamaesipho brunnea*, Chc - *Ch. columna*, Epp - *Epopella plicata*, Myg - *Mytilus galloprovincialis*, NtR - *Notoacmea* sp., Rsv - *Risellopsis varia*, Xnp - *Xenostrobus pulex.*

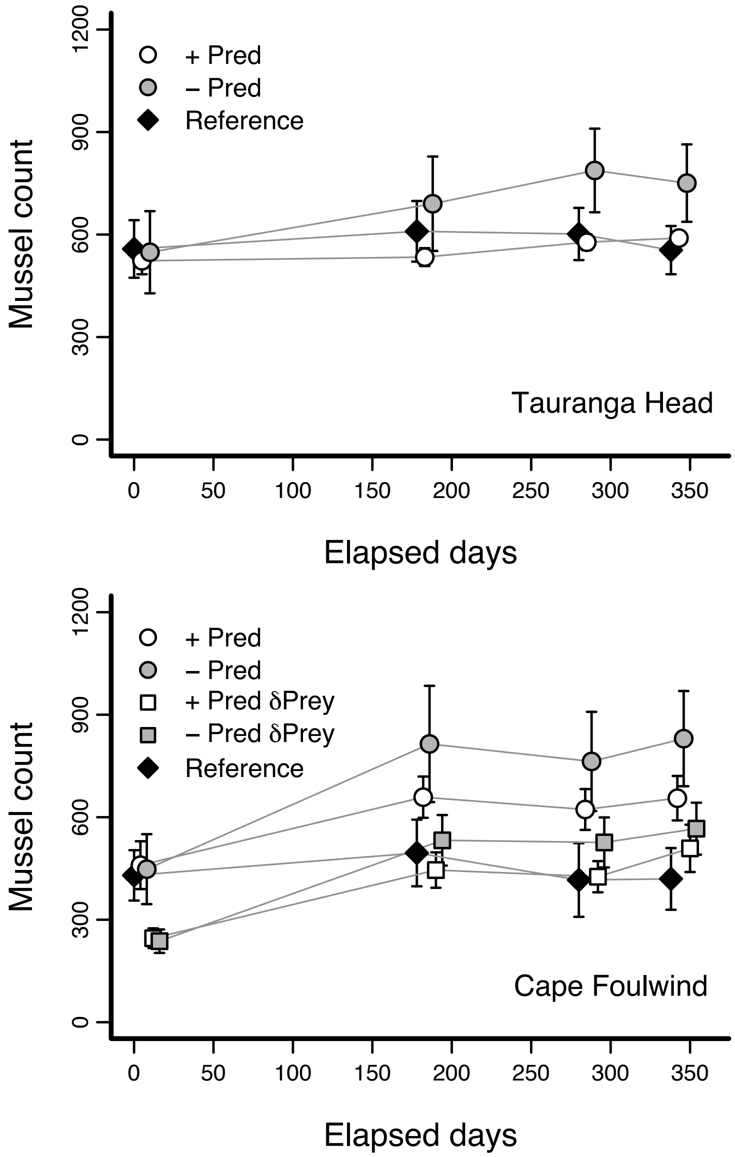

Figure 3.4. *Xenostrobus* mussel population dynamics (mean ± SE) observed in the experimentally manipulated presence and absence of *Haustrum* predation. Points staggered for clarity.

Tauranga Head ($t_{42} = 3.02$, $p = 0.004$), but only marginally so at Cape Foulwind ($t_{80} = 1.94$, $p = 0.056$) where a model including time as a polynomial term fit significantly better than a model with only a linear time term (Likelihood ratio = 24.2, $p < 0.001$). Population dynamics did not differ between the *Haustrum*-enclosure cages and the cage-free reference plots at Tauranga Head ($t_{42} = 1.11$, $p = 0.27$), but densities did increase in the *Haustrum*-enclosure cages relative to the reference plots at Cape Foulwind ($t_{80} = 5.40$, $p < 0.001$). Only five stocked *Haustrum* individuals escaped between censuses, and invaders and hatchlings (1.5 cage^{-1} census^{-1}) are unlikely to have caused significant predation pressure on mussels due to their small size (mean = 7 *mm*).

In model-fitting, nine of the twelve hypothesized models that included a predation term performed better in describing prey dynamics than did the remaining six models that did not (Table 3.3). The three best performing models effectively performed equally well ($\Delta_i < 4$, Burnham and Anderson 2002), and had site-specific parameters that included predation terms assuming a linear functional response. The overall best performing model had site-specific immigration, self-limitation, and linear predation terms. This model suggested higher mussel immigration and self-limitation rates, and lower *Haustrum* attack rates, at Cape Foulwind than at Tauranga Head (Table 3.4).

The best performing nonlinear model also included only mussel immigration and self-limitation rates on a site-specific basis (Table 3.3). It too suggested higher immigration and self-limitation rates, and lower feeding rates, at Cape Foulwind than at Tauranga Head (Table 3.5). The model’s per capita attack rate estimate closely matched

Table 3.3. AIC$_c$ comparisons of competing models fit to the time-series dynamics of *Xenostrobus* mussels in the experimental presence or absence of *Haustrum* whelks.

Site-specific parameters	**Predator functional response**	**Prey self-limitation**	**Density-independent prey mortality**	***k***	***L***	**AIC$_c$**	Δ_i
No	No predator effect	No	Yes	3	592.2	1190.7	11.9
No	No predator effect	Yes	No	3	592.1	1190.4	11.5
No	No predator effect	Yes	Yes	4	592.0	1192.5	13.7
No	Type I	No	Yes	4	587.7	1183.8	5.0
No	Type I	Yes	No	4	588.3	1185.0	6.1
No	Type I	Yes	Yes	5	587.6	1185.8	7.0
No	Type II	No	Yes	5	587.7	1186.1	7.2
No	Type II	Yes	No	5	588.3	1187.2	8.4
No	Type II	Yes	Yes	6	587.6	1188.1	9.2
Yes	No predator effect	No	Yes	6	587.0	1186.9	8.1
Yes	No predator effect	Yes	No	6	587.2	1187.3	8.5
Yes	No predator effect	Yes	Yes	8	586.6	1190.9	12.0
Yes	Type I	No	Yes	8	580.6	1178.8	*
Yes	Type I	Yes	No	8	581.4	1180.5	1.7
Yes	Type I	Yes	Yes	10	580.0	1182.6	3.7
Yes	Type II	No	Yes	10	580.4	1183.4	4.6
Yes	Type II	Yes	No	10	581.2	1185.0	6.1
Yes	Type II	Yes	Yes	12	580.0	1187.7	8.8

Note: k = number of parameters including error variance, L = negative log-likelihood, Δ_i = difference between the AIC$_c$ of each model and the AIC$_c$ of the best model.

* Lowest AIC$_c$ value.

Table 3.4. Maximum likelihood parameter estimates for the best performing model. Units: I – mussels m^{-2} day^{-1}; n – mussels mussel^{-1} m^{-2} day^{-1}; α – mussels eaten whelk^{-1} mussel^{-1} m^{-2} day^{-1}.

Parameter	**Site**	**Estimate**	**90 % Confidence Interval**	
			Lower	**Upper**
I	Tauranga Head	4.621 x 10^{-2}	2.510 x 10^{-2}	9.667 x 10^{-2}
	Cape Foulwind	7.832 x 10^{2}	5.126 x 10^{-2}	1.241 x 10^{-1}
n	Tauranga Head	2.750 x 10^{-8}	3.666 x 10^{-9}	1.061 x 10^{-7}
	Cape Foulwind	7.644 x 10^{-8}	5.717 x 10^{-8}	1.713 x 10^{-7}
α	Tauranga Head	1.964 x 10^{-5}	5.299 x 10^{-6}	3.504 x 10^{-5}
	Cape Foulwind	1.242 x 10^{-5}	1.246 x 10^{-6}	2.554 x 10^{-5}

Table 3.5. Maximum likelihood attack rate estimates for the best performing Type II functional response model. Units: mussels eaten whelk^{-1} mussel^{-1} m^{-2} day^{-1}.

Site	**Handling time constrained**	**Estimate**	**90 % Confidence Interval**	
			Lower	**Upper**
Tauranga Head	Yes[1]	2.700 x 10^{-5}	5.198 x 10^{-6}	7.725 x 10^{-5}
Cape Foulwind	Yes[1]	1.757 x 10^{-5}	1.002 x 10^{-6}	6.500 x 10^{-5}
Tauranga Head	No[2]	1.964 x 10^{-5}	6.134 x 10^{-6}	3.743 x 10^{-5}
Cape Foulwind	No[2]	9.463 x 10^{-5}	7.405 x 10^{-7}	4.184 x 10^{-1}
Cape Foulwind[3]	No	1.642 x 10^{-5}	1.557 x 10^{-6}	5.094 x 10^{-3}

[1] Handling time constrained to h_{TH} = 1.24 and h_{CF} = 1.63

[2] Maximum likelihood handling time estimates: h_{TH} = 0 and h_{CF} = 5.53.

[3] Includes only cages with ambient *Xenostrobus* starting density. Maximum likelihood handling time estimate: h_{CF} = 0.

the estimate of the observational method for Tauranga Head (Fig. 3.3). This site's point estimate was within 32% of the observational estimate when handling time was left unconstrained, and was within 5% when handling time was constrained to the mean back-calculated handling time.

Lower feeding rates and increased variation across cages resulted in substantially wider confidence intervals at Cape Foulwind (Table 3.5). Agreement between the point estimates of the two methods nonetheless remained very high at Cape Foulwind (< 31%) when handling time was constrained (Fig. 3.3). Despite the attack rate point estimate of the unconstrained model being substantially higher than that of the observational method, estimates remained of the same order of magnitude (within 610%) and did not differ significantly from one-another. Agreement between the point estimates of the two methods increased when cages with manipulated *Xenostrobus* densities were omitted from the analysis (< 23 %, Table 3.5).

DISCUSSION

Agreement between estimation methods

The principal result of this study was that the fitting of hypothesized models to the time-series of independent manipulative experiments produced per capita attack rate estimates that were in close agreement with the estimates produced by the observational method. When handling times were constrained to their most likely empirical values, the best performing nonlinear model produced point estimates that were within 31% of the estimates produced by the observational method. The fact that point estimates of the two methods agreed well with one-another even when handling times were left unconstrained, bodes well for the use of the observational method in the more species-rich and complex food webs observed in nature.

The close agreement of the two approaches in estimating *Haustrum*'s attack rates on *Xenostrobus* mussels is notable. *Haustrum* was observed feeding on eight other species at the two sites, with observational attack rate estimates for these species varying across two orders of magnitude (Fig. 3.3). While observational estimates on *Xenostrobus* fell at the upper end of this range, both methods agreed that feeding rates on *Xenostrobus* were higher at Tauranga Head than at Cape Foulwind despite the fact that the two populations exhibited equivalent feeding activity levels (22-23% of individuals feeding at any given time). In fact, at Tauranga Head the per capita attack rate was estimated to be an order of magnitude larger on *Xenostrobus* than on *Chamaesipho columna* (Fig. 3.3), the prey observed most frequently in *Haustrum*'s diet (Table 3.A.2).

The close agreement between the two methods is also interesting because the model-fit point estimates were expected to underestimate *Haustrum*'s attack rates on *Xenostrobus* relative to the observational method. While both methods allowed for Type II functional responses, the fitted models assumed a predator responding only to *Xenostrobus* densities and therefore ignored *Haustrum*'s feeding on other prey species, most importantly *Ch. columna*. The observational method, however, assumes a multispecies functional response. The incorporation of this interaction in the denominator of *Haustrum*'s modeled Type II functional response would have increased the inferred attack rate of *Haustrum* on *Xenostrobus*. While technically feasible, the inclusion of *Haustrum*'s feeding on *Ch. columna* in such a more complex model was beyond the scope of this study for three reasons: (1) The counting of this abundant species would have introduced relatively large amounts of observation error due to the small size of individuals (< 3 *mm*). (2) Models incorporating *Ch. columna* would have also needed to include the asymmetric and age-dependent competitive interaction present between the species. *Xenostrobus* preferentially recruit onto barnacles as juveniles, but overgrow and smother them as adults (M. Novak, *pers. obs.*; Luckens 1975a). (3) Despite replication efforts, it is unlikely that the experiments I performed would have provided sufficient data to confidently fit models that included the additionally needed parameters. The close agreement observed between the two methods despite the difference in assumed functional responses suggests that alternative prey had relatively weak effects on the predator's interaction with its *Xenostrobus* prey.

The nonlinearity of species interactions

A second result of this study was that model-selection favored the models that described predation by a linear Type I functional response (Table 3.3). This result seems surprising given that whelks have repeatedly exhibited saturating functional responses under experimental conditions (Murdoch 1969, Katz 1985, Moran 1985, Rodrigues 1986). Linear models may have been favored due to the nature of the criterion I used to compare competing models; AIC_c does tend to favor simpler models (Ward 2008). The substantial AIC_c difference between the best performing linear and nonlinear models nevertheless suggests that the use of this criterion was not problematic (Burnham and Anderson 2002).

A more likely explanation may lie in the known difficulty of using time-series to estimate the parameters of nonlinear functional response models relative to those of linear models (Carpenter et al. 1994). This was reflected in the large confidence intervals of fitted attack rate estimates at Cape Foulwind, and in the maximum likelihood estimates for handling times reducing the best performing nonlinear model to having linear functional responses when cages with manipulated *Xenostrobus* densities were not included in the analysis (Table 3.5). The density reductions that I performed in these additional caging treatments at Cape Foulwind clearly influenced the performance of the nonlinear models.

Rather than being a problem of insufficient replication, this result may provide support to the idea that trophic interactions, especially in multispecies settings, may be approximately linear in the range of mean prey densities actually observed in nature (Wootton and Emmerson 2005). The fact that observational attack rate estimates were so close to model-based estimates suggests that density-dependent feeding rates may not have been high enough for handling times to produce saturated nonlinearity. This suggestion is corroborated by the close agreement observed between attack rate estimates of the best performing linear model and those obtained by applying the log-ratio method of estimating interaction strengths to the experiments (Appendix 3.C). A number of other studies have shown linearly estimated interaction strengths to provide good predictions of independent experimental effects (e.g., Pfister 1995, Schmitz 1997, Wootton 1997), although others have not (Ruesink 1998, Sarnelle 2003).

Estimating interaction strengths in nature

For this study, model-fitting offered the most appropriate way to empirically test the accuracy of the observational method because it avoided a number of implicit assumptions made by alternative experimental methods and was flexible to varied model formulations, including both linear and nonlinear functional responses. Paine's interaction strength index (Paine 1992), for example, assumes a linear model and is inappropriate to the open-recruitment biology of this study's focal prey (Appendix 3.B). Other experimental indices can also be derived (Appendix 3.B), but either produce biased attack rate estimates, or do not provide sufficient sensitivity when applied to this study's experiments (Appendix 3.C).

The observational method does itself assume a particular model and interpretation of the predator-dependent component of prey dynamics, however: a multispecies Type II functional response that assumes nontrivial handling times but trivial post-handling digestion times. While the method appears flexible to near linear interaction forms (*see above*), many other functional response forms have also been proposed to describe predator-prey interactions (reviewed in Jeschke et al. 2002, Gentleman et al. 2003).

Nevertheless, saturating Type II functional responses are among the most common nonlinear forms assumed by theoreticians and empiricists alike, because they, unlike many other response forms, can be derived from first principles and have seen a wealth of empirical evidence to support their use (Murdoch and Oaten , Hassell et al. 1977, Jeschke et al. 2004).

The appeal of the observational approach is that it avoids the potentially confounding physical (Miller and Gaylord 2007), behavioral (Hall et al. 1990), and multi-predator (Menge et al. 2003) effects inherent in experimental predator manipulations. It is unknown, for example, which of these factors contributed to the increased growth of *Xenostrobus* populations in the predator-free cages, relative to reference plots, at Cape Foulwind but not at Tauranga Head (Fig. 3.4). The sources of between-cage variation that resulted in the high uncertainty of experimental attack rate estimates at Cape Foulwind are similarly unclear; the observational method produced estimates with substantially smaller confidence intervals at both sites (Fig. 3.3).

The most notable advantage of the observational approach over other approaches, however, lies in its utility for directly measuring the strengths of all a predator’s trophic interactions concurrently, in natural field settings, and, given sufficient sampling effort, in food webs too species rich and reticulate for complete experimental dissection (see also Wootton 1994, 1997, Woodward et al. 2005). Food webs are certainly far more complex than the food web modules that experimental ecologists typically study (Polis and Strong 1996), but other, non-experimental approaches may make their own unreasonable assumptions (see *Introduction*). This study applied the observational method to a relatively simple system to allow comparison with experiments that reduced the concealment of direct effects by indirect trophic interactions (Yodzis 1988). The method allowed per capita attack rates to be estimated at two sites for nine different prey species, many of which had densities so low, or which were observed being fed upon so infrequently, that feeding rates would have been too low to detect effects in any predator-exclusion experiment (Hall et al. 1990).

Employing the method at seasonal scales also revealed considerable temporal variation in attack rates. This variation will likely have been a function of both the metabolic effects of temperature (Largen 1967, Bayne and Scullard 1978) and the behavioral changes in *Haustrum* associated with seasonal reproductive activity (M. Novak, *pers. obs.*). Many other studies have likewise shown that interaction strengths are dynamic, changing in space and time as species abundances, identities, and environmental contexts vary (Peacor and Werner 2004, Woodward et al. 2005, Navarrete and Berlow 2006). The observational method could easily be used to address such changes by investigating differing spatial (e.g., tide-zone), temporal (e.g., diel), or intraspecific (e.g., ontogenetic) sources of variation in attack rates through the partitioning of an adequate number of surveys (see Novak and Wootton 2008).

The complexity of multispecies interactions poses a significant hurdle for our growing understanding of the structure and dynamics of ecological communities. Progress in understanding such reticulate systems will be made by ensuring that the assumptions inherent in our methods for measuring interaction strengths are appropriate, and that our estimates are applicable to the scales of whole food webs. The results of this study suggest that the observational approach to estimating interaction strengths on a per capita basis provides a reliable means for doing so.

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APPENDIX 3.A: SPECIES ACCUMULATION CURVES, PREY OBSERVATION COUNTS, AND SPECIES ABUNDANCES

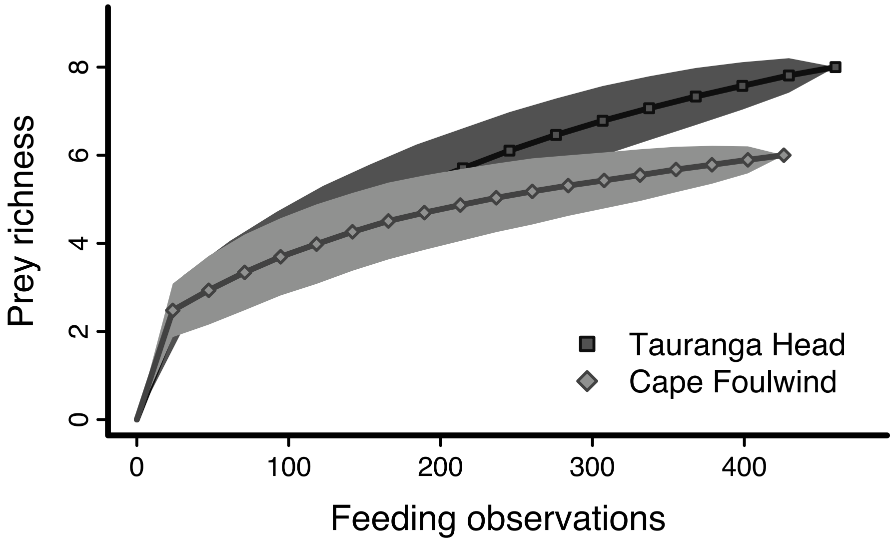

Figure 3.A.1. Species accumulation curves of prey observed in the diet of *Haustrum scobina* (SD), constructed using feeding surveys as the unit of sampling (Gotelli and Colwell, 2001).

Table 3.A.1. Frequency with which prey were observed in the diet of *Haustrum scobina*.

Species	Tauranga Head	Cape Foulwind
Austrolittorina antipodum	3	--
Austrolittorina cincta	2	3
Chamaesipho brunnea	--	1
Chamaesipho columna	265	293
Epopella plicata	2	6
Mytilus galloprovincialis	1	--
Notoacmea sp.	1	--
Risellopsis varia	1	1
Xenostrobus pulex	185	122
Not Feeding	1629	1578

Table 3.A.2. Mean high zone species densities, m^{-2} (± 1 SE).

Species	Tauranga Head	Cape Foulwind
Austrolittorina antipodum	309.6 (60.2)	96.6 (37.6)
Austrolittorina cincta	4685.6 (678.2)	3572.2 (527.7)
Chamaesipho brunnea	2.1 (1.5)	24.6 (14.9)
Chamaesipho columna	106021.3 (4657.1)	68682.4 (4210.7)
Epopella plicata	838.2 (136.6)	4374.9 (386.2)
Haustrum scobina	60.4 (7.2)	92.9 (8.4)
Mytilus galloprovincialis	9.3 (3.5)	12.4 (3.8)
Notoacmea sp.	144.8 (28.7)	209.8 (24.5)
Risellopsis varia	122.2 (36.1)	40.6 (9.6)
Xenostrobus pulex	3529.1 (639.3)	3527.9 (673.5)

APPENDIX 3.B: CLARIFICATION AND DERIVATION OF EXPERIMENTAL INDICES

This appendix attempts to clarify some of the assumptions made in the application of the two commonly used experimental interaction strength indices: Paine's index and the dynamic index. It also introduces two further indices: a reformulation of Paine's index applicable to one type of open-recruitment system, and an extension of the dynamic index applicable to predators exhibiting Type II functional responses.

Paine's Index

The index proposed by Paine (1992) for estimating the per capita interaction strength of a predator on its prey using a caging experiment is

$$PI = \frac{N_{+P} - N_{-P}}{PN_{-P}}, \tag{3.B.1}$$

where P is the abundance of the predator and N is the abundance of the prey in the experimentally manipulated presence (+P) or absence (-P) of the predator. Strictly speaking, the this index estimates -α, the per capita attack rate assuming a linear functional response, if the prey dynamics of a Lotka-Volterra predator-prey model are formulated, using logistic prey growth, as

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K} - \alpha P\right), \tag{3.B.2}$$

where r is the prey populations' intrinsic growth rate and K its carrying capacity. The theoretical justification of Paine's index proceeds as follows: Assume that prey populations are at equilibrium abundance N^*, such that $dN/dt = 0$ in both the presence and absence of the predator. Rearranging Eq. 3.B.2 to isolate N^* leads to

$$N^*_{+P} = K - K\alpha P \tag{3.B.3}$$

in the predator-enclosure treatment, and

$$N^*_{-P} = K \tag{3.B.4}$$

in the predator-exclusion treatment ($P = 0$). Applying Paine's index leads to the cancellation of all parameters except $-\alpha$ (Laska and Wootton 1998).

This model formulation (Eq. 3.B.2), however, implicitly treats α as being scaled to r. Paine's index does not, therefore, produce estimates consistent with empirical per capita attack rate estimates (i.e., number of prey eaten per predator per prey per time). This is clarified by formulating prey dynamics as

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - \alpha PN\,, \tag{3.B.5}$$

where α is not implicitly scaled to r. An application of Paine's index to this formulation leads to an estimate of $-\alpha/r$ (Abrams 2001). Therefore, in either model formulation, the use of Paine's index to estimate predator per capita attack rate requires an additional independent measurement of the prey intrinsic per capita growth rates if the interaction strengths of different species-pairs in a food web are to be compared.

Which predator-prey model is assumed to underlie the prey dynamics of an empirical system is also of importance in regards to the application of Paine's index under other model formulations. Thus, while Paine's index was originally conceived and applied to an intertidal system (Paine 1992), and intertidal biologists have been among its most frequent subsequent users, the index is in fact not appropriate in experimental situations open to outside immigration or recruitment. Application of Paine's index to the three predator-prey models with immigration and linear functional responses utilized in the main text (Eq. 3.3, where *m* is substituted for *r* and *n* is substituted 1/*K*), for example, leads to estimates of

$$\alpha/(m+\alpha P) \tag{3.B.6}$$

for the model assuming only a density-independent prey mortality rate (*m*);

$$\frac{\alpha P + 2\sqrt{I}\sqrt{n} + \sqrt{\alpha^2 P^2 + 4In}}{2P\sqrt{I}\sqrt{n}} \tag{3.B.7}$$

when only a density-dependent self-limitation rate (*n*) is assumed; and

$$\frac{\alpha P - \sqrt{m^2 + 4In} + \sqrt{m^2 + 2\alpha m P + \alpha^2 P^2 + 4IN}}{mP + P\sqrt{m^2 + 4In}} \tag{3.B.8}$$

for the full model including both mortality and self-limitation.

A subtle reformulation of Paine's index as

$$PI = \frac{N_{+P} - N_{-P}}{PN_{+P}} \tag{3.B.9}$$

provides a more straightforward means to isolate α in the simplest immigration model assuming only density-dependent mortality, but also estimates a scaled attack rate, $-\alpha/m$ (J.T. Wootton, *pers. comm.*).

The Dynamic Index

A second interaction strength index proposed to estimate per capita attack rates that is known as the log-ratio method (Billick and Case 1994, Osenberg et al. 1997, Wootton 1997) or as the Dynamic index (Berlow et al. 1999), is commonly written as

$$DI = \frac{ln\left(\frac{N_{+P}}{N_{-P}}\right)}{P\Delta t} \tag{3.B.10}$$

where N is the abundance of the prey in the experimental presence or absence of a predator after time Δt has elapsed. The index is derived from a Ricker-type predator-prey model, analogous to Eq. 3.B.2 but formulated in discrete-time, written as

$$N_{t+\Delta t} = N_t e^{(r-N_t/K-\alpha P)\Delta t}, \tag{3.B.11}$$

and therefore also assumes a linear functional response.

While Eq. 3.B.10 estimates an unbiased - when prey populations in the two treatments are exactly equal at time t (i.e., at the start of the experiment), this is rarely the case in empirical situations. If abundances at time t are sufficiently similar, however, such that differences in the effects of intraspecific density dependence can be assumed to be unimportant, then an empirically more practical formulation of the dynamic index estimates -α using not the difference in final prey abundances, but the difference in prey growth rates between the two treatments, and is written as

$$DI = \frac{ln\left(\frac{N_{+P,t+\Delta t}}{N_{+P,t}}\right) - ln\left(\frac{N_{-P,t+\Delta t}}{N_{-P,t}}\right)}{P\Delta t} \tag{3.B.12}$$

(J.T. Wootton, *pers. comm.*). Note that Eq. 3.B.12 reduces to Eq. 3.B.10 if $N_{-P,t} = N_{+P,t}$.

Unlike Paine's index, the dynamic index need not be affected by the inclusion of outside immigration or recruitment. For example, applying the index to prey dynamics formulated as

$$N_{t+\Delta t} = N_t e^{(I/N_t - n - mN_t - \alpha P)\Delta t}, \tag{3.B.13}$$

analogous to the full linear model of the main text (Eq. 3.3), returns an unbiased estimate of α.

An extension of the dynamic index can also be derived for situations where the predator's feeding rate exhibits a nonlinear Type II functional response to changes in the prey's density, such as

$$N_{t+\Delta t} = N_t e^{\left(r - \frac{N_t}{K} - \frac{cP}{1+chN_t}\right)\Delta t}. \tag{3.B.14}$$

This model is a slight simplification of the model used in simulations of Berlow et al. (1999) written in discrete time, and does not assume outside immigration. The extension requires a total of four experimental treatments: the standard predator enclosure and exclusion treatments where prey densities are left un-manipulated, and two predator enclosure and exclusion treatments in which prey densities are reduced by a proportion δ (J.T. Wootton, *pers. comm.*). Letting R_x stand for the log ratio of prey abundances at time $t + \Delta t$ and time t in treatment x,

$$DI_{TypeII} = \frac{(R_{-P,\delta} - R_{+P,\delta})(R_{+P} - R_{-P})(1-\delta)}{(\delta(R_{-P,\delta} - R_{+P,\delta}) - (R_{-P} + R_{+P}))P\Delta t}. \tag{3.B.15}$$

This index estimates -*c*, the attack rate constant that describes the rate at which a predator approaches the saturation point of its functional response as the abundance of its prey increases. It shares all other assumptions of the original dynamic index.

With four treatments it is also possible to derive estimates of other model parameters. Assuming Eq. 3.B.14, the time that a predator spends handling all the prey it eats is estimated by

$$H = ch = \frac{R_{+P,\delta} - R_{-P,\delta} - R_{+P} + R_{-P}}{(R_{+P} - R_{-P} + \delta(R_{-P,\delta} - R_{+P,\delta}))N_{-P,t}}\ . \tag{3.B.16}$$

The prey populations intrinsic growth rate is estimated by

$$r = \frac{R_{-P,\delta} - \delta R_{-P}}{(1-\delta)\Delta t}\ . \tag{3.B.17}$$

Finally, the prey's carrying capacity is estimated by

$$K = \frac{(R_{-P,\delta} - \delta R_{-P})N_{-P,t}}{R_{-P,\delta} - R_{-P}}\ . \tag{3.B.18}$$

APPENDIX 3.C: PERFORMANCE OF EXPERIMENTAL INDICES

The two indices used most frequently in experimental investigations seeking to estimate interaction strengths are Paine's index (Paine 1992) and the dynamic index (Billick and Case 1994, Osenberg et al. 1997, Wootton 1997). Paine's index estimates interaction strengths as the attack rate scaled to the prey population's growth rate. Though it is inappropriately applied to situations with open-recruitment (see Appendix 3.B), it has seen frequent use in intertidal systems. Two further variants of these indices – a reformulation of Paine's index applicable to one type of open-recruitment situation, and an extension of the dynamic index applicable to Type II functional response predators – are described in Appendix 3.B. This appendix details the results of applying these four indices to the responses of *Xenostrobus* mussel populations in the experimentally manipulated presence and absence of *Haustrum* whelks.

Paine's index (Eq. 3.B.1) assumes that prey abundances have returned to equilibrium after the removal of the predator (Laska and Wootton 1998). This is true for its reformulated version as well (Eq. 3.B.9). The dynamic index (Eq. 3.B.10 and 3.B.12), on the other hand, performs best when population sizes are closest to their starting conditions (Laska and Wootton 1998), which may or not correspond to the prey's equilibrium abundance (c.f. Berlow et al. 1999). This is because of the discrete-time nature of the model on which this index is based (Eq. 3.B.11), which assumes that population trajectories depend only on initial conditions with no continuous-time changes in population density occurring between time-intervals (J.T. Wootton, *pers. comm.*, see also Deng 2008). This is also true for the index's extension that assumes that predators exhibit a Type II functional response (Eq. 3.B.15; M. Novak, *unpubl. simulations*).

In applying the four indices to the experimental times-series of *Xenostrobus* dynamics in the presence and absence of *Haustrum scobina*, I therefore used the abundances of *Xenostrobus* at the end of the experiment for both Paine's index and its reformulated variation, and the abundances of *Xenostrobus* observed during the second census ($\Delta t = 178$) for both dynamic indices. The loss of cages due to storms reduced the number of blocked $+P$ and $-P$ treatment pairs to 5 at Tauranga Head and 10 at Cape Foulwind (4 for the Type II dynamic index). I therefore treated each cage as independent and obtained estimates for each index by nonparametric bootstrapping. In applying the Type II dynamic index to the Cape Foulwind experiment, I estimated each block's α by the quotient of the abundance in its reduced *Xenostrobus* cages and its un-manipulated cages at the start of the experiment.

Because Paine's index and its reformulated variation estimate α/r rather than α itself (Appendix 3.B), estimates produced by the two indices are two orders of magnitude larger than those produced by the observational method or by maximum likelihood estimation using explicit model-fitting (contrast Tables 3.C.1 and 3.C.2 with Tables 3.2 and 3.4).

Despite being more appropriate to the nonlinear functional response biology of the predator, the extension of the dynamic index produces an attack rate point estimate that is an order of magnitude smaller than those produced by either the observational

Table 3.C.1. Bootstrapped mean per capita interaction strengths as estimated by Paine's index.

Site	Prey Treatment	Estimate	90 % Confidence Interval	
			Lower	Upper
Cape Foulwind	Ambient	1.298×10^{-3}	-6.795×10^{-3}	7.245×10^{-3}
	Reduced	-1.138×10^{-4}	-1.454×10^{-2}	6.137×10^{-3}
Tauranga Head	Ambient	1.840×10^{-3}	-5.288×10^{-3}	6.413×10^{-3}

Table 3.C.2. Bootstrapped mean per capita interaction strengths as estimated by the reformulated version of Paine's index.

Site	Prey Treatment	Estimate	90 % Confidence Interval	
			Lower	Upper
Cape Foulwind	Ambient	4.008×10^{-3}	-4.200×10^{-3}	2.122×10^{-2}
	Reduced	2.327×10^{-3}	-6.262×10^{-3}	1.388×10^{-2}
Tauranga Head	Ambient	4.039×10^{-3}	-3.887×10^{-3}	1.140×10^{-2}

Table 3.C.3 Bootstrapped mean parameter estimates as estimated at Cape Foulwind using the Type II dynamic index.

Parameter	Estimate	90 % Confidence Interval	
		Lower	Upper
c	5.477×10^{-6}	-1.161×10^{-4}	8.562×10^{-5}
ch	4.900×10^{-3}	-8.885×10^{-3}	1.836×10^{-2}
r	5.498×10^{-3}	-2.728×10^{-3}	1.271×10^{-2}
K	3.532×10^{2}	-1.025×10^{3}	1.523×10^{3}

Table 3.C.4. Bootstrapped mean per capita attack rate estimates, α, of the dynamic index.

Site	Prey Treatment	Estimate	90 % Confidence Interval	
			Lower	Upper
Cape Foulwind	Ambient	1.360×10^{-5}	-1.738×10^{-5}	4.379×10^{-5}
	Reduced	1.26×10^{-5}	-5.313×10^{-5}	7.493×10^{-5}
Tauranga Head	Ambient	2.130×10^{-5}	-1.191×10^{-5}	5.815×10^{-5}

method or by model-fitting (contrast Table 3.C.3 with Tables 3.2 and 3.5). It is unclear whether this lack of correspondence is due to insufficient sample sizes or the inappropriateness of the model lacking immigration that is assumed to underlie the dynamics of *Xenostrobus* by application of this index.

Application of the standard dynamic index, however, produces point estimates quite similar to those of best performing linear model fit to the time-series of *Xenostrobus* dynamics (contrast Table 3.C.4 with Table 3.4). Estimates from the dynamic index suggest that attack rates were higher at Tauranga Head than at Cape Foulwind, just as did the best performing linear model. Although index estimates are larger than model-fit estimates at both sites, this is not surprising given that they were estimated with only the data from the first time period of the experiment when abundances diverged most dramatically.

CHAPTER IV

TROPHIC OMNIVORY ACROSS A PRODUCTIVITY GRADIENT: INTRAGUILD PREDATION THEORY AND THE STRUCTURE AND STRENGTH OF SPECIES INTERACTIONS

ABSTRACT

A well developed theory of intraguild predation makes two key predictions: (1) For three species – an omnivore, an intermediate predator (IGPrey), and a shared prey – to coexist, the IGPrey must be superior to the omnivore at competing for the shared prey. (2) Increases in productivity will cause a decline in IGPrey's abundance when all three species coexist. In this study I assess the robustness of IGP theory in species-rich systems by testing these predictions with a series of omnivorous food webs situated along a strong gradient of productivity on New Zealand rocky shores. I focused my study on two dominant predatory whelks, *Haustrum haustorium*, a trophic omnivore, and *H. scobina*, the IGPrey, and collected data to document the structure and strengths of their food web interactions. I show that the IGPrey is the superior competitor for shared prey species, as predicted by IGP theory, but that the omnivore is the superior competitor when both shared and unshared prey are considered. In further contrast to theory, I document an increase in the abundance of the IGPrey with increasing system productivity. My data reveal clear and remarkably regular cross-gradient shifts in the food web structure and strengths of species interactions and suggest that adaptive and optimal foraging behavior, and interactions among basal prey species, may play an important role in the structuring omnivorous food webs.

Keywords: food webs, community structure, interaction strengths, intraguild predation, competition, alternative prey, New Zealand marine intertidal, dogwhelks, cannibalism, functional response, optimal foraging, adaptive foraging.

INTRODUCTION

Trophic omnivores – species that feed at multiple trophic levels – are central to our understanding of the structure, dynamics, and functioning of food webs. Many analyses have now shown that trophic omnivores are ubiquitous and often over-represented in ecological communities (Polis et al. 1989, Rosenheim et al. 1995, Coll and Guershon 2002, Arim and Marquet 2004, Williams and Martinez 2004, Bascompte and Melian 2005, Stouffer et al. 2007, Thompson et al. 2007). Their presence in food webs complicates the predictive power of trophic cascades and undermines the utility of the trophic level concept itself (Cousins 1987, Polis and Strong 1996). This is particularly true when omnivores engage in intraguild predation (IGP) by feeding on a second consumer with whom they share prey (a.k.a. closed-loop omnivory, Polis et al. 1989). In IGP systems, changes to one consumer's abundance may generate no change in the abundance of another (reviewed by Diehl 1993, Janssen et al. 2007, Vance-Chalcraft et al. 2007) when the strength of the direct interaction between two species is of equal magnitude to the effect of the indirect interactions linking them via the third species (Gard 1982, Yodzis 1988, Dambacher et al. 2002).

Theory on IGP systems offers unique and interesting predictions regarding the mechanisms governing species coexistence in omnivorous food webs, and how the structure of communities should change across gradients of system productivity (Polis and Holt 1992, Holt and Polis 1997). Two predictions are common to current models of IGP theory: (1) For three species – an omnivore, an intermediate predator, and a shared prey – to coexist, the intermediate predator (henceforth referred to as the IGPrey) must be superior to the omnivore at competing for the shared prey, and (2) that when all three species do coexist, increases in productivity will cause the IGPrey's equilibrium abundance to decline (Table 4.1). The IGPrey's decline occurs even as the shared prey's abundance increases because the omnivore's abundance also increases, causing top-down control of the IGPrey to strengthen as competition between predators declines. The incorporation of age-structure and life-history omnivory or Type II functional responses does not alter these predictions of IGP theory (Table 4.1), although Type II functional responses may make the predicted change of the omnivore's abundance indeterminate (Diehl and Feißel 2000). Further models that include predation refuges for the IGPrey by incorporating predation-free time periods, prey vigilance, or explicit Type III functional responses in the omnivore's feeding rate, as well as models incorporating

Table 4.1. A review of the biological details incorporated into IGP models and their predictions regarding the competitive superiority of the IGPrey and its response to increases in system productivity when all species coexist.

Modeled process	**IGPrey is superior competitor**	**IGPrey response to productivity**	**Source**
Basic IGP module	Yes	Decrease	A
Age-structure and life-history omnivory	Yes	Decrease	B
Type II functional responses	Yes	Decrease	C
IGPrey refuges			
Type III functional responses	Yes	Decrease	D
Predation-free time periods	Yes	Decrease	E
Prey vigilance	Yes	Decrease	F
Predator-specific differences in:			
Prey quality	Yes	Decrease	G
Diet requirements	Yes	Decrease	H
Mortality rates	Yes	Decrease	I
Immigration	Yes	Decrease	J
Alternative prey[1]	Yes[2]	Decrease	K
Metacommunity patch structure	Yes	Increase or decrease[3]	L
Negative intraspecific density-dependence			
Cannibalism	Yes or No[4]	Increase or decrease[4]	M
Ratio-dependent functional responses	Yes	Increase	N
Adaptive foraging	Yes	Increase or decrease[5]	O

[1] Mylius et al. (2001) have suggested that the addition of exclusive prey to the IGPrey is unlikely to affect equilibrium coexistence when consumers have type II functional responses, but see Holt and Huxel (2007).

[2] The IGPrey must be the overall superior competitor across all shared and unshared prey, but may be inferior on the shared prey alone (Daugherty et al. 2007).

[3] The IGPrey's response is dependent upon the relative between-patch dispersal rate of the omnivore relative to the IGPrey's dispersal rate (Amarasekare 2007a).

[4] An increase in the IGPrey's abundance requires that cannibalism in the omnivore be greater than its feeding on the IGPrey, and the omnivore is the superior competitor (Rudolf 2007).

[5] An increase in the IGPrey's abundance requires an evolutionary-scale tradeoff for the omnivore between feeding on the shared prey and the IGPrey (Křivan and Diehl 2005).

Sources: (A) Gard 1982, Polis et al. 1989, Polis and Holt 1992, Holt and Polis 1997, Diehl and Feißel 2000, Borer et al. 2003, Borer et al. 2007, Takimoto et al. 2007; (B) Pimm and Rice 1987, Holt and Polis 1997, Mylius et al. 2001, Borer 2006, van de Wolfshaar et al. 2006, Amarasekare 2007b, Rudolf 2007, Amarasekare 2008; (C) Holt and Polis 1997, Diehl and Feißel 2000, Mylius et al. 2001, Hart 2002, Revilla 2002, Kuijper et al. 2003, van de Wolfshaar et al. 2006; (D) Gismervik and Andersen 1997, HilleRisLambers et al. 2006; (E) Amarasekare 2007b, 2008; (F) Kimbrell et al. 2007; (G) Diehl 2003, Borer 2006; (H) HilleRisLambers et al. 2006; (I) Holt and Polis 1997, Briggs and Borer 2005, Daugherty et al. 2007, Holt and Huxel 2007, Rudolf 2007, Hatcher et al. 2008, Namba et al. 2008; (J) Appendix 4.A, see also Briggs and Borer 2005, Velazquez et al. 2005; (K) Gard 1982, Holt and Polis 1997, Heithaus 2001, Mylius et al. 2001, Briggs and Borer 2005, Daugherty et al. 2007, Holt and Huxel 2007, Kimbrell et al. 2007, Kondoh 2008; (L) Snyder et al. 2005, Amarasekare 2006, 2007a, Su et al. 2008; (M) Hart 2002, Amarasekare 2007b, Rudolf 2007, Amarasekare 2008; (N) Hart 2002; (O) Matsuda et al. 1986, Holt and Polis 1997, Lalonde et al. 1999, Křivan 2000, Křivan and Schmitz 2003, Křivan and Diehl 2005.

consumer-specific differences in prey quality, diet requirements, or mortality rates, may prevent the high productivity extinction of IGPrey predicted by other models, but still do not alter the qualitative predictions for how the abundance of coexisting species should change over the productivity gradient (Table 4.1).

While the development of theory regarding the effects of IGP and trophic omnivory on food webs has, to date, far outpaced empirical assessments, tests of IGP theory's predictions are increasing in number. A recent meta-analysis of manipulative experiments has indicated that IGPrey typically are superior competitors for the shared prey, reducing the shared prey's abundance more so than their omnivorous counterparts (Vance-Chalcraft et al. 2007). However, IGP models relate to long-term equilibrium conditions, while experiments are typically conducted over much shorter transient time-scales. The appropriateness of these studies is thus debatable (Holt and Polis 1997, Briggs and Borer 2005, but see Vance-Chalcraft and Soluk 2005). Empirical studies testing equilibrium conditions have been more limited, and have largely been restricted to arthropod (often parasitoid) or microbial systems whose species' generation times are sufficiently short (Morin 1999, Amarasekare 2000, Diehl and Feißel 2000, Diehl and Feissel 2001, Borer et al. 2003, Trzcinski et al. 2005, Liess and Diehl 2006, Amarasekare 2007b, Kneitel 2007, Montserrat et al. 2008). These tests have offered somewhat mixed support for IGP theory's predictions (e.g., Borer et al. 2003, Liess and Diehl 2006, Montserrat et al. 2008). While no studies have documented the complete extinction of the IGPrey at the highest productivity levels tested, a number have shown the IGPrey to depress the shared prey's equilibrium abundance more so than the omnivore (e.g., Diehl and Feissel 2001). Lower resource depression at equilibrium does indicate competitive superiority (all else, such as predator intrinsic mortality rates, being equal; Holt and Polis 1997), but competitive superiority – as measured by the relative per capita bottom-up impact received by a predator from the shared prey – could be achieved in a number of ways: A predator could be superior by having higher per capita attack rates, shorter handling times, or better conversion rates of prey into predator biomass. Such mechanisms have not been investigated.

Of greater concern is that models and empirical manipulations of tightly coupled three-species IGP systems do not capture the complexities of the reticulate, species-rich food webs of natural communities where omnivory may be more diffuse (Rosenheim et al. 1995, Kondoh 2008). Recent theoretical efforts have begun to address this issue by adding alternative prey to the basic IGP module (Table 4.1). Not surprisingly, alternative prey exclusive to the omnivore strengthen the predictions of three-species models, requiring an even stronger competitive superiority for the IGPrey and decreasing the range of productivities where coexistence is feasible. The addition of prey exclusive to the IGPrey, on the other hand, can make unnecessary the IGPrey's competitive superiority on the shared prey and can allow indefinite coexistence at high productivities (Daugherty et al. 2007, Holt and Huxel 2007). The IGPrey must still be the overall superior competitor however (Daugherty et al. 2007, see also Kondoh 2008), and increasing productivity remains favorable to the omnivore such that the IGPrey's equilibrium abundance is still predicted to decline (Holt and Huxel 2007).

Here I assess the robustness of IGP theory in species-rich systems by testing its two key predictions with a series of omnivorous food webs situated along a strong gradient of productivity on New Zealand rocky shores. I focused my study on the dominant predatory whelks, *Haustrum haustorium*, the trophic omnivore, and *H. scobina*, the IGPrey, and collected data to document the structure and strengths of their food web interactions. I show that the IGPrey is the superior competitor for shared prey species, as predicted by IGP theory, but that the omnivore is the superior competitor when both shared and unshared prey are considered. In further contrast to theoretical predictions, I document an increase in the abundance of the IGPrey with increasing system productivity. My data reveal clear and remarkably regular cross-gradient shifts in the food web structure and strengths of species interactions. I suggest that adaptive and optimal foraging behavior, and interactions among basal species, may play an important role in structuring omnivorous food webs.

STUDY SYSTEM

An omnivorous food web

Haustrum haustorium and *H. scobina* (= *Lepsiella scobina*, Beu 2004) are muricid whelks common to the rocky shores of New Zealand (Morton and Miller 1968, Tan 2003). *H. haustorium*'s diet typically consists of limpets, chitons, and snails (Plate

4.1), but may also consist of acorn barnacles, mussels, and other whelk species, particularly *H. scobina*. (R.T. Paine, *unpubl. data*; Morton and Miller 1968, McKoy 1969, Luckens 1975b, Ottaway 1977, Walsby 1977, Walsby and Morton 1982, Patrick 2001, and see below). *H. scobina* is a relative specialist whose diet consists primarily of mussels, acorn barnacles and oysters, but may also include limpets, snails, and tubeworms (Clark 1957, Fearon 1962, Morton and Miller 1968, Luckens 1975b, Gardner 1978, McKillup 1982, Menge et al. 1999). Muricid whelks like the two *Haustrum* species are classic Type II functional response predators (*sensu* Holling 1959), typically needing to drill through the shells of their prey in order to feed. Whelk handling times – the time needed to drill and ingest a prey item – may vary on the order of hours to days (*Chapter III*) and may limit feeding rates at high prey densities (*Chapter V,* Murdoch 1969, Katz 1985, Moran 1985, Rodrigues 1986).

Little is known about *Haustrum*'s predators. The only reported predation on either species comes from Paine (1971) who observed a single individual of the seastar *Stichaster australis* feeding on an *H. scobina*. Other seastars (but see Town 1979, Town 1980), fishes (particularly labrids, Denny and Schiel 2001), crabs (particularly *Cancer novaezelandiae*, Creswell and Marsden 1990), oystercatchers (Baker 1974), and gulls probably also consume whelks as they do on other rocky shores around the world (e.g., Wootton 1997).

H. haustorium individuals appear to become reproductively mature at 24-30 mm, while individuals of *H. scobina* do so at 9-12 mm (based on dissections and the minimum

Plate 4.1. *Haustrum haustorium* feeding on a *Cellana ornata* limpet at Cape Foulwind. *Xenostrobus pulex* mussels, *Epopella plicata* barnacles and *Austrolittorina antipodum* snails in the foreground, and an *H. scobina* on the right.

size of individuals observed in breeding aggregations; M. Novak, *unpubl. data*). Both *Haustrum* species lay benthic egg masses that hatch to locally dispersing crawl-away larvae (Graham 1941, Pilkington 1974), but *H. haustorium*'s eggs are larger than *H. scobina*'s (~ 4.5 x 4.5 mm vs. 3 x 3 mm, respectively, Graham 1941, Tan 2003). The two whelk's prey species exhibit diverse larval dispersal modes, with some species having direct-developing crawl-away larvae, and others (e.g., mussels and barnacles) having lecithotrophic or planktotrophic larvae that can disperse long distances in the water column before recruiting to the shore (Graham 1941, Pilkington 1974).

A benthic productivity gradient

Menge and colleagues (Menge et al. 1999, Menge et al. 2002, Menge et al. 2003, Rilov et al. 2008) have demonstrated that mussels and barnacles – the primary prey shared by *Haustrum* whelks – exhibit marked regional differences both in recruitment and growth around the South Island of New Zealand. Most clearly illustrated by Menge et al. (2003), recruitment rates (recruits per collector per month, RCM) are highest along the northwest coast (~900-1100 mussel RCM, ~2000 – 6000 barnacle RCM), are much lower along the southwest coast (~125 mussel RCM, ~50 barnacle RCM), and are even lower along the east coast, particularly in the northeast (~10 mussel RCM, ~50 barnacle RCM). Individual mussel and barnacle growth rates (as judged by RNA:DNA ratios or the growth of recruited individuals, respectively) are more than twice as high along the northwest coast as they are on the east coast (Menge et al. 1999, Menge et al. 2003).

Menge and colleagues have attributed this gradient of effective basal productivity to the nearshore oceanographic conditions surrounding the South Island. Situated in the path of the eastward flowing Tasman Current, the South Island's west coast causes the current to bifurcate into two water masses (Fig. 4.1). Wind events and the northward flowing Westland Current cause upwelling along the northwest coast, intermittently bringing deep, nutrient rich water to the surface (Stanton 1976, Vincent et al. 1991, Stanton and Moore 1992). This upwelling spurs shallow water primary production (Bradford and Roberts 1978, Chang and Bradford 1985, Bradford and Chang 1987, Chang et al. 1995, Murphy et al. 2001). The position and strength with which the Tasman Current intersects the South Island appears variable (Vincent et al. 1991, Stanton and Moore 1992, Uddstrom and Oien 1999). This suggests that less consistent upwelling and downwelling conditions typify the southwest coast, as the southward flowing tongue of the Tasman Current – the Southland Current – curls around the southern end of the South Island. The nearshore northeast coast, on the other hand, appears to observe little to no current-driven upwelling (Vincent et al. 1991). While wind-driven upwelling events do occur (Heath 1972, Chiswell and Schiel 2001), and upwelling caused in the nearby Kaikoura Canyon supports a productive pelagic system (Murphy et al. 2001), these do not appear to translate to onshore productivity in mussels and barnacles (Menge et al. 1999, Menge et al. 2002, Menge et al. 2003, Seaward 2006, Rilov et al. 2008). Macroalgae remain at low abundance in both the mid and high midlittoral zones of

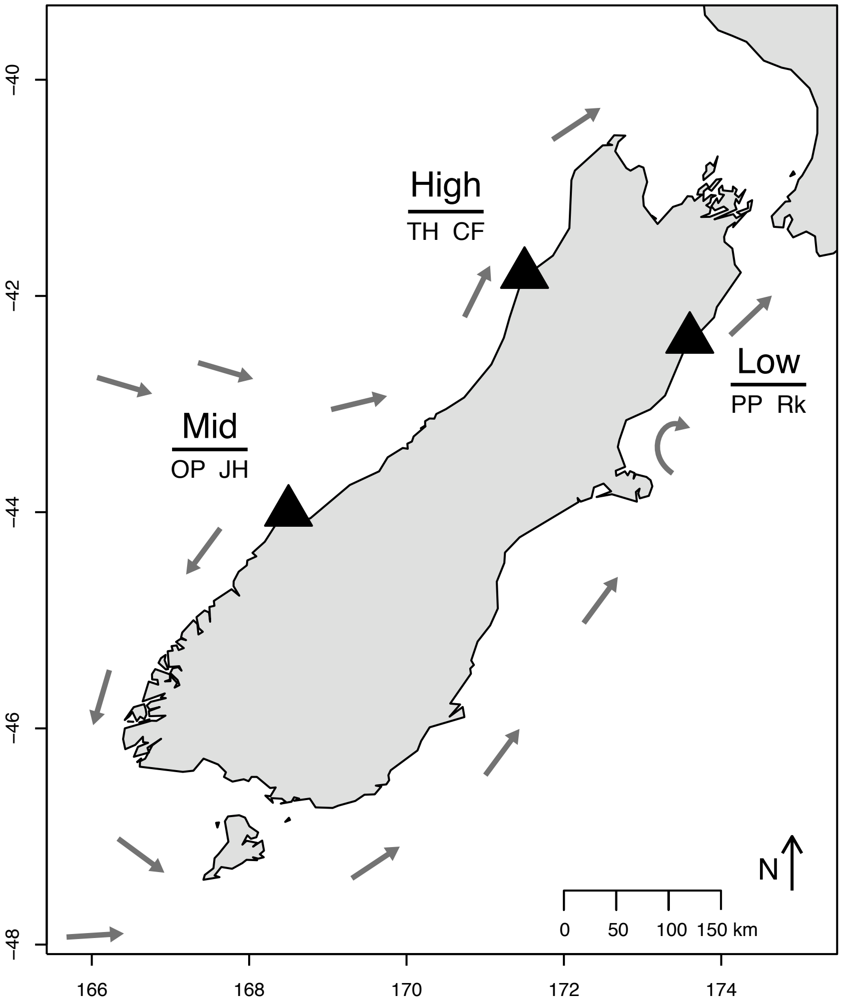

Figure 4.1. Map of New Zealand's South Island and nearshore oceanography (after Heath, 1985) indicating regional locations of study sites and associated productivity levels as reflected by mussel and barnacle growth and recruitment rates.

exposed sites throughout the South Island, becoming dominant only in the lower midlittoral zone (Menge et al. 2003, and see below).

METHODS

I tested the predictions of IGP theory by studying the food webs of *Haustrum haustorium* and *H. scobina* at a series of sites situated along this productivity gradient. At each site I determined each predator's diet, documented the structure of the community, and contrasted the two predator's competitive advantages by assessing three interaction-strength components contributing to the species-specific bottom-up prey impacts they receive from their prey: (1) their handling times, (2) their per capita attack rates, and (3) their feeding rates. I did so while incorporating species-specific differences in prey body-mass and each predator's prey-size selection. I then investigated cross-gradient changes in food web structure and interaction strengths to understand the discrepancies I observed between IGP theory's predictions and the patterns my data revealed.

Study sites

Six study sites were chosen around New Zealand's South Island to represent the regional productivity gradient in barnacle and mussel growth and recruitment rates (Fig. 4.1). Two "low productivity" east coast sites, Paia Point (PP) and Rakautara (Rk), respectively located 14 km south and 20 km north of the Kaikoura Peninsula; two "mid productivity" southwest coast sites, Jackson Head (JH) and Okahu Point (OP), located on

Table 4.2. Locations of focal study sites.

Site name	Abbreviation	Coast	Location
Tauranga Head	TH	Northwest	41°46′26″ S, 171°27′20″ E
Cape Foulwind	CF	Northwest	41°45′09″ S, 171°27′31″ E
Okahu Point	OP	Southwest	43°57′55″ S, 168°36′16″ E
Jackson Head	JH	Southwest	43°57′53″ S, 168°36′23″ E
Paia Point	PP	East	42°28′24″ S, 173°32′12″ E
Rakautara	Rk	East	42°15′38″ S, 173°48′43″ E

the westward side of Jackson Head; and two "high productivity" northwest coast sites, Tauranga Head (TH) and Cape Foulwind (CF), located to the west of Westport (Table 4.2). PP is located 2 km south of Menge et al.'s (2003) northeast coast site; JH is the same as their southwest site; and TH is located 29 km north of their northernmost west coast site. All localities are generally similar in character to those used by Menge et al. (2003). The study areas chosen within JH, TH and CF, however, are more protected than Menge et al.'s since they are situated behind seaward rock outcrops rather than being fully exposed to incoming waves. This was done in order to maintain consistent exposure across all study sites.

The intertidal substrate of PP and Rk consists of greywacke bedrock extending through the shallow subtidal. The substrate of JH and OP consisted of areas of sandstone and sandstone with beach conglomerates, and turned to sandstone outcrops surrounded by beach sand in the shallow subtidal. The substrate of TH and CF consisted of gneiss bedrock that also turned to loose sand in the shallow subtidal. JH and TH were adjacent to sandy beaches and often showed evidence of scouring in the low intertidal. TH, CF and Rk were also located within 14 km of the mouth of rivers. These sites likely experienced periodically reduced salinities as a result of river discharge (Bradford 1983, Stanton and Moore 1992).

Determining the diet of *Haustrum haustorium* and *H. scobina*

I determined predator diets at each site by conducting systematic, predator-specific searches of predefined areas of the shore (Connell 1961). Surveys were performed during both day and nighttime low tides, and were not repeated in the same area for at least four high tides. Preliminary surveys repeated more frequently suggested that four high-tides was ample time for whelks to commence normal feeding activity between surveys. All individuals found during a survey were carefully examined and picked up to determine whether or not they were feeding. I recorded the identity and size (± 1 mm) of prey items, and the location (tide-zone) and size (± 1 mm) of all feeding and non-feeding whelks.

Assessing cross-gradient changes in community structure

Species densities

I estimated mean species population densities in both the mid and high zones of the midlittoral at each site using three haphazardly located 20 m transects per zone with five randomly positioned quadrats (0.25 m^2, subdivided into 100 5x5 cm subquadrats) per transect. One or two of the transects in each zone was surveyed at night. I counted mobile species and estimated percent cover for sessile species, bare space, and macroalgae. A small subset of exceptionally abundant mobile species (e.g., Austrolittorine spp.) was subsampled at some sites, and was not counted in the quadrats of the third transect. Surveys were repeated three times at PP, Rk, TH and CF, and twice at OP and JH, between 2005-2006. Densities were therefore estimated using 40-90 quadrats per species.

To account for cross-quadrat variation in bedrock topography I divided each mobile species' quadrat count by the ratio of the minimum distance between opposing quadrat corners ($\sqrt{0.5}$ m) and the average distance between quadrat corners measured by following the topography of the substrate surface with a flexible line. I converted sessile species percent-cover estimates to densities with site- and species-specific cover-count conversion relationships determined for each site using haphazardly placed 0.0025 m^2 quadrats.

Species biomass

I estimated species-specific biomass using size-frequency distributions obtained by systematically measuring all individuals of a species in additional 0.25 m^2 quadrats positioned randomly along the shore. For most species this resulted in measurements on $\geq$50 individuals per species. Size-measurements for exceptionally abundant species were obtained by subsampling quadrats to increase spatial coverage, while size-measurements for rare species were supplemented by systematic searches of the shore. Barnacle sizes were obtained by measuring randomly chosen individuals from within photographed 5 x 5 cm quadrats positioned at random along the shore.

I converted the sizes of all individuals to wet weights (shell and tissue) using allometric relationships determined from individuals collected on both coasts (M. Novak, *unpubl. data*). A species' mean population biomass was then estimated by multiplying its individuals' mean weight by its mean density which assumed independence in these variables (Welsh et al. 1988).

Estimating predator-prey handling times

In order to estimate the expected handling time of a feeding event observed in the field, I measured the temperature-dependent time needed for a whelk of a given size to drill and ingest a prey item of a given size in the laboratory (see *Chapter III* for details). To do so, I collected whelks and their prey from Tauranga Head and multiple east coast sites nearer the Edward Percival Field Station, Kaikoura. Prey were then maintained in aquaria with flowing sea water (~9-11°C) filtered to 40 m, while whelks were kept under a 12:12-hr day:night cycle in aerated aquaria maintained at ~10, 14, or 18°C – the latitudinal and seasonal range of mean ocean temperatures around the South Island (Uddstrom and Oien 1999). After a ≥ 3 day acclimation and ≥ 5 day starvation period, individually housed whelks were measured (± 0.1 mm) and provided with 6 or 10 individuals of a given prey species. All prey individuals within a group were of similar size, but whelk and prey size combinations were varied to maximize the range of relative sizes. Each whelk was subsequently checked on an hourly basis and classified as either feeding or not feeding. I measured the prey of all successful predation events (± 0.1 mm) and visually estimated the proportion of unconsumed tissue remaining.

To measure the handling times of barnacles, I placed one or two whelks into aquaria with independent and continuously flowing filtered sea-water, the temperature of which varied over the course of a field season. Barnacles were introduced to the aquaria on cement tiles to which they had naturally recruited at an east coast site. I then monitored whelk feeding using low-light video cameras under natural day:night lighting conditions supplemented by a red light at night. Barnacle prey were measured under a dissecting microscope (± 0.1 mm).

Since monitoring was done on an hourly basis, exact handling times were unknown; feeding events had both a minimum and a maximum possible duration. I therefore used the duration midpoints of all feeding events (h_{ij}, days) in a multiple regression of predator j and prey i shell length (L, mm), and temperature (T, °C), where

$$\ln\ h_{ij} = \beta_1 + \beta_2\ \ln L_j + \beta_3\ \ln L_i + \beta_4\ \ln T + \epsilon\ . \tag{4.1}$$

Since feeding event durations were often more tightly constrained by more frequent feeding checks (or video-surveillance), I performed these regressions with feeding events weighted by the inverse of their maximum possible time duration. A handling time that had been constrained to within 1 hr therefore received less weight than a handling time constrained to 10 min. Only those feeding events for which handling times had been well-constrained (both the start- and end-time within a 1/10th day total window, or a maximum possible start- to end-time difference of ≤ 80% of the estimated midpoint time; 1119 of 1819 feeding events) and in which ≥ 80% of prey tissue had been consumed (1099 of the 1119 feeding events with only 65 events < 100%) were included in the analysis.

I then calculated the expected handling time of each feeding event observed in the field using (i) the laboratory-based handling time regression coefficients, (ii) the field temperature observed during the month of a feeding survey (mean of air and water), and (iii) the observed whelk and prey sizes. Field temperatures were obtained using Stowaway® TidbiT™ temperature loggers (Onset Computer, Pocasset, MA) positioned in the lower midlittoral zone of each site to record low-tide air and high-tide water temperatures at ½ hr intervals. Prey species whose handling times were not measured in the laboratory were assigned handling time regression coefficients of the measured species considered most similar on taxonomic, morphological, and behavioral grounds.

Estimating per capita attack rates

Species-specific per capita attack rates (c_{ij}) – the average number of prey eaten per predator per prey per m^2 per day – which reflect a predator's prey preferences (Chesson 1983), were estimated at each site using the observational method of Novak and Wootton (2008). I have shown previously that this method performs well at estimating per capita interaction strengths in the New Zealand system (*Chapter III*). The method estimates species-specific per capita attack rates by

$$c_{ij} = \frac{F_{ij} A_{xj}}{(F_{xj} - A_{xj}) h_{ij} N_{i}}, \tag{4.2}$$

where A_{ij} as the proportion of all individuals of predator j (feeding and not feeding) that are observed to be feeding on prey species i over the course of all feeding surveys, F_{ij} is the proportion of all feeding individuals of predator j that are observed to be feeding on prey i, h_{ij} is the mean estimated field handling time of the predator-prey pair, and N_i is the focal prey's mean site-level density. I used the prey observed most frequently in each predator's diet as prey x, following Novak and Wootton (2008). Prey species not observed during quadrat-based abundance sampling were assigned ½ the estimated density of the least abundant species. This applied to 21 of the 202 observed predator-prey interactions.

Estimating feeding rates

I then calculated species-specific feeding rates (f_{ij}) – the average number of prey eaten per predator per m^2 per day – as

$$f_{ij} = \frac{c_{ij} N_i}{1 + \sum_{k=1}^{S} c_{ik} h_{ik} N_k} \tag{4.3}$$

(e.g., Murdoch 1973), where S is the total number of prey species observed in a predator's site-specific diet. Eq. 4.3 is the multispecies Type II functional response on which the derivation of Eq. 4.2 is based (Novak and Wootton 2008), and assumes constant prey preferences and thus no switching between prey species (Murdoch and Oaten 1975).

Estimating bottom-up prey impacts

Finally, I estimated specific-specific bottom-up prey impacts (b_{ji}) by the average grams of prey tissue consumed per predator and converted to predator tissue mass per m^2 per day. I calculated this as

$$b_{ji} = e_{ji} w_i f_{ij} \tag{4.4}$$

(*cf.* Holt 1983), where w_i is the dry tissue weight of prey i individuals (estimated from prey shell length, using species-specific allometric relationships; M. Novak *unpubl. data*) averaged across all prey i individuals that were observed being fed upon in the feeding surveys, and e_{ji} is the conversion efficiency (assimilation and production) by which prey i tissue is converted to predator j tissue. I therefore assumed that the numerical response of the predator populations was a linear function of their feeding rate (Lawton et al. 1975, Abrams and Ginzburg 2000), and that 100% of prey tissue was consumed. This latter assumption is reasonable given the low frequency at which < 100% of prey tissue was consumed in the handling time experiments (*see above*).

Lacking species-specific estimates, I set e_{ji} to 0.25 for all predator-prey combinations. This value is the median gross conversion and growth efficiency observed among studies of other muricid whelks which have suggested widely varying efficiencies for even the same prey species (Paine 1965, Hughes 1972, Bayne and Scullard 1978, Stickle and Bayne 1987, Burrows and Hughes 1990). The assumption of a constant, tissue weight-corrected conversion efficiency across all prey species is supported by the observation that C:N ratios vary little among prey species (M. Novak, *unpubl. data*). Furthermore, while no information exists on the number of eggs laid per female, the hatchling size of *H. haustorium* is larger than that of *H. scobina* (see *Study System*). Thus, *H. haustorium* is likely to require more units of resource to produce hatchlings than is *H. scobina*, making bottom-up prey impact estimates conservative regarding the IGP predictions of competitive superiority being tested.

TESTING THE PREDICTIONS OF INTRAGUILD PREDATION THEORY

Cross-gradient changes in community structure

To test the predictions made by IGP theory regarding the expected changes in the abundance of species across the productivity gradient, I assigned all observed prey species into three exclusive prey groups – a shared prey group, an omnivore's alternative prey group, and an IGPrey's alternative prey group – and summed their mean site-level densities and biomass estimates accordingly. Because *H. haustorium* showed relatively large cross-site variation in the proportion of individuals that were of small size, I also calculated the proportion of individuals that had been measured during the feeding surveys as having been ≤ 25 mm in order to partition population-level densities into juvenile and adult size-classes.

The relative superiority of competing predators

To test the prediction that the IGPrey was the superior competitor for the prey it shared with the omnivore, I compared the summed bottom-up prey impacts the two whelk species obtained from their shared prey. This comparison is analogous to the R^* concept of competitive exclusion (Tilman 1982, see also Kondoh 2008, *Appendix 4.B*). To determine the species-specific mechanistic basis of any shared-prey competitive superiority, I then compared the two predators by contrasting the log ratio of each of their four interaction strength components, calculated as the across-site average of

$$LR = \log\left(\frac{\bar{x}_{Hs}}{\bar{x}_{Hh}}\right), \tag{4.5}$$

where x was substituted by per capita attack rates (c_{ij}), handling times (h_{ij}), feeding rates (f_{ij}), and bottom-up prey impact (b_{ji}), for each shared prey species. The competitive superiority of the IGPrey for a specific prey species is thereby indicated by an LR value < 0 for handling time, or by $LR > 0$ for per capita attack rates and feeding rates of the predator and bottom-up impacts of the prey.

To test for the overall competitive superiority of the IGPrey across all prey, I then compared the summed bottom-up impacts the two whelk species obtained from the consumption of all the prey species on which they fed (Tilman 1982, Kondoh 2008).

Cross-gradient changes in food web structure and interaction strengths

Finally, I investigated cross-gradient changes in the structure of the two predators' food webs. I did so on a species-specific basis, and in an IGP framework with prey species aggregated into shared prey or alternative prey groups. In order to gain insight into the mechanistic basis of these structural changes, I also investigated the cross-gradient changes in per capita attack rates and feeding rates. To do so within the IGP framework, I simply summed these terms for each prey group at each site. To do so on a species-specific basis, I used one-sided Spearman's rank correlation tests. More specifically, I correlated the magnitude of each predator's per capita attack rates and feeding rates across the six sites on a site-specific pair-wise basis in three different ways: (1) Considering all potential prey that were present but not necessarily fed upon by a predator at either site, (2) considering all prey present and fed upon at at least one of the two paired sites, and (3) considering only prey species fed upon at all six sites. In combination, these analyses allowed me to tease apart the relative strength and consistency of predator-specific prey preferences, feeding rates, and the availability of potential prey species within and across the productivity gradient. A combination of high per capita attack rate correlations and low feeding rate correlations, for example, would be indicative of an across-gradient consistency in a predator's relative prey preferences (Chesson 1983) that was not reflected in its realized species-specific feeding rates due to changes in the availability, relative abundance, or handling times of its prey species.

RESULTS

The diet of *Haustrum haustorium* and *H. scobina*

In total I performed between 29-59 *H. haustorium* surveys, and between 20-34 *H. scobina* surveys at each site. *H. haustorium* surveys lasted an average (± SD) of 47 ± 21 min., while *H. scobina* surveys lasted 39 ± 16 min.. On average, 9.3% (± 0.08, range: 0-40.5%) of *H. haustorium* individuals and 21.0% (± 0.10, 0-49.0%) of *H. scobina* individuals were observed in the process of feeding during any given feeding survey. Thus, a total of 2,142 *H. haustorium* feeding observations and 3,526 *H. scobina* feeding observations were made by examining a total of 21,028 *H. haustorium* and 17,293 *H. scobina* individuals across all surveys combined. Site-specific species accumulation curves suggest that enough surveys were performed at each site to ensure the accuracy of the observational method of inferring species-specific per capita attack rates (Fig. 4.2, see Novak and Wootton 2008).

Across all sites, *H. haustorium* was observed feeding on a total of 44 species, while *H. scobina* was observed feeding on 19 species. Neither species was ever observed scavenging. The richness of each predator's diet varied markedly across the productivity gradient (Fig. 4.2). Both whelks exhibited the highest rarefied diet richness at the two low-productivity sites. *H. scobina*'s diet richness then decreased with increasing productivity; its high-productivity populations had diets that were roughly half as species rich as those of the low-productivity populations. *H. haustorium*'s rarefied diet richness,

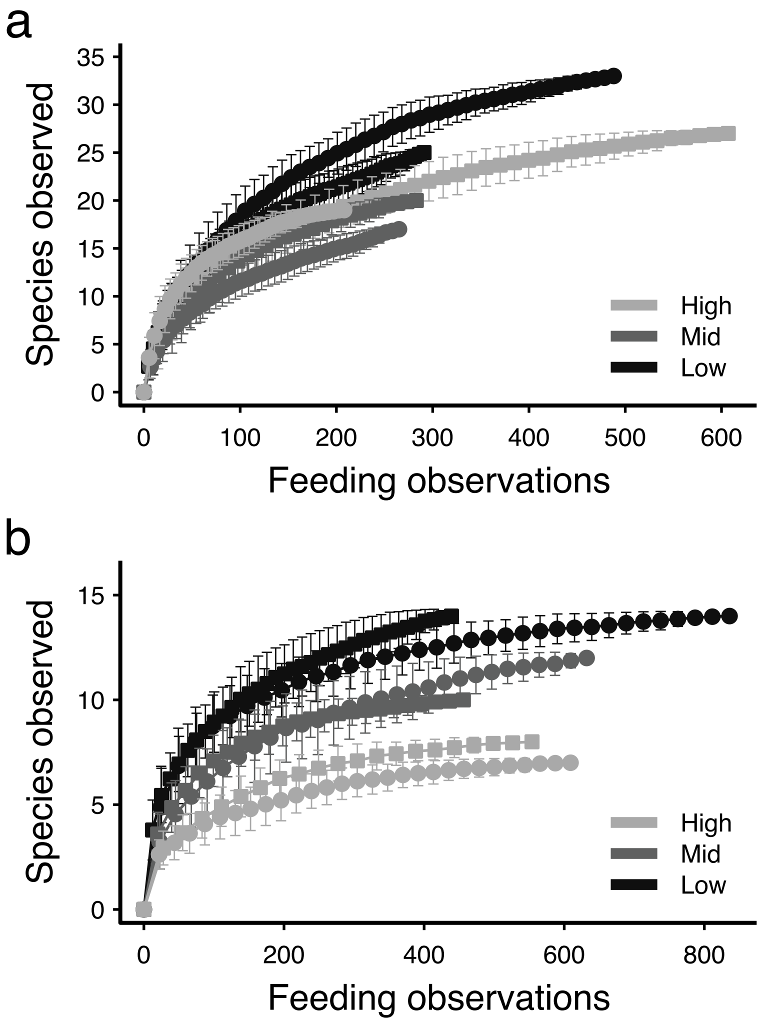

Figure 4.2. Species accumulation curves of prey observed in the diet of (a) the omnivore, *Haustrum haustorium*, and (b) the IGPrey, *H. scobina*, (± SD), as a function of the shared prey's productivity, constructed using feeding surveys as the unit of sampling (Gotelli and Colwell 2001). Site symbols: PP, JH, CF (○); Rk, OP, TH (□).

however, was lowest at one of the mid-productivity sites, and was at intermediate levels at the remaining two high- and one mid-productivity sites.

Mussels and acorn barnacles were the dominant prey species shared by the two predators. In total, however, seven species were judged as being the main prey species shared between the two predators, either by occurring in both predator's diets at all productivity levels or by representing a significant number of each predator's feeding observations at a subset of cross-gradient sites. These were the barnacles *Chamaesipho columna*, *Ch. brunnea* and *Epopella plicata*, the mussels *Xenostrobus pulex* and *Mytilus galloprovincialis*, the snail *Risellopsis varia*, and a limpet from the poorly resolved *Notoacmea* genus (Nakano and Spencer 2007). Nine other species were also considered shared, but contributed too few feeding observations for the mechanisms of a predator's competitive superiority to be assessed. Together, shared prey species comprised 28.0% of the feeding observations made for *H. haustorium*, and 88.6% of the observations made for *H. scobina*. Of the remaining documented prey species, 27 were considered to be primarily the omnivore's alternative prey (mostly Cellanid and Pulmonate limpets, chitons, and other large gastropods), and 3 were considered to be primarily the IGPrey's alternative prey (two Austrolittorines and a Veneroid clam).

Cross-gradient changes in community structure

Omnivore and IG prey

In contrast to the predictions of IGP theory, the abundance of the IGPrey, *H. scobina*, increased with increasing productivity, whereas the omnivore, *H. haustorium,* did not change in density or biomass (Fig. 4.3). *H. haustorium*'s abundance was ~2-3 times higher at PP and TH than at the remaining sites, a difference driven primarily by an increased number of juveniles. *H. scobina*'s density increased by up to 110-times between low and high-productivity sites, but its abundance did not increase significantly between low- and mid-productivity sites.

Shared prey

The abundance of shared prey species increased with increasing productivity (Fig. 4.4a-b). The mean density and biomass of mussels was lowest at the low-productivity sites, was intermediate at the mid-productivity sites, and was highest at the high-productivity sites. Acorn barnacles showed a similar cross-gradient increase in densities but did not have higher densities at CF than at JH. Barnacle biomass was more variable and showed a substantial increase only at the high-productivity CF site. This variation was due to changes in the both the relative abundance of the large *Epopella plicata* barnacle and the reduced mean size of *Chamaesipho* barnacle individuals at the mid-productivity sites.

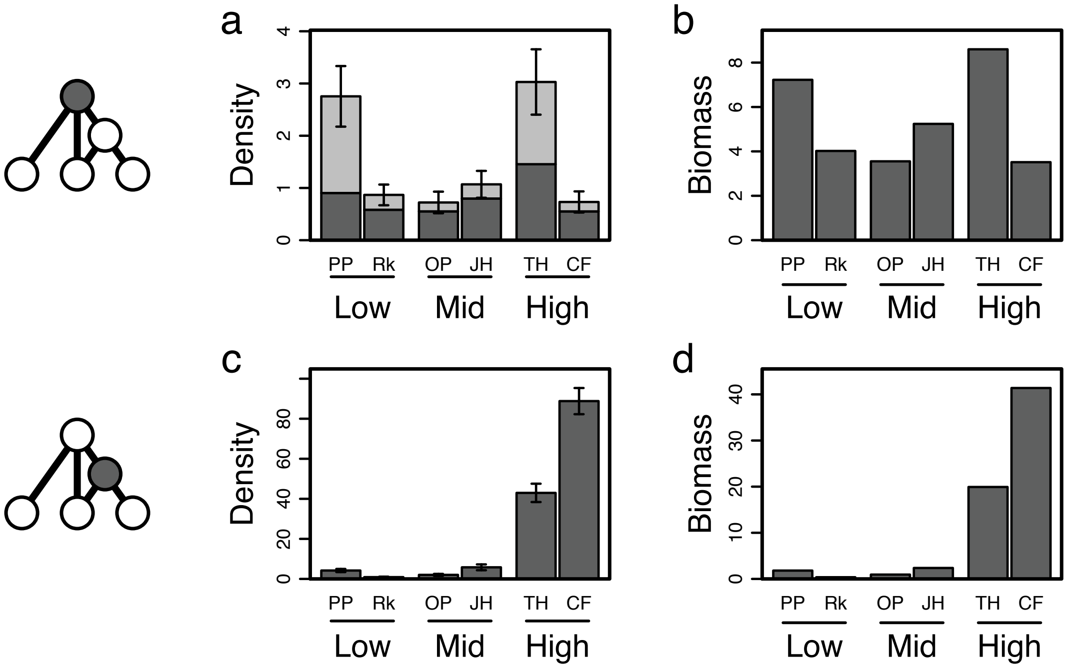

Figure 4.3. Changes in the density, m^{-2}, and total biomass, g m^{-2}, of (a-b) the omnivore, *Haustrum haustorium*, and (c-d) the IGPrey, *H. scobina* as a function of the productivity of their shared prey. *H. haustorium* densities split into adult (dark fill) and juvenile (light fill) size classes based on their proportion abundance in feeding surveys. Error bars indicate ± 1 SE.

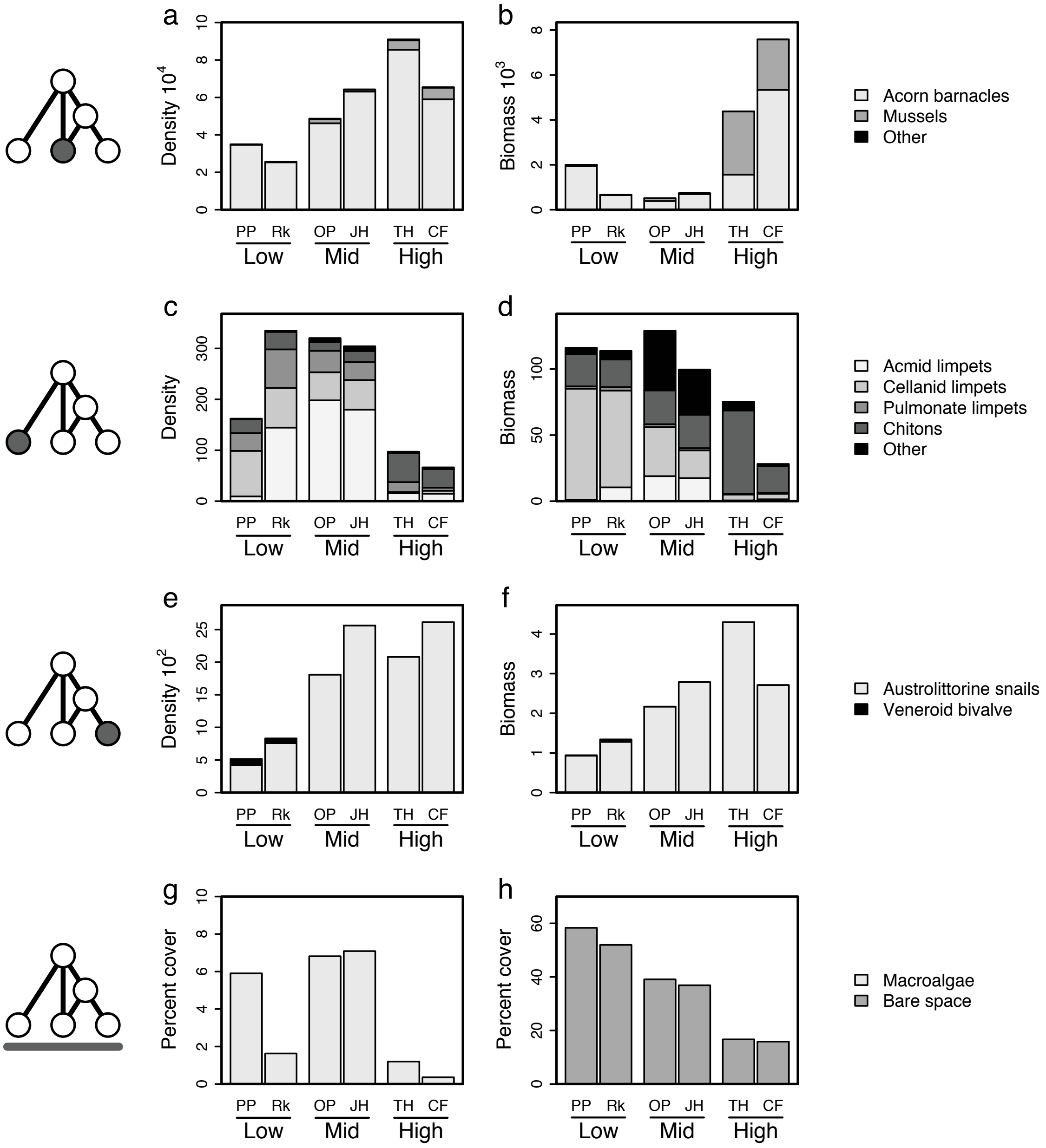

Figure 4.4. Cross-gradient changes in community structure as illustrated by the cumulative density, m^{-2}, and total biomass, g m^{-2}, of prey species grouped into (a-b) shared prey, (c-d) the omnivore's alternative prey, and (e-f) the IGPrey's alternative prey, and in the percent cover of (g) macroalgae and (h) bare space.

Omnivore's alternative prey

The total abundance of the omnivore's alternative prey was generally similar at the low- and mid-productivity sites, but decreased markedly at the high- productivity sites (Fig. 4.4c-d). Acmid limpets, primarily *Patelloida corticata*, generated the only major exception to this overall pattern, being relatively scarce at the low-productivity PP site.

IGPrey's alternative prey

The total abundance of *H. scobina*'s alternative prey increased from low- to mid-productivity sites, but was roughly similar at mid- and high-productivity sites, although the mean size and thus biomass of *Austrolittorina cincta* was substantially higher at TH than at CF (Fig. 4.4e-f). The overall pattern was driven primarily by changes in the abundance of the Austrolittorines, as the bivalve *Lasaea rubra hinemoa* was scarce and present only at low- and mid-productivity sites.

Community diversity

The mean proportion of secondary (canopy) space occupied by macroalgae was low across all sites (< 7.1 %), but was highest at the southwest coast mid-productivity sites (Fig. 4.4g). The mean percent cover of bare space, on the other hand, was highest at the low-productivity sites and decreased with increasing with increasing productivity (Fig. 4.4h).

Despite the marked cross-gradient changes observed in species abundances, the total extrapolated species richness of potential prey remained remarkably constant across the six sites (Fig. 4.5). Only 8 of the 46 documented potential prey species were not observed across all six sites. Both the potential prey diversity and the total species diversity was lower at the two mid-productivity sites due to a decreased evenness in relative species abundances (Fig. 4.6).

The relative superiority of competing predators

In agreement with IGP theory, the IGPrey was a superior competitor to the omnivore when only shared prey were considered. The cumulative bottom-up impacts that *H. scobina* received from shared prey outweighed the impacts that *H. haustorium* received from these prey at all six sites along the productivity gradient (contrast Fig. 4.7b with Fig. 4.7f). The IGPrey was not, however, superior at competing for all shared prey species individually. When averaged across the six sites, *H. scobina*'s feeding rates were larger than *H. haustorium*'s for up to five of these species (Fig. 4.8a), but because of differences in prey size, mean bottom-up impacts were larger on *H. scobina* from only four of these species (Fig. 4.8b).

Competitive superiority on shared prey species was achieved between the two predators in different ways for different prey species. *H. scobina*'s per capita attack rates were higher than those of *H. haustorium* for the same five species for which its feeding rates were higher (Fig. 4.8c). *H. scobina*'s handling times, however, were significantly

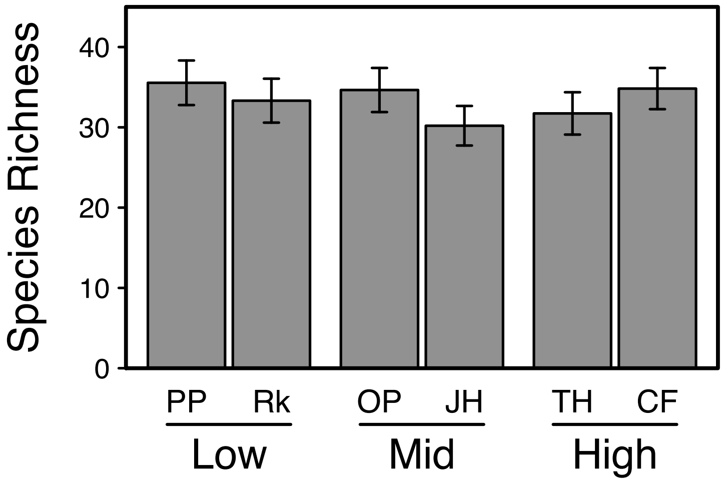

Figure 4.5. Extrapolated richness of prey species available as a function of shared prey productivity-levels (± SE), estimated by abundance coverage estimator method (Chao and Lee 1992, O'Hara 2005) treating species of incidence < 10 as rare.

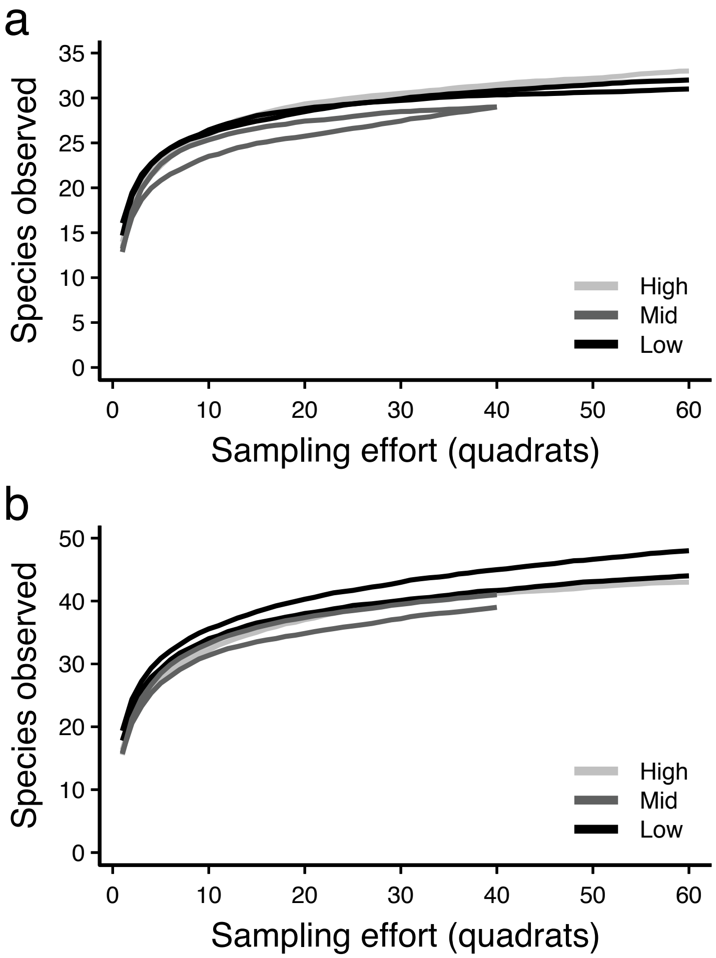

Figure 4.6. Site-specific accumulation curves for (a) documented prey species only, and (b) all species observed during quadrat-based abundance surveys, excluding the 3rd transects in which not all species were counted (see *Methods*). Confidence intervals omitted for clarity.

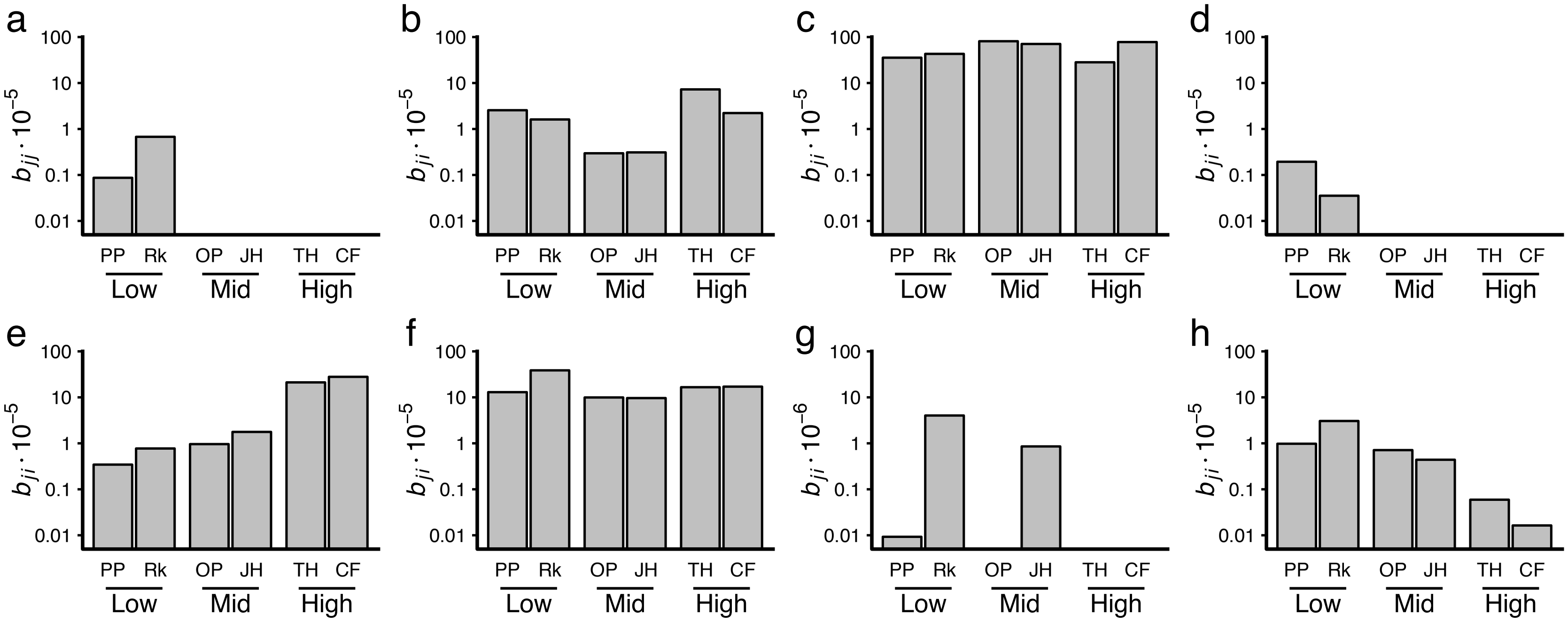

Figure 4.7. Cross-gradient changes in the bottom-up impact derived by the omnivore from (a) itself, (b) the shared prey, (c) its own alternative prey, (d) the IGPrey's prey, and (e) the IGPrey, and similarly, derived by the IGPrey from (f) the shared prey, (g) the omnivore's alternative prey, and (h) its own alternative prey. Note unique y-axis scale of (g).

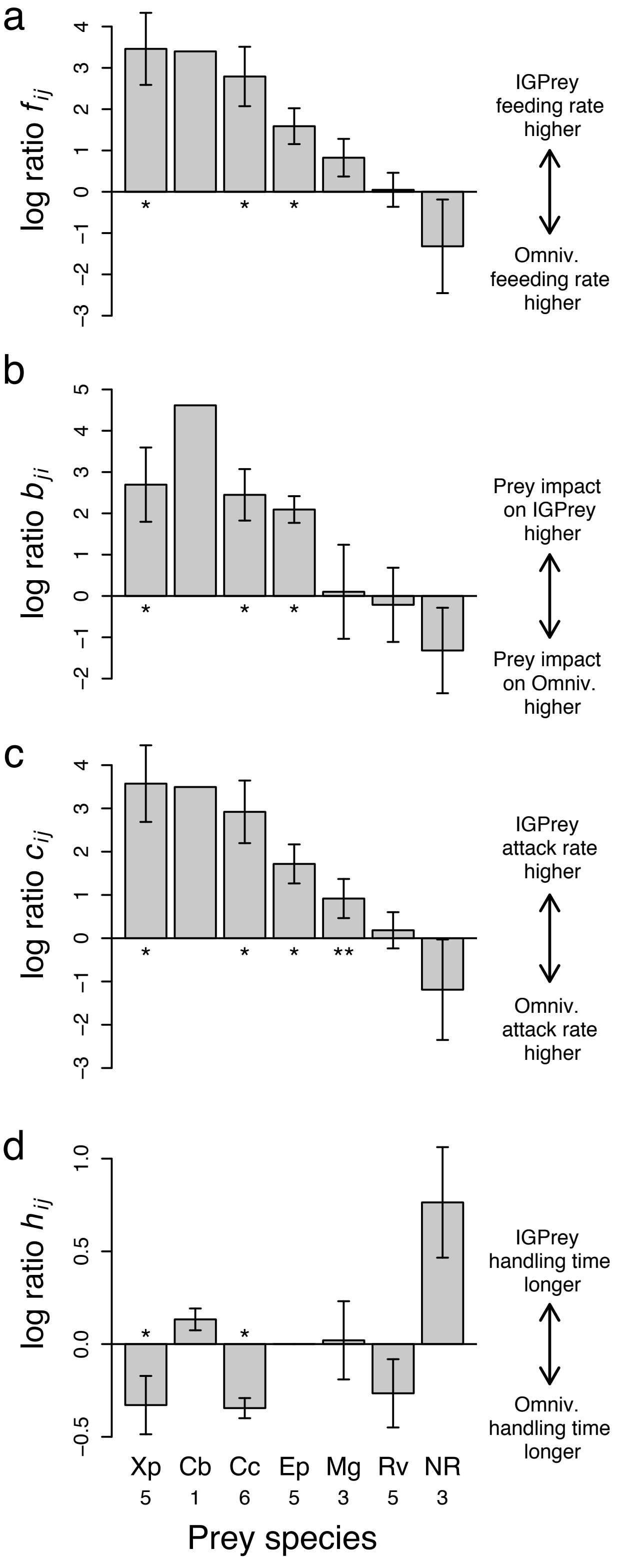

Figure 4.8. Mean relative competitive abilities (± SE) of the IGPrey and the omnivore as assessed by the log-ratio of their mean population level (a) feeding rates, (b) bottom-up prey impacts, (c) per capita attack rates, and (d) handling times on each of their shared prey species. Asterisks indicate significance after one-sided t-test (* $p < 0.05$, ** $p < 0.1$). Prey abbreviations: Xp - *Xenostrobus pulex*, Cb - *Chamaesipho brunnea*, Cc - *Ch. columna*, Ep - *Epopella plicata*, Mg - *Mytilus galloprovincialis*, Rv - *Risellopsis varia*, NR - *Notoacmea* sp. Radialspokes. Numbers below abbreviations indicate number of sites at which the prey was shared. Handling time SE for Cb derived from within-site variation across individuals.

shorter for only two of these five species (*Chamaesipho columna* and *Xenostrobus pulex*), as well as a third species (*Risellopsis varia*) for which the two predator's per capita attack rates, feeding rates, and bottom-up impacts were, on average, of equal magnitude (Fig. 4.8d). *H. scobina*'s shorter handling times on *Ch. columna* and *R. varia* were caused by its increased efficiency at handling these species. Its shorter handling times on *X. pulex*, however, were the result of its having larger predator-prey size ratios than *H. haustorium*. The only shared prey species for which *H. haustorium* had higher mean per capita attack rates, feeding rates and bottom-up prey impacts was the Notoacmid limpet. *H. haustorium* had shorter handling times for this species by being ~1.5 times larger relative to its limpet prey than was *H. scobina*.

In contrast to the predictions of IGP theory, and despite being superior at competing for shared prey species, the IGPrey was not the overall superior competitor when both shared and unshared prey were considered together. At all six sites along the productivity gradient the cumulative bottom-up impacts that the omnivore, *H. haustorium*, received from all its prey outweighed the impacts that *H. scobina* received from its prey species (contrast Fig. 4.7a-e with Fig. 4.7f-h).

Cross-gradient changes in food web structure and interaction strengths

Food web structure

Changes in predator diets caused the structure of the food web to change in a directional manner across the productivity gradient (Figs. 4.9-4.10).

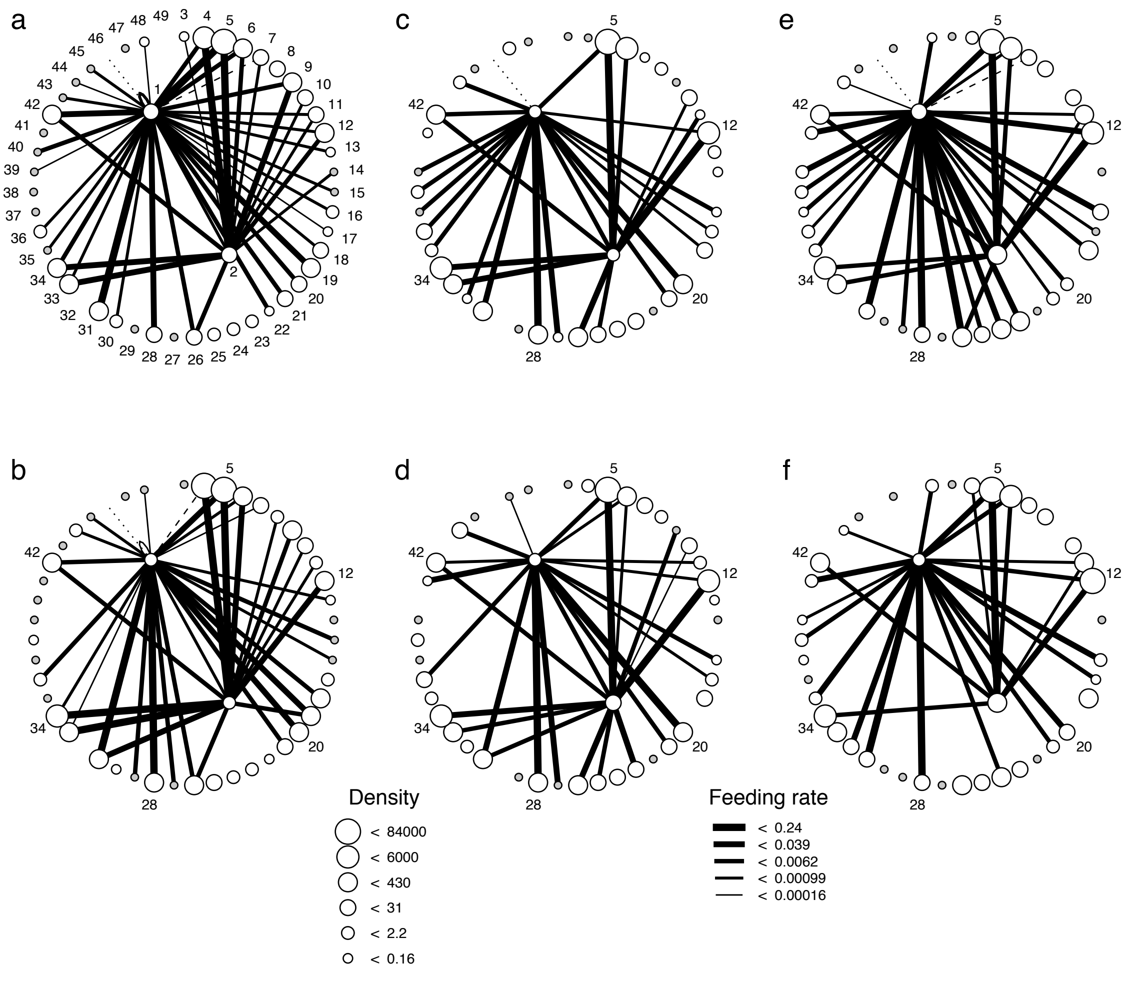

Figure 4.9. Cross-gradient changes in food web structure, species-specific densities, and feeding rates across sites of low (a - PP, b - Rk), mid (c - OP, d - JH), and high (e - TH, f - CF) productivity-levels of the shared prey species. See Table 4.3 for species identification codes.

Table 4.3. Summary of species names, abbreviations, taxonomic groups, assigned IGP groups, and associated identification codes.

Species	Abb.	Group	IGP group	ID
Haustrum haustorium	Hh	Whelk	Omnivore	1
Haustrum scobina	Hs	Whelk	IGPrey	2
Balanus sp.	-	Barnacle – Acorn	Shared prey	3
Chamaesipho brunnea	Cb	Barnacle – Acorn	Shared prey	4
Chamaesipho columna	Cc	Barnacle – Acorn	Shared prey	5
Epopella plicata	Ep	Barnacle – Acorn	Shared prey	6
Calantica spinosa	-	Barnacle – Gooseneck	Shared prey	7
Calantica villosa	-	Barnacle – Gooseneck	Shared prey	8
Lasaea rubra hinemoa	-	Bivalve – Veneroid	IGPrey prey	9
Aulacomya atra maoriana	Am	Bivalve – Mussel	Shared prey	10
Mytilus galloprovincialis	Mg	Bivalve – Mussel	Shared prey	11
Xenostrobus pulex	Xp	Bivalve – Mussel	Shared prey	12
Acanthochitona zelandica	-	Chiton	Omnivore prey	13
Chiton glaucus	-	Chiton	Omnivore prey	14
Onithochiton neglectus neglectus	-	Chiton	Omnivore prey	15
Plaxiphora caelata	Pl	Chiton	Omnivore prey	16
Plaxiphora obtecta	-	Chiton	Omnivore prey	17
Sypharochiton pelliserpentis	Sp	Chiton	Omnivore prey	18
Cellana denticulata	-	Limpet	Omnivore prey	19
Cellana ornata	Co	Limpet	Omnivore prey	20
Cellana radians	Cr	Limpet	Omnivore prey	21
Atalacmea fragilis	-	Limpet – Acmid	Omnivore prey	22
Notoacmea sp. 2spokes	-	Limpet – Acmid	Shared prey	23
Notoacmea sp. Black	-	Limpet – Acmid	Shared prey	24
Notoacmea sp. Net	-	Limpet – Acmid	Shared prey	25
Notoacmea sp. Radialspokes	NR	Limpet – Acmid	Shared prey	26
Notoacmea daedala	-	Limpet – Acmid	Shared prey	27
Patelloida corticata	Pt	Limpet – Acmid	Omnivore prey	28
Notoacmea sp.	-	Limpet – Acmid	Shared prey	29
Montfortula chathamensis	-	Limpet – Fissurelid	Omnivore prey	30
Siphonaria australis	Sa	Limpet – Pulmonate	Omnivore prey	31
Trimusculus conicus	-	Limpet – Pulmonate	Omnivore prey	32
Austrolittorina antipodum	Aa	Snail	IGPrey prey	33
Austrolittorina cincta	Ac	Snail	IGPrey prey	34
Cantharidella tesselata	Ct	Snail	Omnivore prey	35

Table 4.3. Summary of species names, abbreviations, taxonomic groups, assigned IGP groups, and associated identification codes, continued.

Species	Abb.	Group	IGP group	ID
Diloma aethiops	De	Snail	Omnivore prey	36
Diloma arida	Da	Snail	Omnivore prey	37
Diloma bicanaliculata	Db	Snail	Omnivore prey	38
Diloma nigerrima	Dn	Snail	Omnivore prey	39
Eatoniella sp.	-	Snail	Omnivore prey	40
Margarella sp.	-	Snail	Omnivore prey	41
Risellopsis varia	Rv	Snail	Shared prey	42
Thoristella chathamensis	-	Snail	Omnivore prey	43
Turbo smaragdus	Ts	Snail	Omnivore prey	44
Zeacumantus subcarinatus	-	Snail	Omnivore prey	45
Unidentified	-	NA	NA	46
Buccinulum sp.	-	Whelk	Omnivore prey	47
Haustrum lacunosus	-	Whelk	Omnivore prey	48
Paratrophon patens	Pp	Whelk	Omnivore prey	49

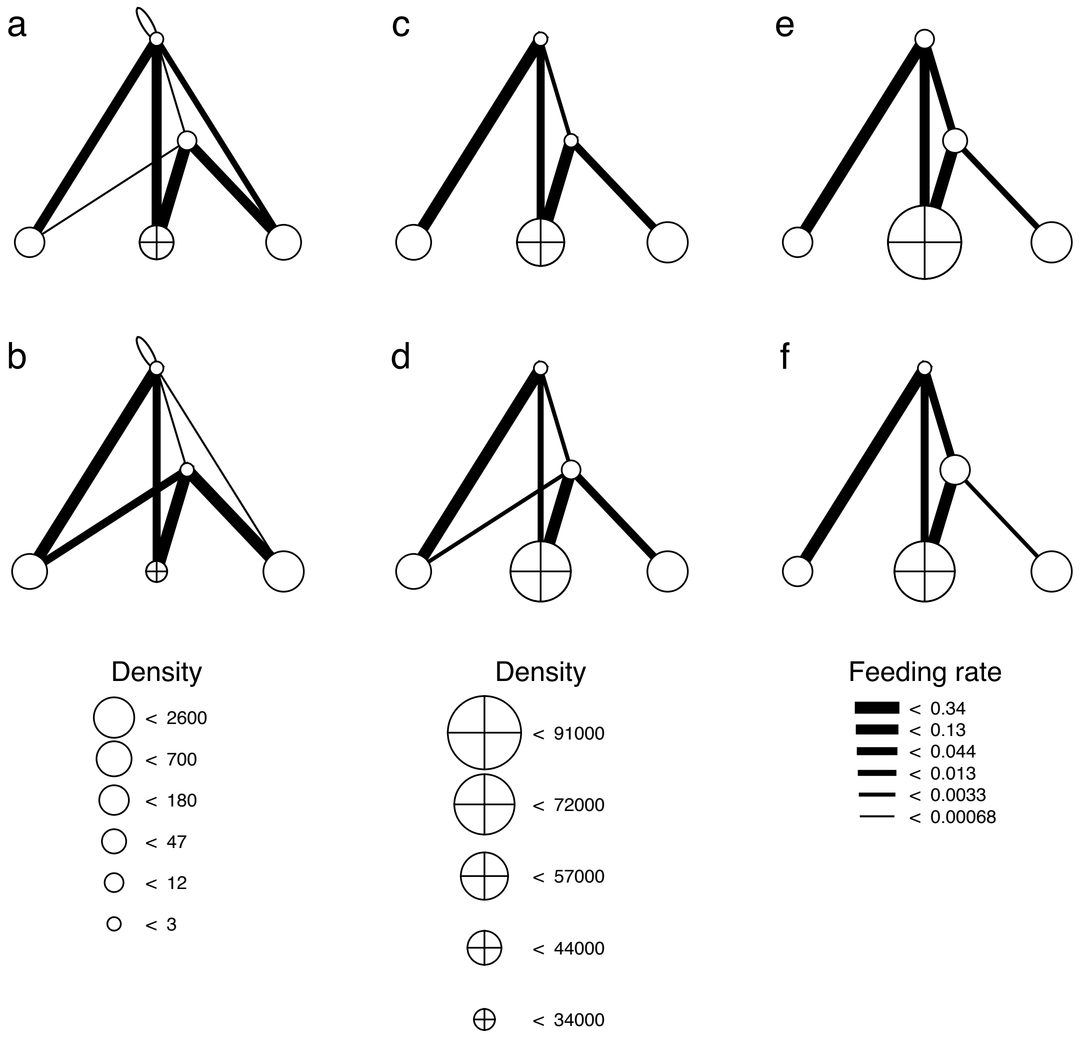

Figure 4.10. IGP-aggregated cross-gradient changes in food web structure, population density, and feeding rates across sites of low (a - PP, b - Rk), mid (c - OP, d - JH), and high (e - TH, f - CF) productivity-levels of the shared prey species. Note that shared prey densities are on a different scale.

The simplest food web structure was observed at two high- and one mid-productivity site (JH). At these sites, *H. haustorium* fed on *H. scobina*, both predators fed on the shared prey group, and each predator fed on a prey group exclusive to itself. The structural complexity of the food web then increased with decreasing productivity. First, at the second mid-productivity site, *H. scobina* fed on species previously exclusive to *H. haustorium*. Then, at the low-productivity sites, *H. haustorium* also fed on both the prey group previously exclusive to *H. scobina* and upon itself as well.

IGP-grouped interaction strengths

Across sites, species-specific per capita attack rates and feeding rates respectively varied across seven and four orders of magnitude. Within a site, they varied by a minimum of six and three orders of magnitude. Among the IGP-grouped interactions that occurred across all sites, cumulative feeding rates of *H. haustorium* on its alternative prey, and of *H. scobina* on the shared prey, were relatively constant, respectively varying by less than three- and two-fold across the productivity gradient (Fig. 4.11). In contrast, *H. scobina*'s feeding rates on its alternative prey showed an exponential decline from low- to high-productivity sites, decreasing by up to almost two orders of magnitude. In contrast as well, *H. haustorium*'s feeding rates on *H. scobina* increased at a faster-than-exponential rate, being up to 46-times higher at high-productivity sites than at low-productivity sites. *H. haustorium*'s feeding rates on the shared prey were more variable across the sites, but were generally lower at the mid-productivity sites.

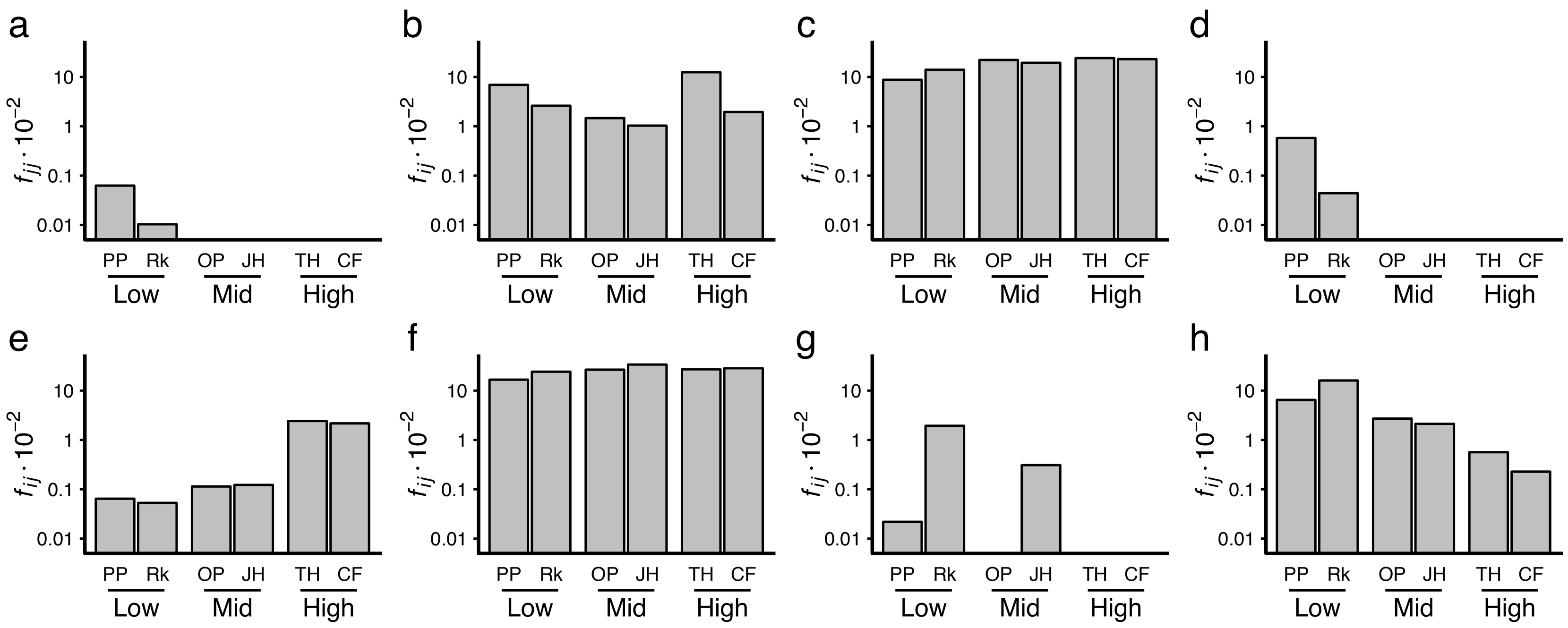

Figure 4.11. Cross-gradient changes in the feeding rates of the omnivore on (a) itself, (b) the shared prey, (c) its own alternative prey, (d) the IGPrey's prey, and (e) the IGPrey, and similarly, of the IGPrey on (f) the shared prey, (g) the omnivore's alternative prey, and (h) its own alternative prey.

Cross-productivity changes in feeding rates were not always reflected by changes in per capita attack rates. Unlike its feeding rates, *H. haustorium*'s per capita attack rates on *H. scobina* remained roughly constant across the gradient, varying by less than four-fold across the sites (Fig. 4.12). *H. haustorium*'s attack rates on its alternative prey group, however, increased with increasing productivity (by up to 20-times). As with its feeding rates, its attack rates on the shared prey were quite variable, being more than two orders of magnitude higher at one mid-productivity site (OP) than the other sites. *H. scobina*'s attack rates on shared prey remained relatively constant between low- and mid-productivity sites, but declined by at least 20-times at the high-productivity sites. Its attack rates on its own alternative prey declined by up to three orders of magnitude from low- to high-productivity sites.

Species-specific interaction strengths.

The across-site correlations of each predator's feeding rates tended to be positive when prey species present at both and fed upon at at least one of the two sites were considered (Fig. 4.13a-*Site pair*; mean r_s of all pairwise correlations = 0.36, range = -0.01-0.82, $p < 0.1$ for 9 of 30 comparisons). Correlations were more strongly positive when only species that were fed upon across all sites were considered (Fig. 4.13a-*All sites*; mean $r_s = 0.67$, range = 0.10-1.00, $p < 0.1$ for 16 of 30 comparisons). Feeding rates thus tended to be consistently high on some species and low on others across all sites of the productivity gradient (*cf.* Fig. 4.9).

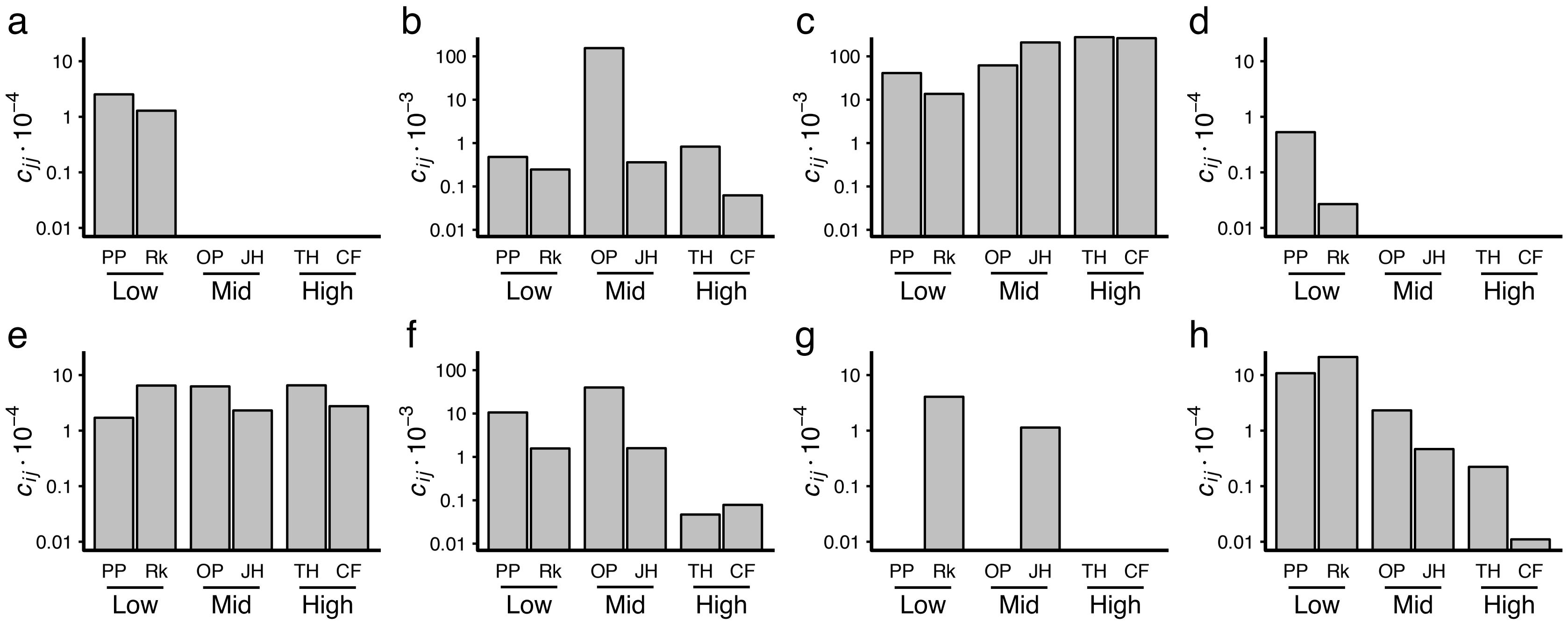

Figure 4.12. Cross-gradient changes in the per capita attack rates of the omnivore on (a) itself, (b) the shared prey, (c) its own alternative prey, (d) the IGPrey's prey, and (e) the IGPrey, and similarly, of the IGPrey on (f) the shared prey, (g) the omnivore's alternative prey, and (h) its own alternative prey. Note variable scales on y-axes. Prey species not observed in abundance surveys excluded (e.g., PP in (g)). Due to their low assumed densities (see *Methods*), these species had very high per capita attack rate estimates, but contributed to only 1% of the cumulative feeding rates and bottom-up species impacts.

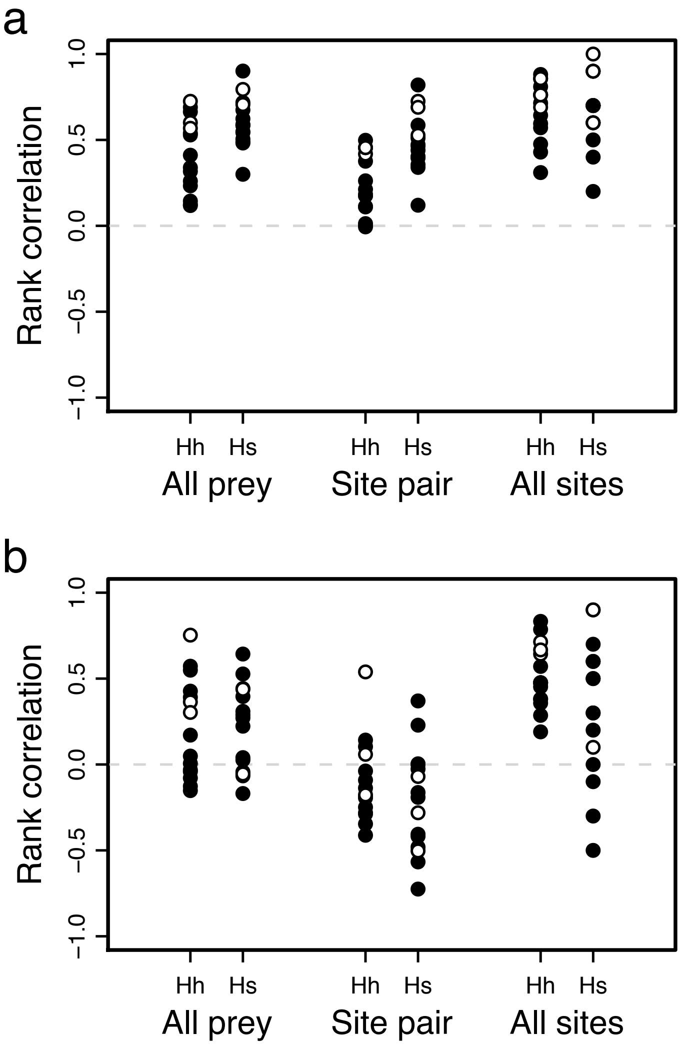

Figure 4.13. Pairwise site-to-site Spearman's rank correlations of species-specific (a) feeding rates and (b) per capita attack rates for the omnivore, *Haustrum haustorium* (Hh), and the IGPrey, *H. scobina* (Hs), when considering: all potential prey present but not necessarily fed upon at either site (All prey), all prey present and fed upon at at least one of the two paired sites (Site pair), and only prey species fed upon across all six sites (All sites). Site-pair combinations contrasting sites within a productivity region (i.e., within the northwest, southwest, or east coast) are indicated by open-circles.

There was little across-site correlation among either predator's per capita attack rates when considering only species present at both and fed upon at at least one of the two paired sites (Fig. 4.13b-*Site pair*; mean $r_s = -0.16$, range = -0.72-0.54, $p < 0.1$ for 1 of 30 comparison). Correlations between sites became more positive when only species that were fed upon across all sites were considered (Fig. 4.13b-*All sites*; mean $r_s = 0.41$, range = -0.50-0.90, $p < 0.1$ for 8 of 30 comparisons). The cross-site consistency in relative feeding rates was therefore less driven by relative predator preferences for prey species than by prey abundances, handling times, or its feeding on alternate prey species.

Across-site correlations tended to be higher when the feeding rates of all potential prey species present but not necessarily fed upon at either of the paired sites was considered (Fig. 4.13a-*All prey*; mean $r_s = 0.51$, range = 0.12-0.90, $p < 0.1$ for 26 of 30 comparisons), but were lower when per capita attack rate on these species were considered (Fig. 4.13b-*All prey*; mean $r_s = 0.21$, range = -0.17-0.75, $p < 0.1$ for 12 of 30 comparisons). Prey on which a predator fed with low feeding rates at some sites therefore tended to be the species that were dropped from its diet at other sites (*cf.* Fig. 4.9), but this was again less strongly driven by predator preferences than by prey abundances, handling times, or its feeding on alternate prey species.

DISCUSSION

IGP theory makes two key predictions: First, that for three-species coexistence to occur, the IGPrey must be superior to the trophic omnivore at competing for their shared basal prey. Second, that despite its competitive superiority, the equilibrium abundance of the IGPrey will decline as the productivity of basal prey increases when the omnivore is also present. These theoretical predictions are robust to a variety of biologically relevant details and, under particular conditions, to the addition of prey species exclusive to each predator (Table 4.1, and see below). In this study the IGPrey, *Haustrum scobina*, was indeed the superior competitor for the species it shared with the omnivore, *H. haustorium*. It was not, however, the overall superior competitor when non-shared prey were also considered. The manner in which *H. scobina*'s abundance changed as a function of the productivity of the shared prey species was also strongly counter to the prediction of IGP theory.

The relative superiority of competing predators

Superiority for shared prey

A number of studies have shown the IGPrey of many IGP systems to be superior to their omnivorous competitors because they are able to reduce the abundance of shared prey at a faster rate (see *Introduction*). The mechanisms behind this superiority have remained largely unknown. In this study, *H. scobina* fed at a higher rate on at least four of the seven main prey species it shared with *H. haustorium*. The resultant bottom-up impacts it derived from these four species exceeded the impacts that *H. haustorium* derived from all shared prey combined. *H. scobina* was therefore the superior competitor for shared prey.

The manner by which *H. scobina* achieved its competitive superiority differed between the shared prey species. For two species, *H. scobina* achieved superiority by having both higher per capita attack rates and shorter handling times. Shorter handling times were the results of *H. scobina* having a higher efficiency at drilling and ingesting prey individuals, or by the selection of smaller prey individuals relative to its own size, than did *H. haustorium*. For two other species, *H. scobina* achieved superiority by having sufficiently high per capita attack rates for its lack of higher handling time efficiency to be overcome. Such variation in competitive mechanisms could have important consequences for the dynamics of species interactions and the coexistence of species in species-rich food webs (Armstrong and Mcgehee 1980, Schreiber and Vejdani 2006). Furthermore, the magnitude by which *H. scobina*'s species-specific per capita attack rates differed from those of *H. haustorium*, relative to the magnitude by which their species-specific handling times differed (Fig. 4.8), suggests that attack rates are more easily learned or evolved. This pattern is consistent with the more general observations of Blomberg et al. (2003) that behavioral traits (i.e., prey preferences) are more labile than physiological traits (i.e., digestion or enzyme-mediated drilling rates), and should therefore be considered in future comparative studies of IGP systems.

Superiority for all prey

Despite being the superior competitor for shared prey species, and counter to IGP theory, the IGPrey was not the overall superior competitor when all prey species were considered. Theory predicts that the IGPrey must be the overall superior exploiter when alternative prey are considered (Daugherty et al. 2007, Holt and Huxel 2007). More specifically, it must gain a sufficiently large impact from all its prey to outweigh the negative top-down effects of the omnivore's predation and its own intrinsic mortality rate (Daugherty et al. 2007). IGP theory would predict the ultimate extinction of *H. scobina* because its alternate prey species did not have large enough bottom-up effects to outweigh the substantial bottom-up effect that *H. haustorium* received from its alternate prey (Kondoh 2008). Local extinctions do not appear common, for both species have coexisted at other sites for at least four decades (R.T. Paine, *unpubl. data*).

A similar lack of IGPrey exclusion by a competitively superior omnivore has also been observed in other IGP systems (e.g., Navarrete et al. 2000). These observations imply that *H. haustorium* does not strongly control the abundance of *H. scobina*. Its own abundance must therefore be limited by more than just its consumption rates, perhaps by having higher mortality rates than *H. scobina*. Although the relative body sizes of the two predators suggest that the smaller *H. scobina* should experience the higher intrinsic and extrinsic mortality rates (Sinclair et al. 2003, McCoy and Gillooly 2008), I explore this possibility in *Appendix 4.B* by estimating the expected mortality rates that would satisfy coexistence requirements. In *Appendix 4.B*, I also estimate how much higher *H. scobina*'s efficiencies at converting prey into offspring would need to be for it to have received bottom-up prey impacts equal to those received by *H. haustorium*.

Cross-gradient changes in community structure

The overall abundance of shared prey species increased across the gradient of increasing mussel and barnacle growth and recruitment rates. Counter to the predictions of IGP theory, *H. scobina*'s abundance increased across the gradient, and *H. haustorium*'s abundance remained unchanged. Current IGP theory has not sufficiently explored predictions regarding the cross-gradient changes in the abundance of each predator's alternative prey groups. Interestingly, the two groups responded in opposite direction, with *H. haustorium*'s alternative prey decreasing, and *H. scobina*'s alternative prey increasing with productivity.

Diehl and Feißel (2000) have suggested that a saturating Type II functional response in the omnivore with respect to the IGPrey may cause the direction of the omnivore's response in abundance to be indeterminate. An omnivore's abundance, therefore, could remain unchanged with increasing productivity if its feeding rate is sufficiently reduced by the saturating effects of its prey. The analyses of *Chapter V*, however, suggest that *H. haustorium*'s feeding rates are not strongly reduced. Furthermore, the IGPrey's abundance is still predicted to decline even if the omnivore's feeding rate is saturated (Diehl and Feißel 2000). *H. scobina*'s increase in abundance therefore adds a second piece of evidence suggesting only weak top-down control of its populations by *H. haustorium*.

Only a handful of possible mechanisms have been suggested to enable the abundance of the IGPrey to increase with increasing productivity (Table 4.1):

First, Amarasekare (2006, 2007a) has shown that the abundance of the IGPrey may increase in IGP systems across separated sites of increasing productivity using three-species metacommunity patch dynamic models (see also Snyder et al. 2005, Su et al. 2008). In these models the IGPrey is able to persist and increase in abundance at high productivity sites only when the dispersal rate of the omnivore is high enough – relative to the IGPrey's dispersal rate – that it emigrates to low productivity sites at rates that preclude it from controlling the abundance of the IGPrey. The crawl-away larval life-history strategy of *Haustrum* species and the observation that populations of similar, northern hemisphere dogwhelks show low levels of gene flow (e.g., Sanford et al. 2003) suggest that this mechanism is unlikely in the New Zealand system.

Second, Rudolf (2007) has shown that the abundance of the IGPrey may increase with increasing productivity in three-species Lotka-Volterra IGP models when omnivores engage in size-structured cannibalistic interactions (see also Hart 2002, Amarasekare 2007b, 2008). This mechanism requires the omnivore to be the superior competitor for the basal prey and to have a higher per capita attack rate on itself than on the IGPrey. *H. haustorium* did engage in cannibalism and was the overall superior competitor for basal prey. Its per capita attack rate on itself, however, was higher than its attack rate on *H. scobina* only at one low productivity site (Fig. 4.12). Cannibalism was absent at the mid- and high-productivity sites where the cannibalistic mechanism would need to be strongest to explain the patterns observed in New Zealand.

Third, Hart (2002) has shown that the IGPrey will increase with increasing productivity if the omnivore exhibits a multispecies semi-ratio-dependent functional response. The omnivore's feeding rate in Hart's phenomenological models is thus not only a saturating (Type II) function of all its prey's abundances (as is assumed by the observational approach that I employed, Novak and Wootton 2008), but of the relative abundance of the omnivore to its prey as well. Similar to the mechanism of cannibalism, the omnivore's feeding rate is reduced at high density by interference with conspecifics. This negative density-dependence prevents the omnivore from controlling the IGPrey's abundance at high productivity. While such predator-dependent functional responses can arise by a variety of mechanisms (Hart 2002), they have been difficult to assess empirically (Abrams 1994, Abrams and Ginzburg 2000). Their prevalence in nature remains debated in the ecological literature (e.g., Fussmann et al. 2007, Jensen et al. 2007). The few studies that have examined predator-dependence in the functional responses of whelks specifically have provided little support for ratio-dependence (Murdoch 1969, Katz 1985). *H. haustorium*'s densities, furthermore, are typically very low and dispersed, with individuals aggregating in large numbers only during breeding seasons and showing no antagonistic interactions or behavioral modifications in crowded laboratory settings (M. Novak, *pers. obs.*). These observations suggest that ratio-dependence is unlikely to affect *H. haustorium*'s functional response at the ranges of observed prey abundances.

A final previously considered mechanism that could lead to an increase in the IGPrey's abundance is adaptive foraging behavior. With adaptive foraging, the omnivore's per capita attack rate on each of its prey is a function of its prey's potential bottom-up impacts. These depend not only on relative prey abundances, but on the potential per capita bottom-up impact the omnivore would receive by consuming an individual of either prey species. As suggested by Holt and Polis (1997), an IGPrey that is a superior competitor for the shared prey should be able to coexist more easily in the presence of an adaptive omnivore. At high productivity, the omnivore should focus its feeding on shared prey, thereby decreasing predation on the IGPrey. Such adaptive switching has in fact been shown to increase the dynamic stability of IGP systems (Matsuda et al. 1986, Lalonde et al. 1999, Křivan and Diehl 2005). The IGPrey's abundance may therefore increase with productivity as long as the shared prey remains abundant enough to be the more profitable prey for the omnivore.

Křivan and colleagues (Křivan 2000, Křivan and Schmitz 2003, Křivan and Diehl 2005) have addressed the cross-gradient effects of adaptive foraging in three-species IGP models explicitly. Their models predict that the per capita attack rate with which an omnivore feeds on the IGPrey should indeed decrease with increasing productivity when there is a trade-off between feeding on its two prey species (Křivan 2000). Such a decline in per capita attack rates was not observed in the New Zealand system. In fact, *H. haustorium*'s per capita attack rates on both *H. scobina* and on the shared prey group stayed relatively unchanged across the gradient (Fig. 4.12). Furthermore, a switching trade-off such as is required for these models is unlikely to occur in the New Zealand system where prey are encountered in the same fine-grained environment (Holt 1983, Křivan and Diehl 2005). Adaptive foraging does not affect the coexistence window of the IGPrey in models when such an evolutionary-scale trade-off is not incorporated (Křivan and Schmitz 2003). Thus adaptive foraging among individuals (i.e., on ecological time scales) also fails to explain the observed cross-gradient increase in the abundance of *H. scobina*.

Future directions for IGP theory: cross-gradient changes in food web structure and interaction strengths

In summary, there is little support for the mechanisms of current IGP theory in explaining the patterns observed in the food webs of the New Zealand intertidal. One explanation is that the IGP-driven processes predicted for tightly coupled IGP systems are too diffuse in species-rich systems. Having multiple shared and alternative prey may increase the strength of intraspecific interactions in each predator species and reduce the effect of IGP. I therefore suggest that future modeling efforts should consider IGP systems with alternative prey in more detail, and should also focus in particular on the potential for non-trophic interactions to occur between basal prey species (see also Polis and Strong 1996). Changes in community structure observed across the New Zealand productivity gradient suggest that such basal interactions could be very important: Mussels and barnacles are likely to have an indirect facilitative effect on *H. scobina*'s alternative prey (small littorine snails) by the formation of increased structural substrate complexity, and are likely to have indirect negative effect on the abundance of the larger species comprising *H. haustorium*'s alternative prey group (large limpets and snails) which typically prefer less complex surfaces on which to graze (Menge 1995). Such interactions among basal prey are largely disregarded in the models of Daugherty et al. (2007) and Holt and Huxel (2007) whose basal species are made to compete only implicitly, either by each species having a fixed proportion of a shared total carrying capacity (Holt and Huxel 2007) or by each species having a non-shared but equally large carrying capacity (Daugherty et al. 2007).

I also suggest that future modeling efforts should consider that both the structure and interaction strengths of natural food webs are dynamic, particularly over evolutionary time. That the underlying components of species interactions need not be constant has largely been ignored by current theory, but is clearly evidenced by my data. While some interaction strengths did remain constant (e.g., the omnivore's per capita attack rate on the IGPrey), others changed by three orders of magnitude (Fig. 4.12). Hope is offered by the unidirectional nature of the cross-gradient changes observed in both the structure of the food webs and in the interaction strengths themselves.

A similar appeal has been made by Křivan and Schmitz (2003) whose models with adaptive foragers highlight how dynamic food webs can be. Recent work by Petchey et al. (2008), furthermore, has indicated that much of the structural variation observed in food webs in general may be explained by optimal foraging theory. In fact, the cross-gradient changes in food web structure and interaction strengths observed in New Zealand provide evidence suggesting that both adaptive and optimal foraging processes have played a role in structuring this system. Classic optimal foraging theory predicts, for example, that a predator's diet richness will increase as the availability of its primary prey decreases (MacArthur and Pianka 1966, Schoener 1971, Pulliam 1974). This same pattern was noticeably evident across populations of the more specialized IGPrey, *H. scobina*, whose 7-8 prey diet richness at high productivity sites (where its primary prey, mussels and barnacles, were most abundant) steadily increased to 14 prey species at the low productivity sites (where the abundance of mussels and barnacles was low, *cf.* Figs. 4.2 and 4.4). This increase in diet richness was not caused by changes in the available richness of potential prey (Fig. 5). Further evidence that species-specific prey preferences are even more finely developed across populations is given by the high frequency of low correlations in across-site attack rate comparisons (Fig. 4.13b). Relative prey preferences were typically more conserved between adjacent sites and on prey that were consistently observed in each predator's diet, but often diverged quite strongly between more distant sites, particularly for the more specialized *H. scobina*. Evidence for such local selection on predator preferences is strong for similar whelk species of northern hemisphere coasts (Sanford et al. 2003).

Yet despite strong site-to-site variation in prey preferences, between site correlations of species-specific feeding rates were often quite high (Fig. 4.13a). Prey abundances, handling times, and a predator's feeding on alternate prey species all contributed more to a predator's feeding rate on a specific prey species than did just its preference for that species alone. The relative between-species flow of nutrients and energy was therefore quite consistent between sites, especially among adjacent sites having more similar community structure (Fig. 4.7). This consistency offers further hope that the emergent properties of food webs may themselves be still quite predictable despite their reticulate nature.

CONCLUSIONS

The reticulate nature of natural food webs requires us to better understand the role that trophic omnivores play in structuring their communities. No longer in its infancy, IGP theory has already contributed much to our understanding of more complex food webs by integrating our knowledge of how predation and competition, top-down and bottom-up processes, and direct and indirect interactions, affect the coexistence and dynamics of species. While IGP theory's predictions were not supported in this study, the consistent and unidirectional nature of the cross-productivity changes observed in New Zealand suggests hope is warranted for future theoretical developments.

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APPENDIX 4.A: AN INTRAGUILD PREDATION MODEL WITH BASAL IMMIGRATION

Current theoretical models examining the effects of increasing resource productivity on the equilibrium abundances of a three species IGP food web have done so by varying either the local per capita population growth rate or carrying capacity of the shared prey species (but see Holt and Polis 1997). Although Menge and colleagues have shown that the growth rate of individual barnacles and mussels increases from the northeast to southwest to northwest coasts of New Zealand, recruitment rates across these coasts exhibit far more dramatic increases (Menge et al. 1999, Menge et al. 2003). Because recruitment occurs from both local and non-local sources and thus need not be controlled by local process, different degrees of feedback can occur between species such that the existence and stability of IGP food web equilibria and their species abundances can change (Velazquez et al. 2005, Briggs and Borer 2005). Previous studies have only explored the consequences of outside immigration to the consumer populations.

Outside immigration in the shared prey need not, however, alter the qualitative predictions of models with only local processes. To illustrate, consider a three-species model in which the typically used density-dependent local growth term of the shared basal resource (*R*) is replaced by a density-independent immigration term (*I*), as in

$$\frac{dR}{dt} = I - \alpha_{11}RR - \alpha_{12}RP - \alpha_{13}RO, \tag{4.A.1}$$

where α_{11} represents the shared prey's per capita self-limitation rate (1/carrying capacity), and α_{12} and α_{13} are, respectively, the per capita attack rates of the IGPrey (*P*) and the trophic omnivore (*O*) on the shared prey assuming linear functional responses (*cf.* Ruggieri and Schreiber 2005, Takimoto et al. 2007, *Chapter III*). The descriptions of the dynamics of the two predators remain unchanged from their typical Lotka-Volterra representation (e.g., Revilla 2002), and are written as

$$\frac{dP}{dt} = e_{21}\alpha_{12}RP - \alpha_{23}PO - m_2P \tag{4.A.2}$$

and

$$\frac{dO}{dt} = e_{31}\alpha_{13}RO + e_{32}\alpha_{23}PO - m_3O, \tag{4.A.3}$$

where e_{ji} are the numeric efficiency by which prey *i* is converted to predator *j*, and m_j are the density-independent mortality rates of the predators.

A full exploration of this model is beyond the current scope. Not surprisingly, it suggests as do other simple IGP models, that (i.) three-species coexistence can occur at intermediate immigration rates, that (ii.) the IGPrey must be the superior competitor for coexistence to occur, and that (iii.) the equilibrium abundance of the IGPrey within the region of three-species coexistence declines with increasing immigration rates (Fig. 4.A. 1).

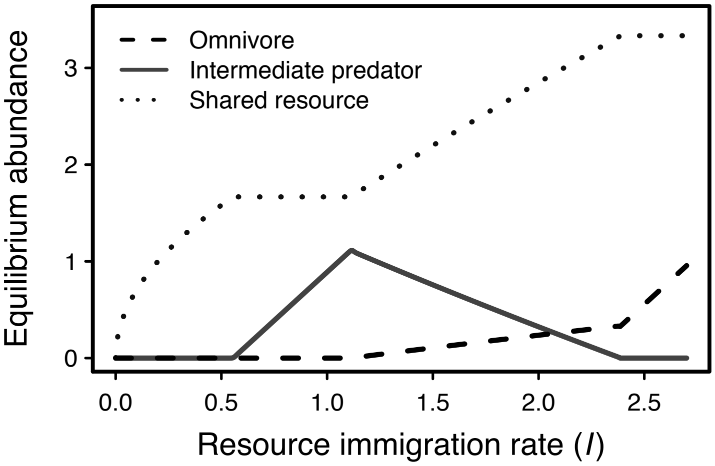

Figure 4.A.1. Illustration of the effects of increasing immigration rate of the shared prey on the equilibrium abundances of the trophic omnivore, the IGPrey, and the shared prey, in a simple intraguild predation model with shared prey recruitment from a non-local source. Equilibrium abundances were obtained by numerical integration. Parameter values are: $\alpha_{11} = 0.2$, $\alpha_{12} = 0.3$, $\alpha_{13} = \alpha_{23} = 0.15$, $e_{21} = 0.1$, $e_{31} = 0.1$, $e_{32} = 0.15$, $m_2 = m_3 = 0.05$.

APPENDIX 4.B: PERSISTENCE BY UNEQUAL MORTALITY AND CONVERSION RATES

For either whelk predator to coexist with the other in an IGP food web with alternative prey species, it must be able to invade a system composed of the other species when it is itself rare. This can occur for the IGPrey when

$$(b_{PAlt} + b_{PSh}) - \left(\frac{b_{OP}N_O}{N_P} + m_P\right) > 0 \quad , \tag{4.B.1}$$

and for the omnivore when

$$b_{OP} + b_{OAlt} + b_{OSh} - m_O > 0, \tag{4.B.2}$$

where b_{ji} are the bottom-up prey impacts of prey species on the IGPrey (P) or omnivore (O) at equilibrium densities N_j, and m_j are each predator's mortality rates (Daugherty et al. 2007). These conditions are analogous to the R^* concept of competitive exclusion (Tilman 1982) in that a predator's R^* is a function of its mortality rate and its attack rates, conversion efficiencies and handling times controlling its bottom-up prey impacts (see also Kondoh 2008). Two nonexclusive hypotheses could therefore explain the persistent coexistence of *Haustrum haustorium* and *H. scobina* in New Zealand within the context of current IGP theory: (i) *H. scobina* convert prey into offspring with higher numeric efficiencies than does *H. haustorium*, and (ii) *H. scobina* exhibit lower mortality rates than *H. haustorium*. The analyses of the main text assumed these two variables were equal between the two predators.

Neither hypothesis on its own appears likely (see also METHODS). To satisfy Eq. B1-2 would require *H. scobina*'s conversion efficiencies to be 1.1 – 7.6 times higher than *H. haustorium*'s if their mortality rates are equal (Table 4.B.1). This would correspond to *H. scobina* having conversion efficiencies greater than 100% at three of the six sites. Similarly, treating observed species densities as the equilibrium densities expected in the absence of the IGPrey lets Eq. B.1-2 be satisfied as long as site-specific m_P are less than the values given in Table 4.B.2 if conversion efficiencies were equal between the two predators. This assumption of equilibrium densities should be conservative given that the abundances of the basal prey and of the omnivore should, respectively, be higher and lower in the absence of the IGPrey than in its presence. Estimated maximum IGPrey mortality rates are remarkably consistent across the six sites (Table 4.B.2). Similarly treating observed species densities as being equilibrium densities in the absence of the omnivore allows Eq. 4.B.1-2 to be satisfied as long as the omnivore's site-specific mortality rates are less than the values given in Table 4.B.2. These estimates are not conservative.

Table 4.B.1. Estimated minimum site-specific conversion efficiencies of *Haustrum scobina* required for coexistence with *H. haustorium*.

Site	**Conversion efficiency**	**Relative to *H. haustorium***
PP	0.69	2.7
Rk	0.27	1.1
OP	1.91	7.6
JH	1.75	7.0
TH	0.53	2.1
CF	1.17	4.7

Table 4.B.2. Estimated maximum site-specific mortality rates of *Haustrum scobina* (m_P) and *H. haustorium* (m_O) allowing coexistence.

Site	m_P	m_O
PP	1.37×10^{-4}	3.85×10^{-4}
Rk	4.13×10^{-4}	4.55×10^{-4}
OP	1.03×10^{-4}	8.23×10^{-4}
JH	0.98×10^{-4}	7.27×10^{-4}
TH	1.52×10^{-4}	5.67×10^{-4}
CF	1.69×10^{-4}	10.80×10^{-4}

Coexistence of all species in the system – the two predators, the shared prey and their alternate prey – is predicted to be achievable only when each predator “specializes” on a different prey species (Daugherty et al. 2007). This occurs when the per capita bottom-up effect of the shared prey on the IGPrey is larger than that of the alternative prey, and the per capita bottom-up effect of the shared prey on the omnivore is smaller than that of the alternative prey, or vice versa (Daugherty et al. 2007), such that

$$\frac{b_{OSh}}{N_{Sh}} < \frac{b_{OAlt}}{N_{Alt}} \tag{4.B.3}$$

and

$$\frac{b_{PSh}}{N_{Sh}} > \frac{b_{PAlt}}{N_{Alt}}\,, \tag{4.B.4}$$

or vice versa. For the New Zealand system, Eq. 4.B.3 is satisfied across all six sites (Table 4.B.3); the omnivore derives a greater per capita impact from the species that are not consistently shared than it does from the seven species that are consistently shared across the sites. Eq. 4.B.4, however, is satisfied only at the two high productivity sites (Table 4.B.3); at the low- and mid-productivity sites, both predators derive greater per capita impacts from the species that are not consistently shared than from the species that are consistently shared.

H. scobina does, however, derive a greater summed impact on a total species-impact (b_{ij}) basis from the shared prey species than it does from the non-shared prey species, across all sites (Fig. 4.10). The apparent inconsistency between the New Zealand

Table 4.B.3. Summed per capita bottom-up impact of prey groups on their predators.

Predator	Prey Group	PP	Rk	OP	JH	TH	CF
H. scobina	Shared	3.71 x 10^{-9}	1.51 x 10^{-8}	2.05 x 10^{-9}	1.50 x 10^{-9}	1.83 x 10^{-9}	2.61 x 10^{-9}
H. scobina	Non-shared	1.87 x 10^{-8}	4.12 x 10^{-8}	7.38 x 10^{-9}	3.34 x 10^{-9}	4.28 x 10^{-10}	9.39 x 10^{-11}
H. haustorium	Shared	7.32 x 10^{-10}	6.32 x 10^{-10}	6.10 x 10^{-11}	4.83 x 10^{-11}	7.99 x 10^{-10}	3.40 x 10^{-10}
H. haustorium	Non-shared	6.82 x 10^{-7}	5.13 x 10^{-7}	3.89 x 10^{-6}	3.46 x 10^{-6}	3.30 x 10^{-6}	1.29 x 10^{-5}
H. haustorium	*H. scobina*	8.20 x 10^{-7}	8.72 x 10^{-6}	4.78 x 10^{-6}	3.05 x 10^{-6}	4.92 x 10^{-6}	3.15 x 10^{-6}

system and the theoretical per capita partitioning predictions of Daugherty et al. (2007) likely arises because per capita attack rates, food web topology, and the relative abundance of shared and non-shared prey are fixed in their models, but vary across sites in the New Zealand system.

Appendix 4.C: Cross-Gradient Changes in Ontogenetic Interactions

Models incorporating age-structure and ontogenetic life-history omnivory do not change IGP theory's predictions regarding either the competitive superiority of the IGPrey or the cross-gradient changes in community structure (Table 4.1). Feeding observations nevertheless suggested that ontogenetic diet changes do occur in *Haustrum haustorium*. I therefore repeated all analyses after splitting *H. haustorium*'s populations into juvenile (≤ 25 mm) and adult size-classes.

Splitting *H. haustorium*'s populations into these two size-classes revealed a considerable amount of ontogenetic diet change in the omnivore (Fig. 4.C.1). At four of the six sites only adult *H. haustorium* engaged in intraguild predation by feeding on *H.*

scobina. Juveniles, on the other hand, were exclusively responsible for feeding on *H. scobina*'s alternative prey at the low-productivity sites where this interaction was observed. Furthermore, only juveniles preyed upon acorn barnacles, and preyed on mussels more often than did adults. They therefore had consistently higher per capita attack rates on shared prey species than did the adult size-class. Even *H. haustorium* juveniles by themselves, however, were competitively inferior to *H. scobina* for these shared prey (Fig. 4.C.2). Unlike each site's entire *H. haustorium* population, juveniles received smaller bottom-up prey impacts from their alternative prey than did *H. scobina* from all of its prey. Thus *H. scobina* populations were overall superior competitors to *H. haustorium* juveniles at all but two of the six sites (OP and TH), receiving greater bottom-up prey impacts from all of their prey species than did *H. haustorium* juveniles from all of their prey.

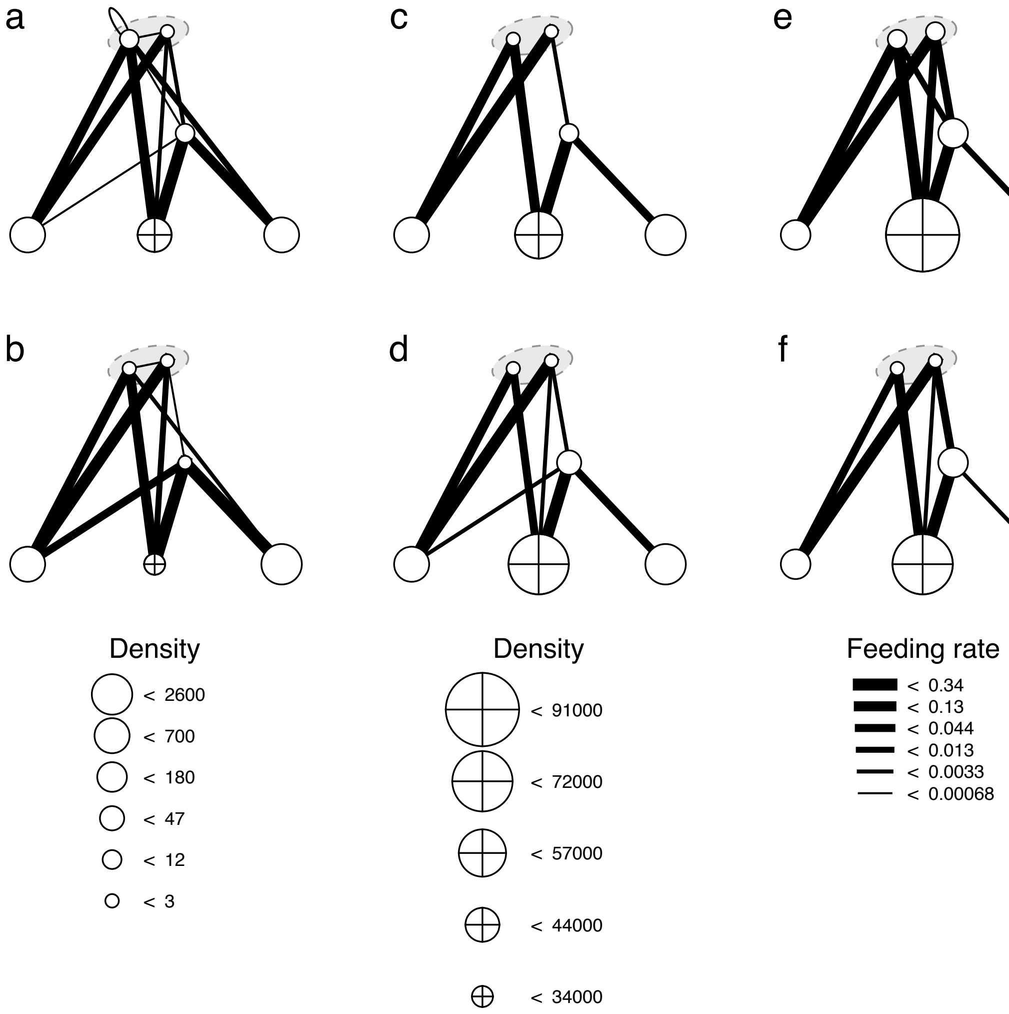

Figure 4.C.1 IGP-aggregated cross-gradient changes in food web structure, population density, and feeding rates across sites of low (a - PP, b - Rk), mid (c - OP, d - JH), and high (e - TH, f - CF) productivity-levels of the shared prey species, with the omnivore's populations split into juvenile (lower left) and adult (upper right) size-classes. Note that shared prey densities are on a different scale.

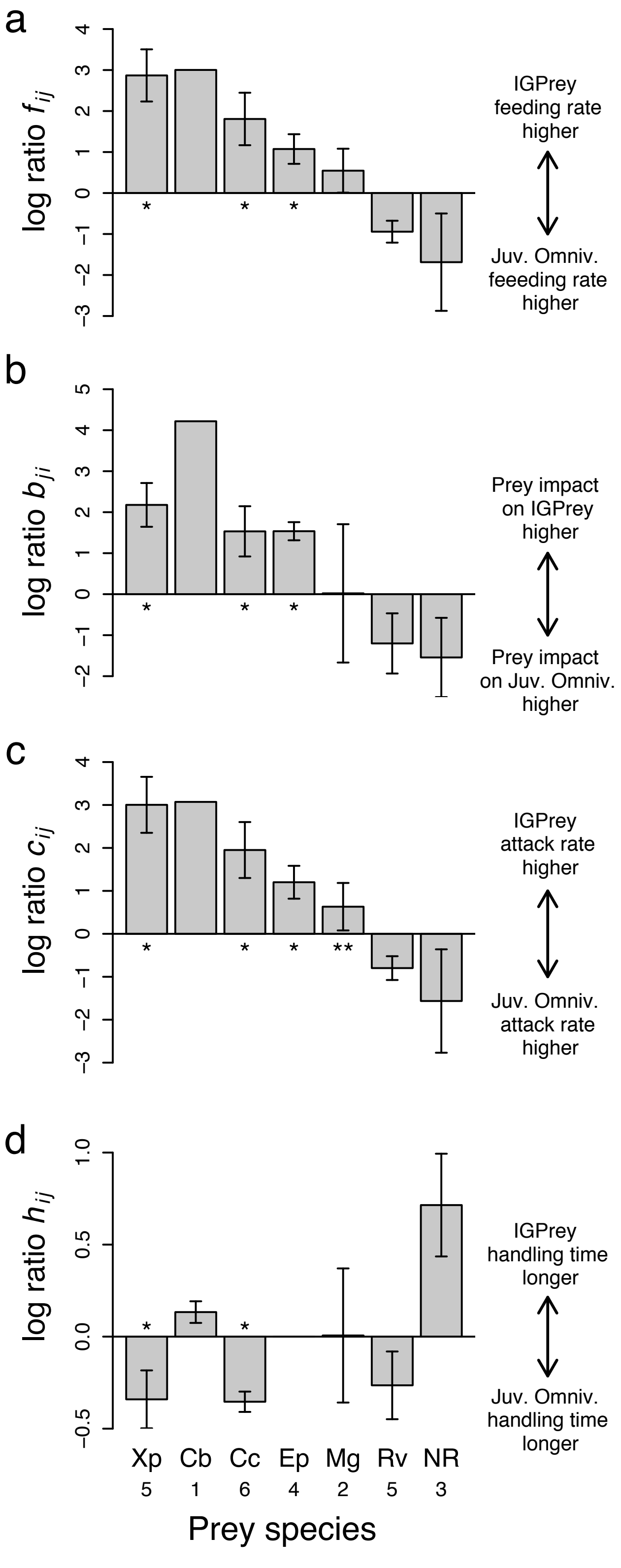

Figure 4.C.2. Mean relative competitive abilities (± SE) of omnivore juveniles (< 25 mm) and IGPrey as assessed by the log-ratio of their mean (a) feeding rates, (b) bottom-up prey impacts, (c) per capita attack rates, and (d) handling times on each of their shared prey species. Asterisks indicate significance after one-side t-test ($p < 0.05$). Prey abbreviations: Xp - *Xenostrobus pulex*, Cb - *Chamaesipho brunnea*, Cc - *Ch. columna*, Ep - *Epopella plicata*, Mg - *Mytilus galloprovincialis*, Rv - *Risellopsis varia*, NR - *Notoacmea* sp. Radialspokes. Numbers below abbreviations indicate number of sites the prey was shared.

CHAPTER V

THE EMPIRICAL NONLINEARITY OF MULTISPECIES FUNCTIONAL RESPONSES AND THE STABILITY OF GENERALIST PREDATOR-PREY INTERACTIONS

ABSTRACT

Most predators exhibit saturating functional responses; their feeding rates becoming increasingly saturated as the abundance of their prey increases. In theory, such saturation is destabilizing, causing predator-prey dynamics to oscillate. Ecologists thus typically invoke low-density prey-switching to account for the empirical persistence and lack of cyclic dynamics in generalist predator-prey interactions. Using data from six intertidal food webs, I ask to what degree the feeding rates of two whelk predators are saturated within the empirical context of their multispecies interactions. I also determine the extent to which prey-attributes can be used to predict prey-specific contributions to the nonlinearity of a predator's functional response, and investigate how a predator's diet richness affects the degree to which it's overall feeding rate is reduced by its prey. By extending and empirically parameterizing the classic Rosenzweig-MacArthur predator-prey model(Rosenzweig and MacArthur 1963), I then ask whether the degree of saturation observed within New Zealand's whelk populations is nonlinear enough to affect the stability of whelk-prey interactions, and how dynamics are affected by predator specialization. My results indicate that whelk feeding rates are generally not strongly saturated, that most prey contribute very little to their predator's saturation, and that increasing diet richness has a non-additive effect on a predator's saturation such that the addition of alternative prey has a stabilizing effect on predator-prey dynamics. I thereby offer a new mechanism by which generalist predators stabilize the dynamics of species-rich food webs which does not rely on density-dependent prey-switching, and an explanation for why predator-removal experiments typically result in linear prey responses despite the inherent nonlinearity of trophic interactions.

Keywords: food webs, functional responses, interaction strength, diversity, stability, specialization, New Zealand, intertidal whelks.

INTRODUCTION

How predator feeding rates may respond to changes in prey abundance underlies the dynamics of all predator-prey interactions. Understanding the empirical nature of these functional responses is central to food web theory and our understanding of the processes controlling the structure and functioning of ecological communities (Abrams and Ginzburg 2000, McCann 2000). Our current understanding of how functional responses affect the dynamics of predator-prey interactions nevertheless harbors three unanswered paradoxes.

The saturation paradox

Most predators exhibit Type II functional responses, their feeding rate becoming increasingly saturated as the abundance of a prey species increases (reviews by Murdoch and Oaten 1975, Hassell et al. 1976, Jeschke et al. 2004). It has long been appreciated, however, that such hyperbolic single-species Type II functional responses tend to destabilize predator-prey interactions (Hassell and May 1973, Oaten and Murdoch 1975). The negative density-dependence of the prey's mortality rate that Type II functional responses exhibit leads to positive density-dependence for the prey population (Gascoigne and Lipcius 2004). If Type II functional responses are both common and destabilizing, how are species-rich food webs maintained in nature (Rosenzweig 1971)?

Ecologists have typically invoked difficult-to-measure low-density prey refuges, predator learning, or density-dependent switching in predator feeding preferences – often encapsulated by the stabilizing sigmoid shape of the Type III functional response – to explain the persistence of predator-prey interactions in nature (e.g., Hassell et al. 1977, Sarnelle and Wilson 2008). Yet Type III responses are themselves only stabilizing below a particular threshold prey density (Murdoch and Oaten 1975). With prey increases above this threshold, Type III responses mimic Type II responses in being destabilizing as predator feeding rates become increasingly unable to control prey abundance. In both laboratory and field functional response studies alike, this threshold density often falls below the maximum density attained by prey in the landscape (e.g., references in Jeschke et al. 2004, see also Middlemas et al. 2006, Englund and Leonardsson 2008, Englund et al. 2008). How do predator-prey interactions persist if predator feeding rates are often saturated with respect to their prey?

The prey dynamics paradox

In theory, the feeding rates of a generalist predator feeding on multiple species with Type II functional responses may effectively exhibit sigmoid (Type III-like) responses to some prey species (Murdoch and Oaten 1975, McCann 2000). The resulting species coexistence requires negative covariance in prey dynamics (increases in the abundance of one prey are associated with decreases in the abundance of another, Murdoch and Oaten 1975) and interaction strengths that are sufficiently skewed towards weak interactions (McCann 2000). Yet while empirical interaction strength distributions in whole communities typically are skewed towards weak interactions (Wootton and Emmerson 2005), empirical time-series indicate that the apparent competition dynamics that could lead to negative covariance among prey are not exhibited by populations of generalist predators (Holt 1977, Murdoch et al. 2002). Only specialist predators exhibit consumer-resource driven cycles (Murdoch et al. 2002). If the dynamics that could lead to persisting predator-prey interactions for generalist predators are shown only by specialist predators, how do the interactions of generalist predators persist?

The linear response paradox

There has been little empirical insight into these first two paradoxes due to the difficulty of measuring the strength and functional form of species interactions in the field, particularly in the species-rich and reticulate food webs that are the norm in nature (Abrams and Ginzburg 2000, Wootton and Emmerson 2005). Most methods for estimating interaction strengths must, perforce, assume unbounded linear Type I functional responses (reviews by Berlow et al. 2004, Wootton and Emmerson 2005, see also Novak and Wootton 2008). These have offered only limited insight because Type I functional responses are by themselves neutrally stable (Murdoch et al. 2003), can make models structurally unstable (Murdoch et al. 2003), and fail to incorporate the dynamic decrease in species-specific feeding rates that must accompany a predator's feeding on alternative prey (see also Abrams 2001, Wootton and Emmerson 2005).

Despite these arguments, methods assuming linear functional responses have proven surprisingly useful for predicting the species-specific effects of many experimental community manipulations (e.g., *Chapter III*, Pfister 1995, Schmitz 1997, Wootton 1997, Berlow 1999). Prey species often respond linearly to experimental changes in the density of their predators. If the functional responses underlying predator-prey interactions are nonlinear, why do prey respond to predator manipulations in ways predicted by models assuming linear functional responses?

Towards a resolution

In this chapter, I offer empirically motivated theory to address these functional response paradoxes. I first use empirical interaction strength estimates from six intertidal food webs to show that the feeding rates of whelks are indeed reduced by the saturating effects of their prey. Most prey, however, contribute so weakly to this nonlinearity that their response to manipulated changes in predator numbers is effectively linear. I then use simulations to show that the degree to which feeding rates are reduced is related directly to the diversity of a predator's diet, but that the effects of increasing prey diversity accumulate in a non-additive manner. Consequently, the feeding rates of specialized predators are more limited by the saturating effects of their prey than are the feeding rates of generalist predators. Finally, I use empirical data to estimate the parameters of a predator-prey model specific to the interactions of two focal whelk populations and their dominant mussel prey and thereby show that feeding on alternative prey stabilizes otherwise oscillatory dynamics. This chapter thereby offers empirically-grounded insight into the way that saturating predator-prey functional responses affect food web dynamics and the persistence of species in diverse ecological communities.

NONLINEARITY IN EMPIRICAL MULTISPECIES FUNCTIONAL RESPONSES

The degree to which a specialist predator's Type II functional response is saturated with respect to its prey species depends on the prey's abundance (N_i), its handling time (h_i), and the predator's per capita attack rate on the prey (c_i):

$$f_i(N_i) = \frac{c_i N_i}{1 + c_i h_i N_i} \tag{5.1}$$

(Holling 1959). Intuitively, the feeding rate of a predator with a larger per capita attack rate or a larger handling time will be more limited at a given prey abundance than a predator with a lower attack rate or more efficient handling time (Fig 5.1).

But while the feeding rate of a fully saturated specialist predator is $1/h_i$, the maximum feeding rate by which a polyphagous generalist predator can feed on a given prey species is limited not only by the focal prey's handling time, but by the predator's feeding on its alternative prey as well. A simple multispecies extension to Eq. 5.1 is

$$f_i(N_i|N_i, ..., N_k) = \frac{c_i N_i}{1 + c_i h_i N_i + \sum_{k \neq i} (c_k h_k N_k)} \tag{5.2}$$

(e.g., Murdoch 1973), whereby the per capita attack rates (= prey preferences, Chesson 1983) are assumed constant such that no density-dependent switching among prey is deemed to occur (Murdoch and Oaten 1975).

Two indices of functional response linearity

To gauge the degree to which predator's feeding rate on prey *i* is limited by the saturating effects of its prey, I define the linearity index μ_i as the slope of the predator's multispecies functional response (Eq. 5.2) evaluated at a given set of prey abundances and divided by its per capita attack rate on prey *i*,

$$\mu_i = \frac{\left.\frac{\partial f_i(N_i|N_i,\ldots,N_k)}{\partial N_i}\right|_N}{c_i} = \frac{1+\sum\limits_{k\neq i}(c_k h_k N_k)}{\left(1+c_i h_i N_i+\sum\limits_{k\neq i}(c_k h_k N_k)\right)^2}. \tag{5.3}$$

Similarly, to gauge the degree to which any given prey species contributes to a predator's saturation, I define a second linearity index σ_i as

$$\sigma_i = \frac{\left.\frac{\partial f_i(N_i)}{\partial N_i}\right|_{N_i}}{c_i} = \frac{1}{(1+c_i h_i N_i)^2}\ , \tag{5.4}$$

letting $\Sigma_{k\neq i}\ c_k h_k N_k = 0$ (Fig. 5.1). Both indices approach a value of 0 as the predator's feeding rate becomes entirely saturated, and equal a value of 1 when the predator's feeding rate is entirely unsaturated (i.e., equivalent to a linear Type I functional response).

The empirical strength of nonlinearities

I applied the two indices to the data set of *Chapter IV* where species-specific per capita attack rates, handling times, and prey densities were estimated for 181 predator-prey interactions of two intertidal whelk predators – *Haustrum scobina* and *H. haustorium* – at six sites along the New Zealand coast. Typically requiring hours to days to drill through the shell of a prey individual, intertidal whelks exhibit classic saturating Type II functional responses to changes in the density of a prey species (Appendix 5.A, Murdoch 1969, Katz 1985, Moran 1985, Rodrigues 1986).

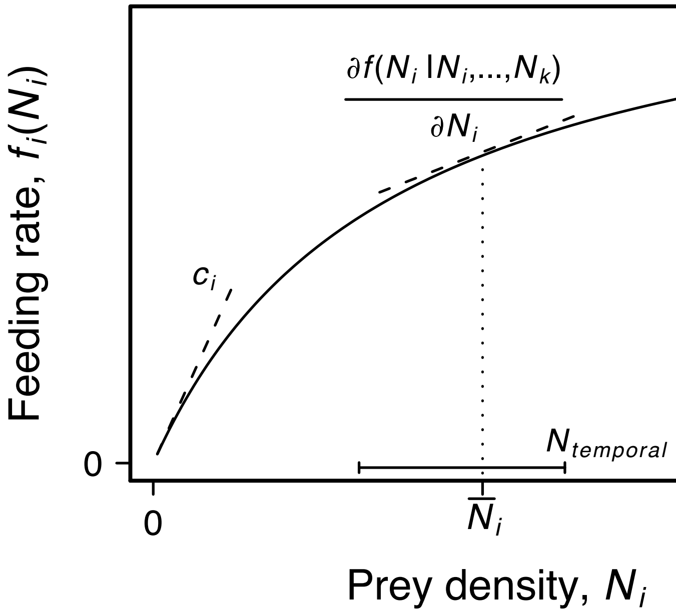

Figure 5.1. Hypothetical Type II functional response curve illustrating the increasing degree to which a predator's feeding rate is saturated as the abundance of its prey increases ($N_{k\neq i}$ constant). The two indices of linearity, μ_i and σ_i, are defined by the slope of the predator's functional response divided by the predator's per capita attack rate, c_i, on the focal prey (Eq. 5.3 and 5.4, respectively). I evaluated both indices using both the slope evaluated at spatiotemporal mean prey densities, $\overline{N}_i$, and the upper 95th percentile of the temporal variation in mean density of the focal prey observed across biannual site-specific surveys (max. $N_{temporal}$).

As described in *Chapter IV*, species densities were estimated using standard quadrat-based survey techniques repeated multiple times at each site. I used both a species' site-specific grand mean density and the 95th percentile of its temporal variation in mean densities observed across these surveys in applying the two nonlinearity indices (see Fig. 5.1). Field-based species-specific handling times were estimated using empirical relationships between handling time, predator and prey identity and body size, and temperature derived from laboratory experiments (see *Chapters III* and *IV*). Per capita attack rates were estimated in *Chapter IV* using the method derived in Novak and Wootton (2008). This method uses estimates of prey densities and handling times, and two pieces of information derived from predator feeding surveys (A_{ij} – the fraction of a predator j population observed feeding on prey i, and F_{ij} – the fraction of all feeding individuals observed feeding on prey i) to estimate per capita attack rates as

$$c_{ij} = \frac{F_{ij} A_{xj}}{(F_{xj} - A_{xj}) h_{ij} N_i} \tag{5.5}$$

where species x is an arbitrarily chosen species used throughout the calculation of all attack rates (Novak and Wootton 2008).

Several patterns emerge when the two linearity indices are applied to these data (Fig. 5.2). First, predator feeding rates are not strongly limited, with even the most saturated of interactions having $\mu_i > 0.66$. (All interactions have $\mu_i > 0.62$ when the upper 95th percentile of a species' temporal variation in site-level mean density is used.) Second, relatively few prey species contribute strongly to a predator's saturation level,

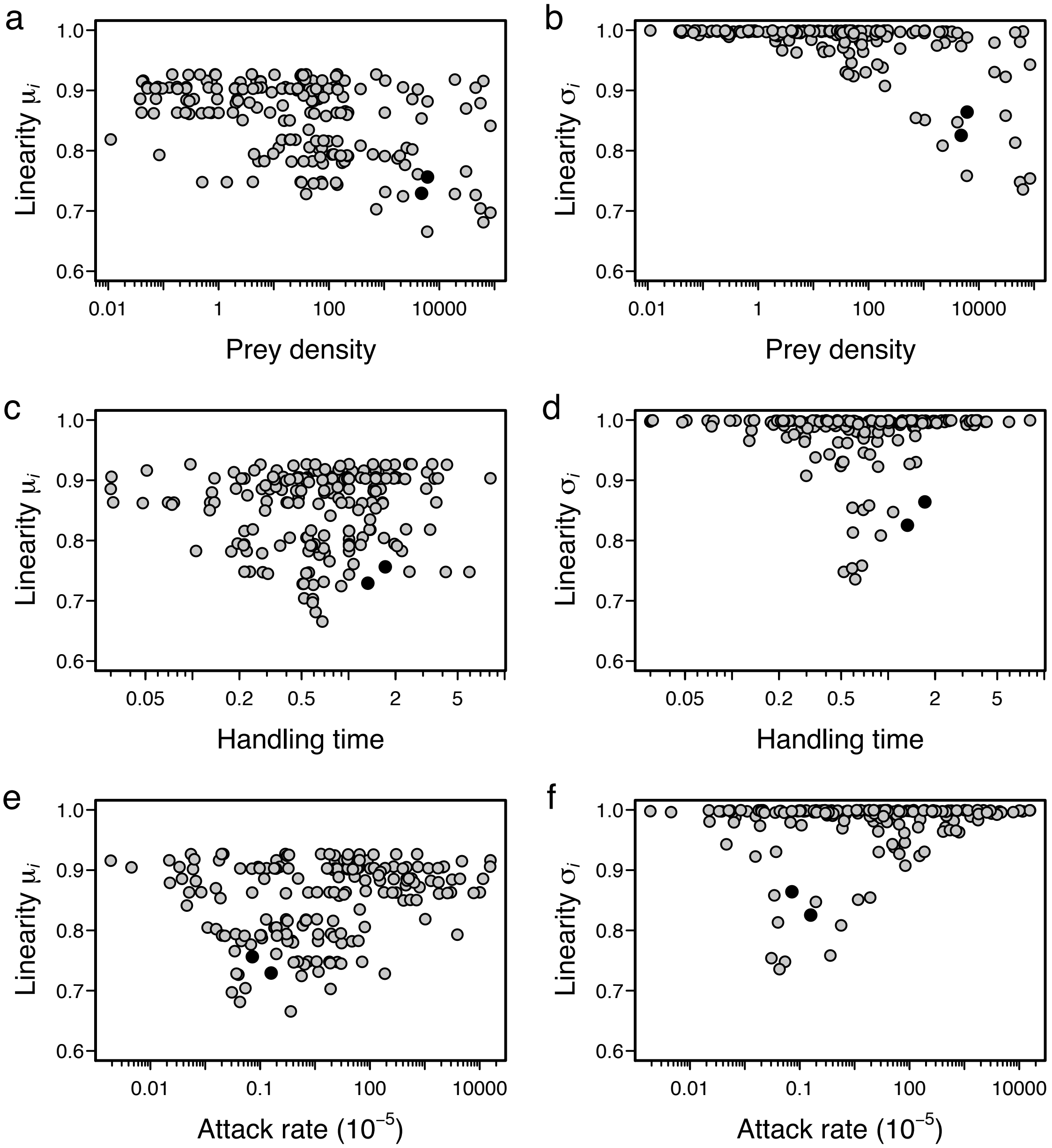

Figure 5.2. Relationships between μ_i – the linearity of the predator's prey-specific functional response – and σ_i – a measure of each prey's contribution to the predator's saturation – and each prey species' (a-b) density (m^{-2}), (c-d) handling time (days), and per capita attack rate (prey eaten $pred^{-1}$ $prey^{-1}$ m^{-2} day^{-1}) ($n = 181$). Black points indicate focal interactions of *Haustrum scobina* whelks and *Xenostrobus pulex* mussels.

with only 23 of 181 interactions having σ_i values < 0.95 (25 of 181 using the 95th temporal percentile).

As expected, predator feeding rates are likely to be the most limited by prey species having high abundances (Fig. 5.2a-b). However, feeding rates are not likely to be limited by the prey on which predators feed with the highest per capita attack rates, or on which they have the longest handling times. Rather, they are limited most frequently by prey for which they have attack rates and handling times of intermediate magnitude (Fig. 5.2c-f). This may be because predators exhibit low preference for prey with long handling times while prey with short handling times and high per capita attack rates are driven to such low densities that they do not comprise a large proportion of the predator's diet.

In fact, the best predictor of the contribution made by a prey species to the level of a predator's overall saturation is the proportion of the predator's diet that the prey represents; prey representing a large proportion of a predator's diet contribute more to a predator's saturation than rarely fed upon prey (Fig. 5.3a). Feeding rates on these rarely consumed prey are nonetheless also reduced by virtue of the prey dominating the predator's diet, but to a lesser degree (Fig. 5.3b).

It follows that the degree to which a given prey species contributes to a predator's overall saturation should depend upon the predator's level of diet specialization. Prey of a predator with a more species-rich diet each contribute less to the saturation of a predator's feeding rate than do the prey of a predator with a less diverse diet. Patterns

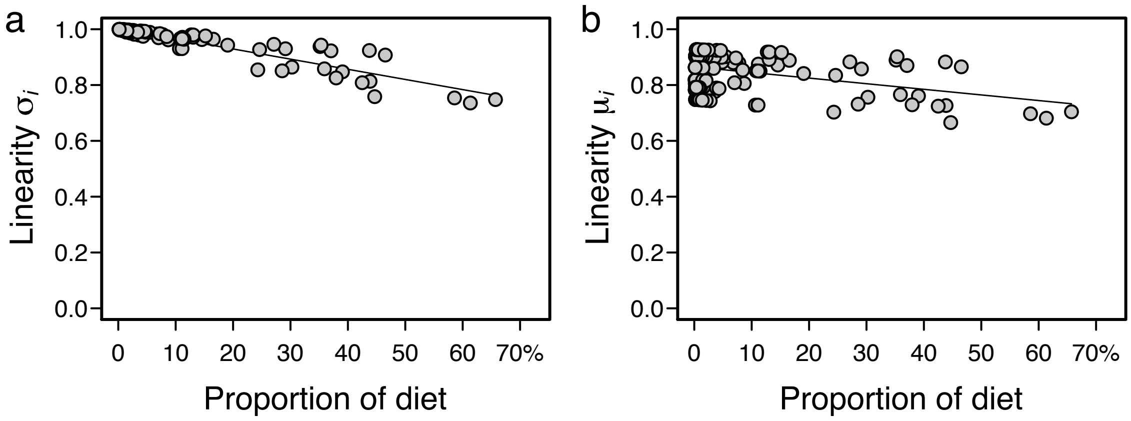

Figure 5.3. Relationships between the proportional frequency by which prey were observed in a whelk population's diet (F_{ij}) and (a) their contribution to the linearity of the predator's functional response, and (b) the degree to which the predator's maximal feeding rate on each prey species is reduced. Least-squares-regression, $y = \beta_1 + \beta_2 x$ (n = 181): (a) $\beta_1 = 1.00$, $\beta_2 = -0.36$, $P < 0.001$, $r^2 = 0.87$; (b) $\beta_1 = 0.86$, $\beta_2 = -0.20$, $P < 0.001$, $r^2 = 0.15$.

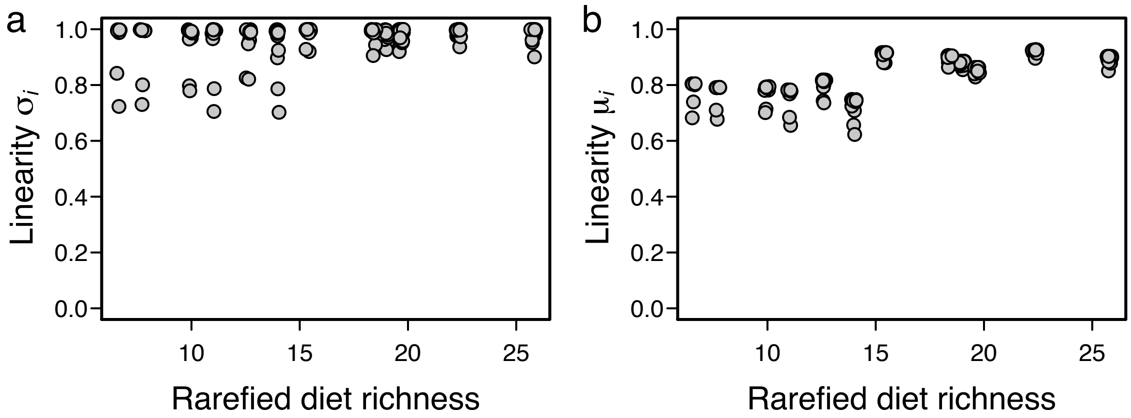

Figure 5.4. Relationships between the predator population's diet richness (rarefied to 208 and 439 feeding observations for *Haustrum haustorium* and *H. scobina*, respectively, and each prey's (a) contribution to the linearity of the predator's functional response, and (b) the degree to which the predator's maximal feeding rate on the prey is reduced.

supporting such a prediction are evident in the New Zealand dataset (Fig. 5.4), but are confounded by covariation in the diet richness and feeding activity levels of the two whelk predators: *H. haustorium*'s populations exhibited species-rich diets (17-33 species) but had low feeding activity levels (an average of 8-16% of individuals were observed feeding during a given survey), while *H. scobina*'s populations exhibited relatively species-poor diets (7-14 species) but had high feeding activity levels (19-28% of individuals feeding). In the next section, I therefore use simulations to tease apart the relationship between diet richness and the degree to which predator feeding rates are saturated by individual prey species.

THE SPECIALIZATION-DEPENDENCE OF PREDATOR SATURATION

How general is the relationship between the degree to which of a predator's species-specific functional responses are saturated and the richness of its diet? I used stochastic individual-based simulations of feeding predator populations to investigate the relationship between a predator's level of saturation (μ_i and σ_i) and its diet richness by controlling for the proportion of its population actively feeding at a given instant in time. Using the same simulation algorithm and parameter values as Novak and Wootton (2008), I simulated predator populations of 10000 individuals feeding on 1, 5, 15 and 30 different prey species, varying each population's level of feeding activity such that 1-80% of the individuals in a population were feeding at any given time. Unlike Novak and Wootton (2008), I drew prey-specific per capita attack rates from a beta distribution (α =

½ , β = 3) multiplied by a maximum possible attack rate (set by the desired feeding activity level and diet richness, see Novak and Wootton 2008) to have their distributions more closely reflect the empirically observed pattern of few strong and many weak attack rates (see Fig. 5.2e-f). Using uniform or truncated lognormal distributions did not change qualitative results. For each simulated diet-richness and activity-level combination I tallied the total number of individuals that were feeding after a burn-in time of 500 time-steps. I then compared the proportion of individuals feeding to each prey species' μ_i and σ_i values, calculated using their drawn c_i, h_i, and N_i values.

Simulation results support the prediction that increasing diet richness reduces the degree to which a generalist predator's feeding rate is reduced by a specific prey species (Fig. 5.5). They also confirm the prediction that even only a few dominant prey species can cause a reduction in a predator's feeding rate on species contributing only weakly to the predator's level of saturation. Importantly, prey contributions to the saturation of a predator's functional response are not additive: The feeding rates of generalist predators are both less reduced (higher μ_i values) and reduced to more similarly degrees (lower variation in μ_i) when a given proportion of their population is feeding, than are those of more specialist predators at the same feeding activity level (Fig. 5.5a). Additional prey in a predator's diet therefore do more than simply diffuse the strength of a its interaction with any specific prey species. Diet richness itself, however, has a much weaker effect on a predator population's saturation level than does its overall feeding activity level.

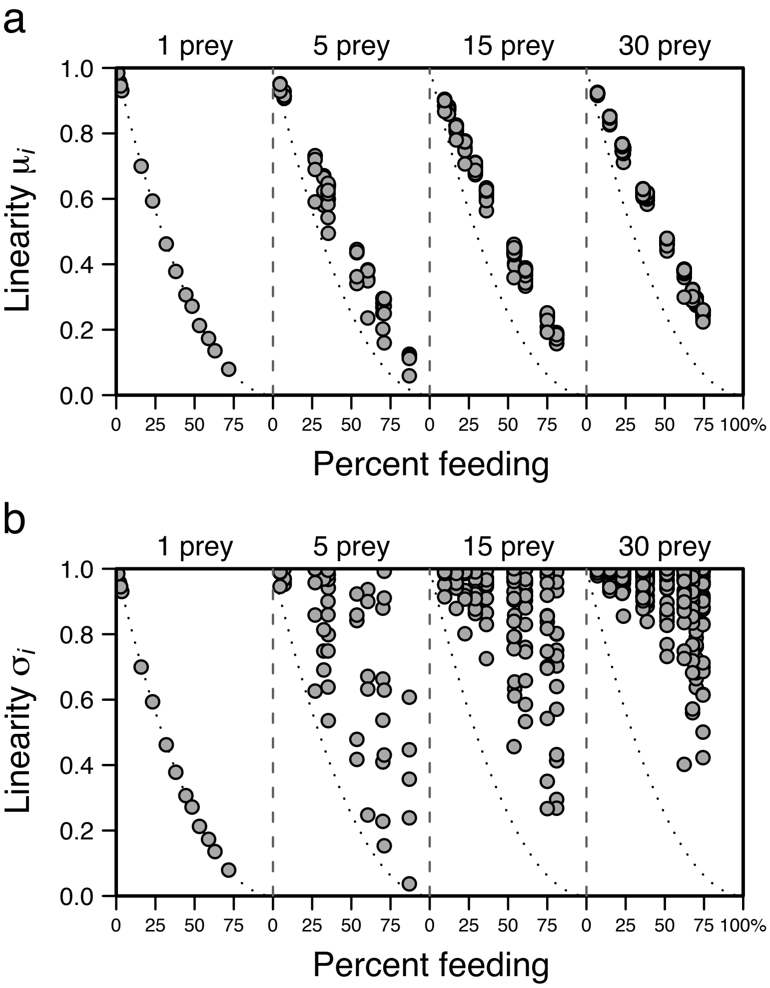

Figure 5.5. The degree to which a predator population's feeding rate is reduced by the saturating effects of its prey species depends upon the proportion of the population that is feeding at any given time (0-100%), and the number of prey species in the predator's diet. (a) Multispecies linearity index reflecting the degree to which a predator's maximal feeding rate on each of its prey species is reduced, and (b) the single-species linearity index reflecting each prey species' contribution to the predator's saturation level. Dashed line is the analytical expectation for specialist predator feeding on a single prey species (Appendix 5.B). Note that $\mu_{\mathrm{i}} = \sigma_i$ for a specialist predator.

THE STABILITY OF GENERALIST PREDATOR-PREY INTERACTIONS

In the previous two sections I have shown that the feeding rates of New Zealand's predatory whelks are reduced by the saturating effects of their prey, and that this nonlinearity in whelk functional responses is affected by the diet richness and the feeding activity level of their populations. A key question remains: how does this nonlinearity affect predator-prey interactions in terms of the predator's control of prey abundance and the stability of the interaction? It has long been appreciated that the saturating nature of the single-species Type II functional responses exhibited by whelks cannot contribute to the stability of a specialized predator-prey interaction (Hassell and May 1973, Oaten and Murdoch 1975, see also Katz 1985). In fact, sufficiently high attack rates and handling times (low μ_i and σ_i values) lead to predator-prey dynamics with populations fluctuating through time in limit cycles rather than tending towards a stable point equilibrium (Rosenzweig 1971, Kot 2001).

I suggest that the feeding on alternative prey increases the range of attack rates that permit stable point equilibrium dynamics. In this section I offer theory to support this assertion and ask whether the observed nonlinearity in whelk functional responses is strong enough to generate limit cycles in the dynamics of their predator-prey interactions.

The boundary conditions for feasible and stable dynamics

To address this question I used a phase-plane analysis of an empirically parameterized extension of the classic Rosenzweig-MacArthur model (Rosenzweig and

MacArthur 1963). My extension more realistically describes the natural history of a specific focal interaction – the predation by *Haustrum scobina* on *Xenostrobus pulex* mussels – by including predation upon multiple prey species and density-independent immigration in the focal prey.

Predator dynamics of this model are described by

$$\frac{dP}{dt} = \frac{e(cN_i + q)P}{1 + chN_i + Q} - mP, \tag{5.6}$$

such that the predator of density P feeds on a focal prey of density N_i with per capita attack rate c and handling time h. The predator has a linear numeric response that converts prey to predators with efficiency e, and dies at rate m. Substituting $q = \Sigma_{k \neq i}\, c_k N_k$ and $Q = \Sigma_{k \neq i}\, c_k h_k N_k$, I reduce the dimensionality of this system by assuming that the density of alternative prey is fixed (see also van Baalen et al. 2001). Prey dynamics are described by

$$\frac{dN_i}{dt} = I + rN_i - \alpha N_i^2 - \frac{cN_i P}{1 + chN_i + Q}, \tag{5.7}$$

where I is the prey's density-independent immigration rate, r is its intrinsic growth rate, and α is its per capita self-limitation rate.

Isoclines of this system are given by

$$N^* = \frac{d(1 + Q) - eq}{c(e - dh)} \tag{5.8}$$

for the predator, and by

$$P^* = \frac{(1 + chN + Q)(I + rN - \alpha N^2)}{cN} \tag{5.9}$$

for the prey. Figure 5.6 illustrates the three regions in which these two isoclines may intersect to produce qualitatively different predator-prey dynamics (Rosenzweig 1971). Two regions occur where population abundances reach stable point equilibria (occurring where the predator isocline intersects the prey isocline at points where it exhibits a negative slope). These flank a third region in which populations fluctuate in periodic limit cycles (occurring where the predator isocline intersects the prey isocline at points with a positive slope). Whereas the hump-shaped nature of the prey isocline (Eq. 5.9) is the key feature of predator-prey interactions having saturating functional responses (Rosenzweig 1969), the leftmost stable region at low prey abundances is caused by the 'refuge' the prey is afforded from predation by its density-independent immigration rate (*cf*. Rosenzweig and MacArthur 1963). This "bottom-up" control of stability (Rosenzweig 1971, van Baalen et al. 2001) is not of relevance to the following argument (Appendix 5.C).

Hopf bifurcation boundaries between regions of stable point equilibria and limit cycles occur where Eq. 5.8 intersects Eq. 5.9 and

$$\frac{\partial P^*}{\partial N} = h(r - 2\alpha N) - \frac{(\alpha N^2 + I)(1 + Q)}{cN^2} = 0 \, . \tag{5.10}$$

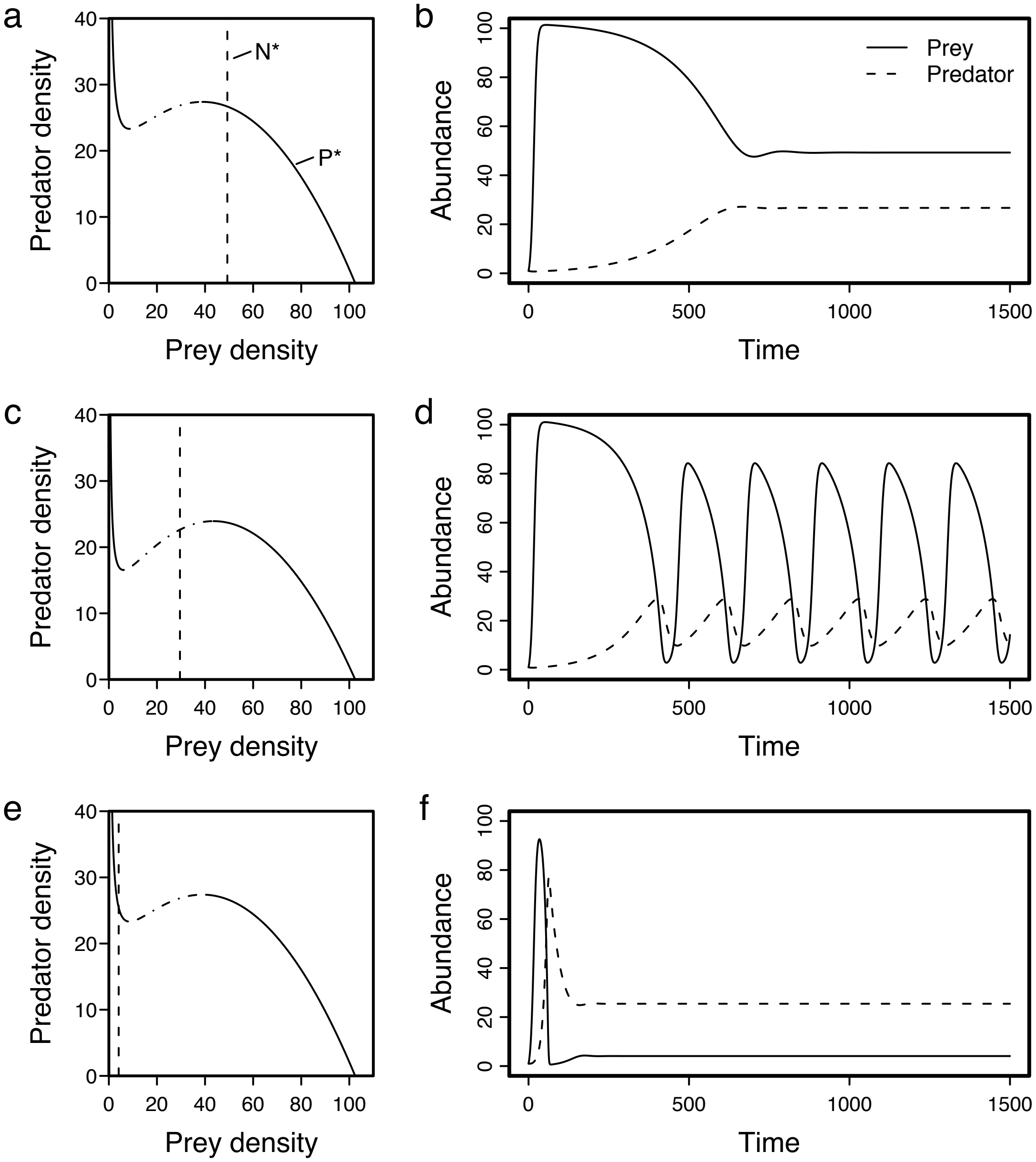

Figure 5.6. Hypothetical examples of predator-prey zero-growth isocline intersections and their associated population dynamics illustrating the regions of stable point equilibria (solid P^*) and limit cycles (dash-dot P^*). Parameter values: (a-b) $I = 0.5$, $r = 0.2$, $a = 0.002$, $h = 3.5$, $c = 0.03$, $m = 0.055$, $e = 0.25$, $q = 0.1$, $Q = 1$, (c-d) $c = 0.05$, (e-f) $e = 0.6$.

The relevant right boundary (i.e., the top of the P* hump) is identified when

$$\frac{\partial^2 P^*}{\partial N^2} = \frac{2I(1+Q)}{cN^3} - 2\alpha h < 0 \,. \tag{5.11}$$

Predator-prey dynamics will thus exhibit both a stable point equilibrium and a feasible predator abundance (i.e., $P > 0$) when

$$\hat{P}^* < N^* < \check{P}^*, \tag{5.12}$$

where the boundary of a feasible predator abundance is

$$\check{P}^* = \frac{r + \sqrt{4\alpha I + r^2}}{2\alpha} \tag{5.13}$$

(i.e., the prey's carrying capacity), and the right-hand boundary between regions of stable point equilibria and limit cycles is

$$\hat{P}^* = \frac{1}{24ach}\left((-4(a(1+Q)-chr)) + \frac{2(1+i\sqrt{3})(a(1+Q)-chr)^2}{\tau^{1/3}} + 2(1-i\sqrt{3})\tau^{1/3}\right), \tag{5.14a}$$

where

$$\tau = a^3(1+Q)^3 + 3ac^2h^2r^2(1+Q) - c^3h^3r^3 - 3a^2ch(1+Q)(-18chI + r(1+Q)) + 6\sqrt{3}\sqrt{\upsilon} \tag{5.14b}$$

and

$$\upsilon = a^2c^2h^2I(1+Q)\omega \tag{5.14c}$$

and

$$\omega = a^3(1+Q)^3 + 3ac^2h^2r^2(1+Q) - c^3h^3r^3 - 3a^2ch(1+Q)(-9chI + r(1+Q)) \,. \tag{5.14d}$$

Numerical analyses indicate that the feeding on alternative prey increases the range of attack rates on a focal prey that satisfy Eq. 5.12 for the focal predator-prey interaction (Appendix 5.C).

The nonlinearity and predicted dynamics of the whelk-mussel interaction

There appears to be no simple way to express both stability and feasibility criteria in terms of the linearity indices (i.e., substituting μ_i for both c and h terms simultaneously). I therefore parameterized the model for the *Haustrum-Xenostrobus* interaction using the species-specific estimates of abundances, attack rates, handling times directly (Table 5.1). Prey immigration and self-limitation rates were estimated by experiments conducted in the high shore zone of two sites (see *Chapter III* for details). *H. scobina*'s predation on *Xenostrobus* at these two sites are among the most nonlinear of the predator-prey interactions observed in the New Zealand system (see Fig. 5.2). The predator's conversion efficiency was set to a value typical for muricid whelks (see *Chapter IV*). I then set N^* equal to the prey's mean density to solve Eq. 5.8 for the predator's death rate, and set P^* equal to the predator's mean density to solve Eq. 5.9 for the prey's growth rate.

Despite the saturating nature of *H. scobina*'s functional response on *Xenostrobus* mussels, the empirically parameterized model predicts that the dynamics of the interaction between *H. scobina* and the mussels will remain effectively linear at both sites and will return to a stable point equilibrium following a perturbation (Fig. 5.7).

Table 5.1. Summary of model parameters and their empirical values estimated for the interaction of *Haustrum scobina* and *Xenostrobus pulex* at Tauranga Head (TH) and Cape Foulwind (CF).

Parameter	**Symbol**	**Value**		**Source**
		TH	**CF**	
Predator density	P	42.97	88.81	*Chapter IV*
Prey density	N_i	4771.44	6112.02	*Chapter IV*
Attack rate on N_i	c	1.574×10^{-5}	7.266×10^{-6}	*Chapter IV*
Handling time on N_i	h	1.341	1.725	*Chapter IV*
$\sum_{k \neq i} (c_k N_k)$	q	2.722×10^{-1}	3.114×10^{-1}	*Chapter IV*
$\sum_{k \neq i} (c_k h_k N_k)$	Q	1.611×10^{-1}	1.658×10^{-1}	*Chapter IV*
Predator conversion efficiency	e	0.25	0.25	*Chapter IV*
Prey immigration rate	I	4.621×10^{-2}	7.832×10^{-2}	*Chapter III*
Prey self-limitation	α	2.750×10^{-8}	7.644×10^{-8}	*Chapter III*
Prey growth rate	r	6.576×10^{-4}	9.738×10^{-4}	See main text
Predator death rate	m	6.881×10^{-2}	7.160×10^{-2}	See main text

Sensitivity analyses indicate, furthermore, that dynamics would remain stable even after an approximately three to five-fold increase in *H. scobina*'s attack rate on *Xenostrobus* (Fig. 5.8a-b). *H. scobina*'s attack rate would have been large enough to induce limit cycles at Tauranga Head, however, had all individuals been observed feeding on *Xenostrobus* mussels (Fig. 5.8c-d). I determined this effect of diet specialization by repeating the above analyses after calculating *H. scobina*'s attack rate on mussels under the hypothetical situation that all feeding individuals had been observed feeding on *Xenostrobus* only (Table 5.2).

Table 5.2. Summary of hypothetical parameter estimates for the interactions of *Haustrum scobina* and *Xenostrobus pulex* at Tauranga Head (TH) and Cape Foulwind (CF) had all feeding individuals been observed feeding on *Xenostrobus* only. In reality, *H. scobina* was observed feeding on 8 species at Tauranga Head and 7 species at Cape Foulwind, with a respective average of 20.7% and 19.4% of their populations having been observed feeding (*Chapter IV*). The additional parameters not listed here are unchanged from Table 5.1.

Parameter	**Symbol**	**Value**	
		TH	**CF**
Attack rate on N_i	c	4.128×10^{-5}	2.298×10^{-5}
$\sum_{k \neq i} (c_k N_k)$	q	0	0
$\sum_{k \neq i} (c_k h_k N_k)$	Q	0	0
Prey growth rate	r	1.525×10^{-3}	2.097×10^{-3}
Predator death rate	m	3.895×10^{-2}	2.826×10^{-2}

DISCUSSION

In this chapter I have used empirically estimated interaction strengths from the food webs of six intertidal whelk populations to address three paradoxes persisting in our understanding of how saturating functional responses affect the dynamics of predator-prey interactions. Two of these paradoxes relate to the persistence of predator-prey interactions that conflict with their destabilizing functional form. The third concerns the paradoxical observation that experimental predator manipulations often affect linear responses in prey despite the nonlinear nature of their predator-prey interactions. My results thereby also speak to the empirical estimation of the strength of predator-prey interactions in general.

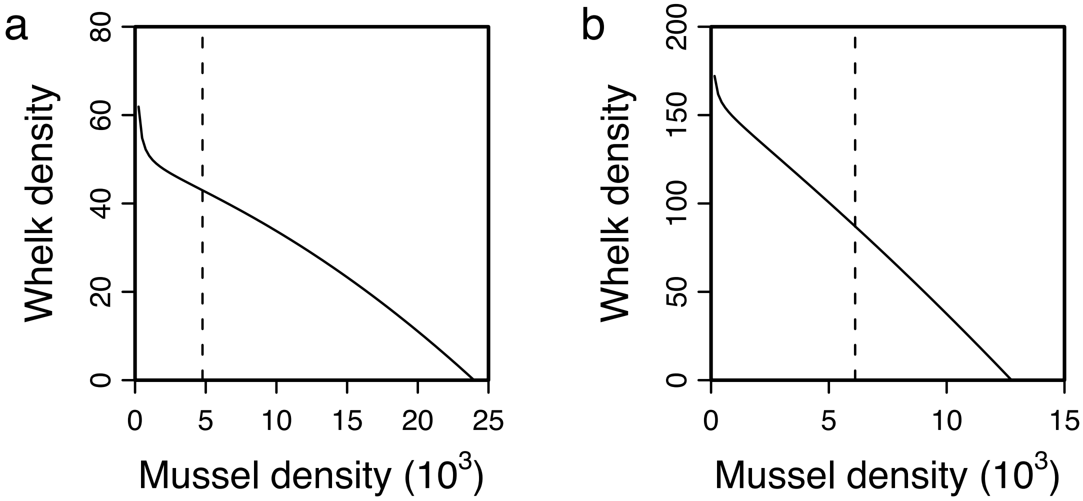

Figure 5.7. Zero-growth isoclines of the model parameterized with empirical data for the *Haustrum scobina – Xenostrobus pulex* interactions at (a) Tauranga Head and (b) Cape Foulwind. *H. scobina*'s feeding rate on alternative prey is sufficiently high that the region of limit cycles has disappeared, with the peak of the prey-isocline having merged into the region of stable point equilibria resulting from the prey's density-independent immigration refuge (see Appendix 5.C).

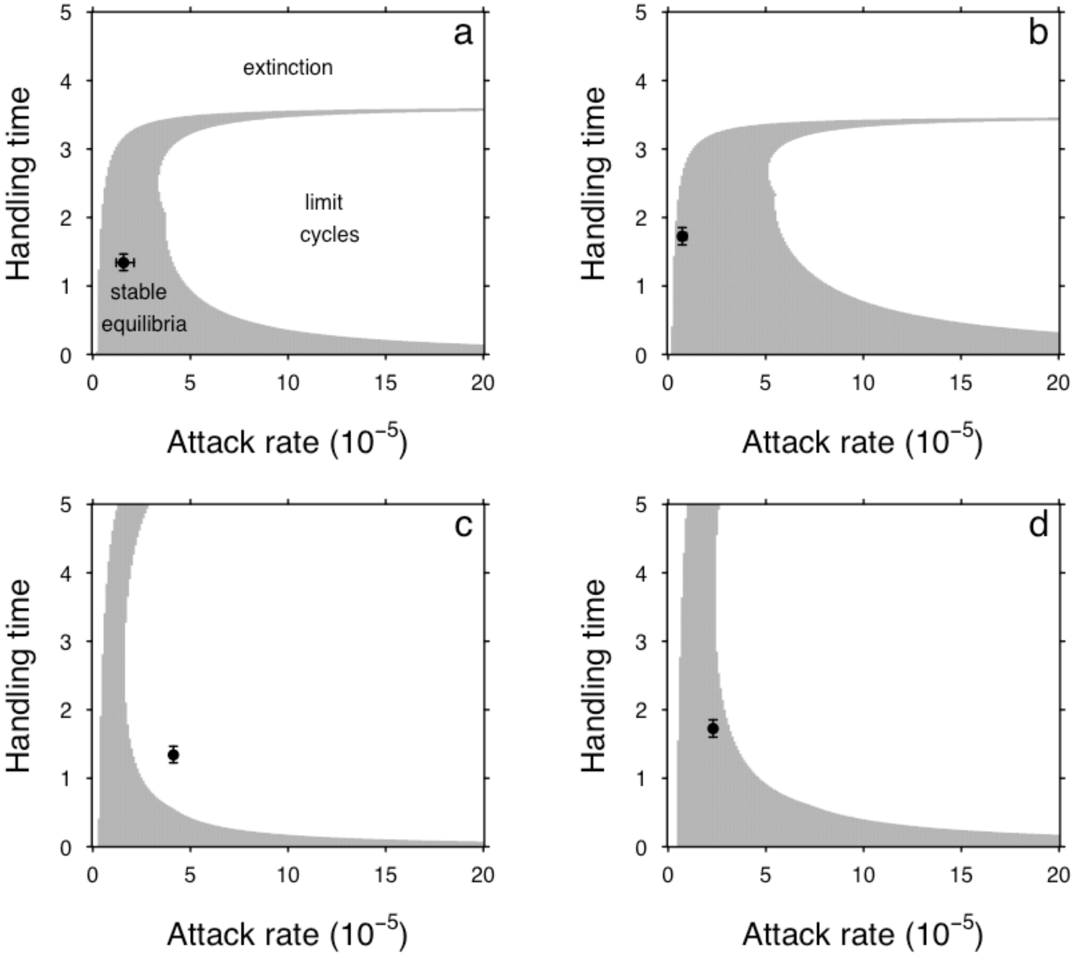

Figure 5.8. Handling time and per capita attack rate combinations leading to stable point equilibria, limit cycles, and predator extinction for the empirically parameterized model of the focal *Haustrum scobina-Xenostrobus pulex* interactions at (a) Tauranga Head and (b) Cape Foulwind, and for a hypothetically specialized *Haustrum scobina-Xenostrobus pulex* interaction at (c) Tauranga Head and (d) Cape Foulwind. Points indicate the empirically estimated mean handling times and per capita attack rates (a-b), and the empirically estimated handling times and hypothetically calculated per capita attack rates had all feeding *H. scobina* been observed feeding on *Xenostrobus* (c-d) with bootstrapped 95% confidence intervals. Y-axes reflect empirical range of handling times (in days) observed across all prey species. Per capita attack rates in units of prey eaten pred^{-1} prey^{-1} m^{-2} day^{-1}.

Estimating interaction strengths in nature

I have shown that the feeding rates of whelks are indeed reduced by the saturating effects of their prey, but that the contributions of particular prey species to this nonlinearity cannot be predicted by knowing either prey abundances, handling times, or a predator's prey preferences alone (Fig. 5.2). Using simulations I then confirmed that the degree to which a predator's feeding rates are saturated with respect to any particular prey species is related directly to the diversity of its diet (Figs. 5.3-5.5). These simulations indicate, however, that the feeding rates of specialized predators are likely to be more reduced on their prey species than are the feeding rates of generalist predators because the saturating contributions of additional prey species do not contribute to the predator's saturation in an additive manner (Fig. 5.5).

The implications of these results are that any attempts to dissect the nonlinear strength of predator-prey interactions by experimentally varying the abundance of isolated prey species (e.g., most references reviewed by Jeschke et al. 2004) will not obtain estimates that can be generalized to the interactions of food webs in nature. The same is true for observational field studies (e.g., Middlemas et al. 2006) that seek to estimate the strength and form of specific predator-prey interactions by correlating the diet of spatially or temporally separated predator populations with the local abundance of a prey species when differences in the abundance of alternative prey are not also considered simultaneously. Species that individually contribute little to the diet of a generalist predator may collectively reduce the predator's feeding rate on a preferred prey, while a dominant prey may limit a predator's feeding rates on rarely observed prey but go unrecognized because it has shorter handling times or the predator shows only an intermediate level of preference for it.

The linear response paradox

Despite the observation that the feeding rates of whelks can become saturated (Appendix 5.A, Murdoch 1969, Katz 1985, Moran 1985, Rodrigues 1986), my data indicate that most prey contribute only weakly to the nonlinearity of their predator's functional response (Fig. 5.2). Under natural conditions, even the most saturating of prey species reduce their predator's feeding rates by less than 38%. The question presented by these data was whether whelk functional responses are thereby made nonlinear enough to generate a nonlinear response of prey populations to an experimental predator manipulation.

The phase-plane analyses of *Section III* suggest that even one of the most saturating of prey species for *Haustrum scobina*, the mussel *Xenostrobus pulex*, will respond to an experimentally manipulated change in the equilibrium abundance of its predator in a manner that is very near linear (Fig. 5.7). This result is more clearly illustrated by hypothetical press experiments (sensu Bender et al. 1984) of *H. scobina*'s populations (Fig. 5.9), and explains the observation made in *Chapter III* that model-selection criteria favor models that describe the experimentally manipulated dynamics of

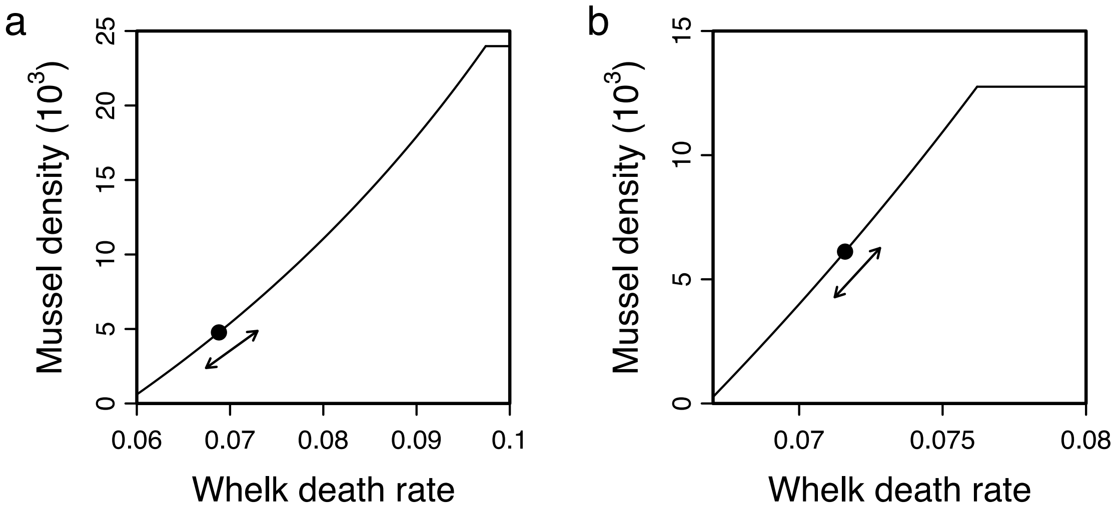

Figure 5.9. Predicted near-linear changes in the equilibrium abundance of *Xenostrobus pulex* mussels following hypothetical press manipulations of their focal predator, *Haustrum scobina*, as affected by experimental changes in the predator's per capita death rate at (a) Tauranga Head, and (b) Cape Foulwind. Sufficiently high death rates would cause the extinction of the predator allowing prey populations to reach their carrying capacity. Points indicate the empirical mussel densities and whelk death rates estimated for each site.

the *H. scobina – Xenostrobus* interaction in a linear manner over models that do so in a nonlinear manner.

It is important to note, however, that these conclusions regarding the near-linear consequences of community manipulations are less likely to apply to experimental manipulations of the prey species. This is because my analyses have assumed the numerical response of the predator to be linear (i.e., *e* is density-independent). While this assumption may indeed be appropriate at the mean prey densities experienced in the field, there will exist threshold minimum prey densities at which predator feeding rates are insufficient to satisfy individual metabolic and reproductive demands (Lawton et al. 1975). Only experimental manipulations maintaining prey abundances above these thresholds are predicted to affect linear changes in the equilibrium abundance of a predator population.

The stability of predator-prey interactions

By empirically parameterizing a model describing the interactions between two focal whelk populations and their dominant mussel prey, I predicted that these interactions would exhibit stable point equilibrium dynamics (Fig. 5.7). Numerical sensitivity analyses indicate that the stability of these interactions should be robust to significant variation in *H. scobina*'s attack rates on *Xenostrobus* that is greater in range than that observed empirically (Fig. 5.8).

The mechanism by which *H. scobina*'s otherwise cyclic dynamics with *Xenostrobus* is stabilized is via *H. scobina*'s feeding on alternative prey. The addition of alternative prey to the diet of a predator reduces the predator's feeding rate on the focal prey (Fig. 5.3, see also McCann et al. 1998), but also increases the degree to which a predator's functional response is saturated by a smaller amount than would an equivalent increase in its feeding rate on the focal prey (Fig. 5.5) and reduces the size of the parameter space with respect to the focal prey in which predator-prey limit cycles would occur (Figs. 5.7-5.8 and 5.C.2). Negative covariance in the dynamics of prey species (Murdoch and Oaten 1975, McCann 2000) is not required for this mechanism to occur. In fact, the mechanism should hold as long as alternative prey abundances do not covary positively, but instead vary independently enough that their combined abundance does not exhibit significant decreases over time. Intuitively, a more generalist diet should include fewer prey exhibiting such positive covariance (Murdoch et al. 2002, Romanuk et al. 2006).

Since the predator-independent prey population parameters (i.e., immigration, growth, and self-limitation rates) undoubtedly differ among prey species and across sites, the conclusions regarding the dynamics of the *H. scobina* – *Xenostrobus* interaction need not apply to all other interactions of the New Zealand system as well. Nevertheless, 14 of the 15 most saturating interactions observed between whelks and their prey are with prey that also have planktonic larval stages that immigrate to the shore when settling (Graham 1941, Pilkington 1974, Goldstien et al. 2006). This suggests that the model-structure

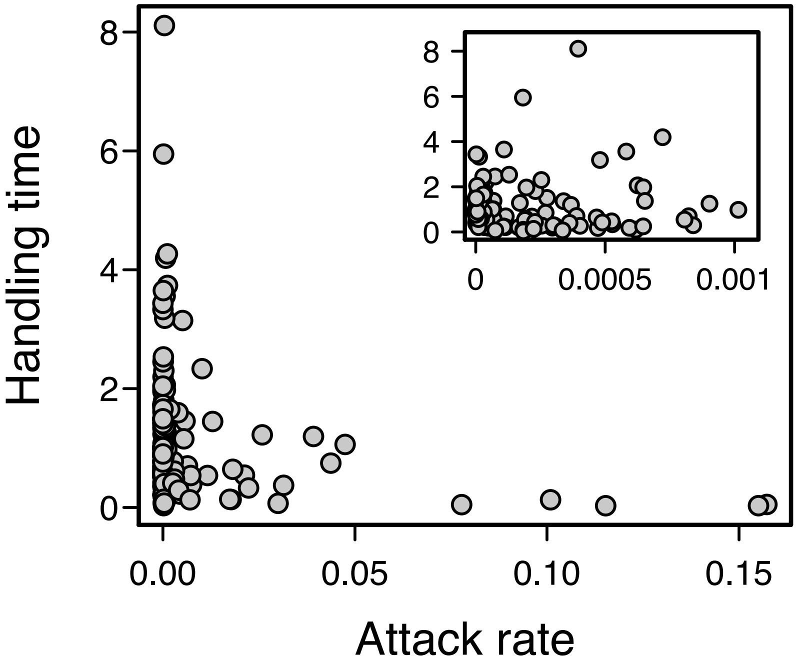

Figure 5.10. Empirical relationship between the species-specific handling times (days) and the per capita attack rates (prey eaten pred^{-1} prey^{-1} m^{-2} day^{-1}) of whelks feeding on their prey (*n* = 181). Inset shows details of the relationship at low attack rates.

itself is generally appropriate. Furthermore, a generally triangular relationship between handling times and per capita attack rates is evident among all empirically estimated interactions (Fig. 5.10) mirroring the relationship between these variables that is necessary for stable point equilibrium dynamics to occur within the *H. scobina* – *Xenostrobus* interaction (Fig. 5.8). Relevant also, is the fact that *H. scobina*'s populations at the two focal study sites exhibit the most specialized of diets observed in the New Zealand system, with > 96% of feeding events observed being represented by only two prey species (33-40% *Xenostrobus pulex* and 60-67%% *Chamaesipho columna*, *Chapter IV*). This suggests an increased likelihood that the stabilizing mechanism of alternative prey is active among the other, more generalized, whelk populations as well.

CONCLUSION

My results suggest that the stabilizing mechanisms encapsulated by the sigmoidal shape of the Type III functional responses may not be necessary to explain the persistence and lack of cyclic dynamics of generalist predator-prey interactions in nature. The dynamics of predator-prey populations interacting with multispecies Type II functional responses may also exhibit stable point equilibria. This is not to say that the effects of prey refuges, predator learning, switching between prey species, and the many other mechanisms that can lead to Type III functional responses are unimportant, for the data and analyses used here have assumed that these do not to occur *a priori* even though they are known to occur in whelks specifically (e.g., Murdoch 1969, West 1986, 1988, Burrows and Hughes 1991, Hughes and Burrows 1991, Sanford et al. 2003). Rather, my results echo the conjecture that generalist predators are more decoupled from the dynamics of their prey species and are thereby less prone to cyclic predator-prey dynamics than their specialist counterparts (Murdoch et al. 2002). Diversity thereby promotes the stability of food webs when predators forage as generalists (MacArthur 1955).

ACKNOWLEDGMENTS

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APPENDIX 5.A: THE NONLINEAR FORM OF WHELK FUNCTIONAL RESPONSES

Intertidal whelks have repeatedly exhibited saturating Type II rather than Type III functional responses (sensu Holling 1959) to density manipulations of their focal prey (Murdoch 1969, Katz 1985, Moran 1985, Rodrigues 1986). A valid criticism that has been applied to many such experimental studies, however, is that prey manipulations have included too few treatments at low prey densities to effectively distinguish between the shape of Type II and Type III responses (e.g., Sarnelle and Wilson 2008). I therefore conducted two mesocosm experiments using *Haustrum haustorium* to evaluate the shape of its single-species functional response at low prey densities.

Both experiments proceeded as follows: Forty *H. haustorium* of 40-50 mm shell length were distributed into ten ~100 liter plastic aquaria (1.46 m^2 surface area) with flowing filtered seawater. After 24 hours, *Diloma aethiops* – a trochid gastropod often found in *H. haustorium*'s diet throughout New Zealand's shores – between 10-15 mm shell length, were placed into the aquaria at 5, 10, 15, 30, 45, 70, 100, 130, 160, and 220 individuals per aquarium. Both *H. haustorium* and *Diloma* had been collected from in front of the Edward Percival Field Station, Kaikoura. Both experiments ran for 29 days, over the course of which all consumed prey were replaced on at least a weekly basis. Some prey escaped their aquaria, but the total number of individuals remaining at the end of experiment was within 2 individuals (10%) of the target number per aquarium. The first experiment started on May 26th, 2007. Water temperatures measured on a half-hour basis using iButton® temperature loggers (Maxim Integrated Products, CA) ranged between 9-15°C, decreasing steadily over the course of the month. The second experiment began on June 25th, 2007. Water temperatures varied between 6-11°C.

The results indicate that the feeding rate of *H. haustorium* individuals clearly became increasingly saturated as the density of their *Diloma* prey increased, and did so following a Type II functional response rather than a Type III response (Fig. 5.A.1). Feeding rates appeared to be temperature-dependent, with fewer *Diloma* being consumed in the second of the two experiments. As a result, the saturation of *Haustrum*'s functional response was not significant in the second experiment; a saturating response did not fit to the data better than a linear response ($F = 2.47$, $P = 0.16$).

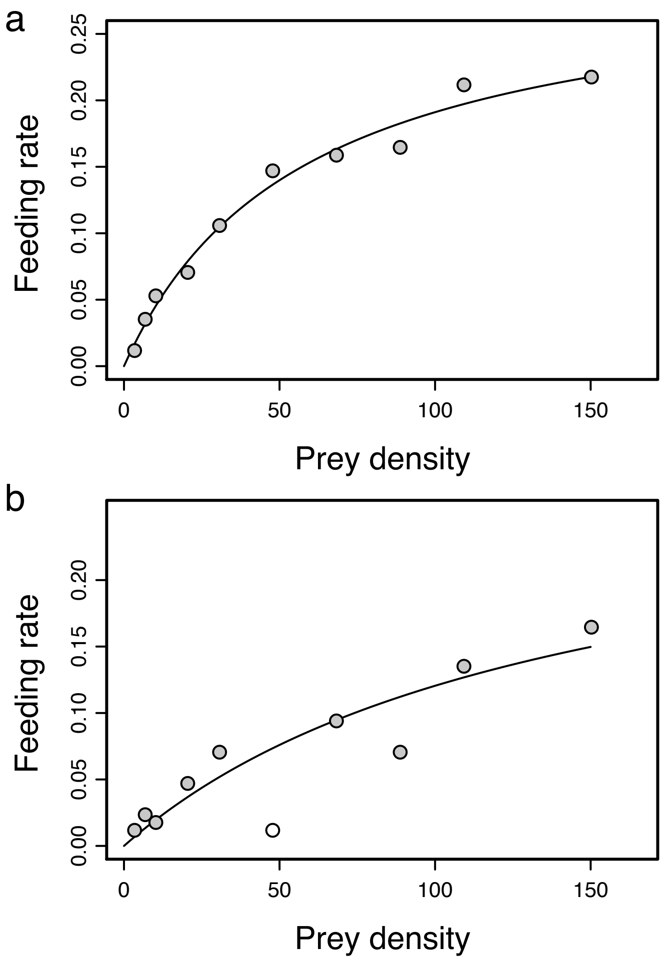

Figure 5.A.1. The single-species functional response of *Haustrum haustorium* feeding on *Diloma aethiops* in the (a) first and (b) second mesocosm experiment. (Density: m^{-2}; Feeding rate: prey eaten predator^{-1} m^{-2} day^{-1}.) Curves fit by nonlinear least squares regression of a Michaelis-Menten function, $y = \beta_1 x / 1+\beta_2 x$, after removing a single outlier treatment (indicated by open-circle) in the second experiment. (a) $\beta_1 = 5.222 \times 10^{-3}$ ($P < 0.001$), $\beta_2 = 1.733 \times 10^{-2}$ ($P < 0.001$); (b) $\beta_1 = 2.057 \times 10^{-3}$ ($P > 0.018$), $\beta_2 = 7.071 \times 10^{-3}$ ($P = 0.22$).

APPENDIX 5.B: ANALYTICAL EXPECTATION FOR A SPECIALIST POPULATION'S SATURATION LEVEL

Consider that an increase in the attack rate or handling time of a specialist predator *j* feeding on one prey species will increase the number of individuals in its population feeding at any given instant in time (its feeding activity level, A_j). If 100% of the population is feeding, increases in the abundance of the prey could elicit no further increase in the population's feeding rate such that it would be completely saturated ($\mu_i = \sigma_i = 0$).

To see how the specialist predator's level of saturation is expected to change as a function of the proportion of it's population that is feeding, substitute Eq 5.5. into Eq. 5.4, and note that for a specialist predator $F_{ij} = F_j = 1$, to obtain

$$\sigma_i = \frac{1}{\left(1 + \frac{1}{1 - A_j}\right)^2}. \tag{5.B.1}$$

No such simple expression relating the μ_i of a generalist predator to its population's feeding activity level exists because F_{ij} and A_{ij} are dependent upon all $c_{ij}h_{ij}N_i$ in concert.

APPENDIX 5.C: PARAMETER-DEPENDENT EFFECTS ON MODEL STABILITY BOUNDARY

Numerical analyses of Eq. 5.12-5.14 suggest that sufficient decreases in the focal prey's immigration and self-limitation rates, or sufficient increases in its growth rate, can cause the dynamics of an interaction at a once stable point equilibrium (i.e. when predator and prey isoclines intersecting to the right of the P^* hump) to cross a Hopf bifurcation boundary and exhibit limit cycles (Fig. 5.C.1). This is not surprising given the strong control that bottom-up processes typically have on stability (Rosenzweig 1971, Kot 2001). Sufficient increases in the predator's attack rate and conversion efficiency, or decreases in death rate, will also cause limit cycles (Fig. 5.C.1, see also Hassell and May 1973, Murdoch and Oaten 1975). The effect of the focal prey's handling time, however, is dependent upon the magnitude of the predator's attack rate (Fig. 5.C.2a). Sufficiently low or sufficiently high handling times permit point stability with higher attack rates than do handling times of intermediate magnitude.

Analyses also indicate that alternative prey increase the range of attack rates on a focal prey that permit stable point equilibria (Fig. 5.C.2b-d). The range of handling times and attack rates permitting stable point equilibria is increased by an increase in the predator's attack rate on alternative prey (or by increasing their abundance, Fig. 5.C.2c), or by an increase in the predator's handling time on alternative prey (Fig. 5.C.2d). Increases in either alternative prey parameters cause the position of the right stability boundary to move towards the left at a faster rate than does the left stability boundary when the sum of alternative prey handling times exceeds one unit of time. The region of limit cycle dynamics thereby disappears with sufficiently high feeding rates on the alternative prey (*cf*. Fig. 5.C.1j) irrespective of the prey's density-independent immigration rate. (In a model without prey immigration, the region of limit cycles would not disappear entirely, but would be increasingly reduced in size.) Nevertheless, increased feeding on alternative prey also increases the minimum permissible attack rate on the focal prey and the maximum permissible handling time on the focal prey which avoid predator extinction (Fig. 5.C.2).

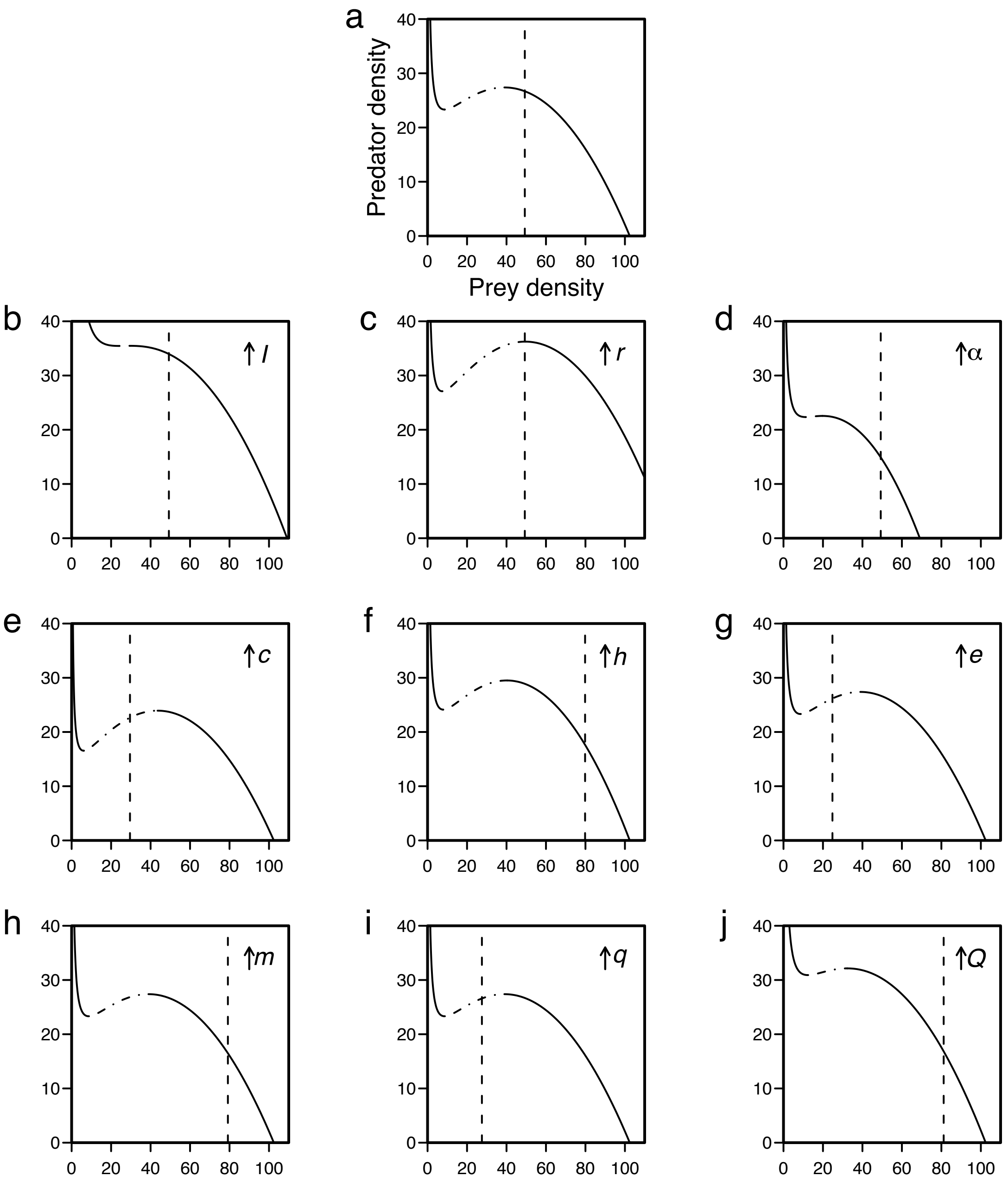

Figure 5.C.1. Effects of prey and predator parameter values on the intersection of predator and prey zero-growth isoclines illustrated at (a) the baseline parameter set of Fig. 6a ($I = 0.5$, $r = 0.2$, $\alpha = 0.002$, $h = 3.5$, $c = 0.03$, $m = 0.055$, $e = 0.25$, $q = 0.1$, $Q = 1$), and after an increase in the prey's (b) immigration rate, $I = 2$, (c) growth rate, $r = 0.24$, (d) self-limitation rate, $\alpha = 0.003$, or the predator's (e) per capita attack rate, $c = 0.05$, (f) handling time, $h = 3.9$, (g) conversion efficiency, $e = 0.3$, (h) death rate, $m = 0.06$, (i) attack rate on alternative prey, $q = 0.25$, holding Q constant, and (j) handling time on alternative prey, $Q = 2$, holding q constant.

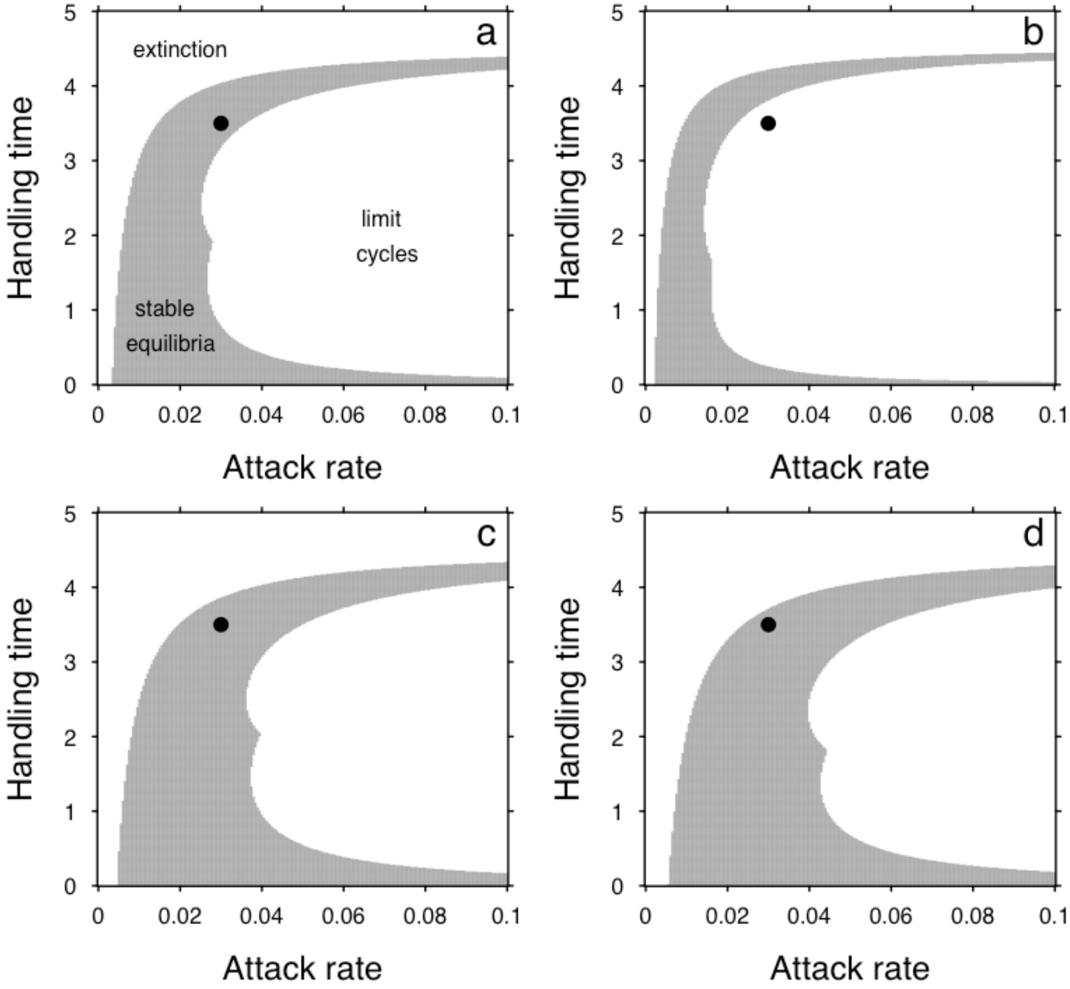

Figure 5.C.2. Attack rate and handling time combinations on the focal prey leading to stable equilibria, limit cycles, and predator extinction for (a) the hypothetical baseline parameter set (see Fig. 6a.), (b) given the cessation of feeding on alternative prey ($q = Q = 0$, c and h unchanged), and after a doubling of the predator's (c) attack rates ($q = 0.2$) and (d) handling times ($Q = 20$) on the alternative prey. Baseline attack rate and handling time on focal prey remain unchanged, and are shown as a point of reference.

APPENDIX 5.D: ASSESSING THE IMPORTANCE OF POST-INGESTION DIGESTION RATES

The observational method of measuring the per capita strength of trophic species interactions proposed by Novak and Wootton (2008) assumes that post-ingestion digestion times do not preclude a predator's ability to search for new prey. In many species these digestion times can be larger, and be more limiting to feeding rates, than the ingestion times (i.e. observable handling times) (Jeschke et al. 2002). Such significant post-handling digestion times would render the application of the observational method as currently proposed invalid.

Several lines of evidence suggest that post-ingestion digestion rates do not limit the feeding rates of intertidal whelks as can their handling times. First among these, is that most digestion of prey tissue occurs during prey handling and ingestion (Boggs et al. 1984) and commences prior to reaching the stomach (Hughes 1986). Second, direct experimental evidence suggests that while prey antigens can remain detectable in whelk stomachs for up to 27 days, stomachs in which prey antigens are detectable are typically already empty after much less than a days time after feeding (Fisher 2008, J. Fisher, *pers. comm.*). Third, the experimental evidence presented in *Chapter III* suggests that application of the observational method can produce accurate estimates of species-specific per capita attack rates despite the fact that it does ignore post-ingestion digestion times.

A fourth line of more direct evidence suggesting that post-ingestion digestion times do not limit feeding rates comes from the laboratory handling time experiments described in *Chapters III* and *IV*. In these experiments I paired individual *Haustrum* spp. whelks with several individuals of a potential prey species to monitor, on an hourly basis, the time that whelks of a given size took to handle prey individuals of a given size at three different temperatures. During these experiments, feeding events frequently began or concluded during the 6-8 hours of the night when hourly monitoring was not conducted, leaving many handling times poorly unconstrained (720 of 1819 feeding events). Whelks and prey individuals were often not replaced when this occurred, but continued to be monitored for a second feeding event. In 70 of these situations representing 14 different prey species, both the conclusion of the first feeding event and the start of the second feeding event were well constrained (both the end- and start-time within a window of 1/10th of a day) and ≥ 80% of the first prey tissue had been consumed.

I used these 70 observations in a multiple-regression to test the hypothesis that post-handling digestion times limit the rate at which whelks are able to feed on their prey. I did so by regressing the time between feeding events on the dried tissue weight of the whelk and its first prey (estimated using species-specific allometric relationships between dry tissue weight and shell length; M. Novak*, unpubl. data*) and temperature, with all variables log-transformed. A significant effect of predator- or prey body size would be evidence suggesting that gut-fullness (i.e., digestion rate) contributed to the speed at which whelks commenced feeding after a meal. A significant negative effect of temperature would, furthermore, provide evidence to suggest that increased metabolic demands reduce the time that whelks spend *not* foraging (i.e. “resting”, Bayne and Scullard 1978).

Results do not support the hypothesis that digestion rates contribute to the rate at which whelks commence feeding. Neither predator- nor prey body size had a significant effect on the time that whelks spent between feeding events (Fig. 5.D.1a-b). Digestion times are thus unlikely to limit the rate at which whelks feed. Temperature did, however, have a weak but significant effect on the time that whelks took between feeding events (Fig. 5.D.1c). Temperature should, therefore, be taken into account not only in the estimation of field handling times using laboratory experiments, but in future spatiotemporal comparisons of attack rates directly as well.

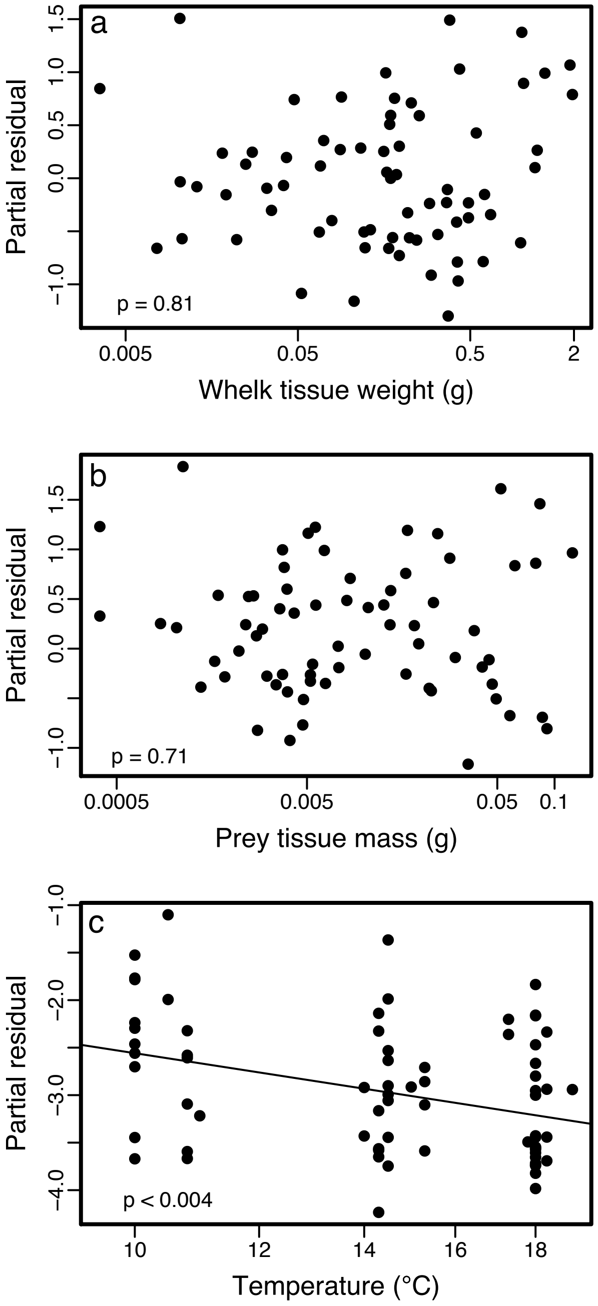

Figure 5.D.1. Partial residual plots demonstrating the contributions of (a) whelk size (b) prey size, and (c) temperature to explaining the time taken by *Haustrum* spp. whelks to commence feeding on a second prey item after a previous feeding event. Axes are log-scaled.

CHAPTER VI

CONCLUSIONS AND FUTURE DIRECTIONS

The research presented in this dissertation primarily addresses two elements of food webs that add significantly to their complexity: the presence of trophic omnivores and the nonlinear nature of predator-prey interactions. Previous efforts to gain insight into the empirical importance of these food web features have largely been hampered by the challenges of measuring the species-specific strengths of trophic interactions in species-rich systems. Logistically feasible methods that can account for the indeterminacy of omnivorous indirect effects and the saturating functional responses that predators exhibit are needed.

In this dissertation, I introduced and tested a new observational method that overcomes these food web complexities (*Chapter II*). I showed that this method worked remarkably well at estimating the species-specific per capita attack rates of a classic Type II functional response predator: intertidal whelks (*Chapter III*). This is the only method to date that has successfully estimated the nonlinear per capita strength of trophic interactions in species-rich and reticulate food webs. In the future, I hope to generalize the method's applicability by addressing two of its main assumptions: that predators consume only one prey item at a time, and that post-ingestion digestion times do not preclude a predator's ability to search for new prey. Although I showed that these assumptions are not violated by New Zealand's whelk populations (*Chapter III* and *V*), this is not true for many other predators (e.g., Polis and Strong 1996 , Jeschke et al. 2002). An extension of this method to eliminate these assumptions will be especially useful because it requires little more logistical field effort than does the reconstruction of a food web's topology in the first place, thus could deepen our understanding of food webs across multiple systems.

Using this new method, I then tested two key predictions of intraguild predation theory by investigating how species abundances, food web structure and species interactions strengths change across six omnivorous food webs situated along a strong gradient of productivity present around New Zealand's coastline (*Chapter IV*). Although the predictions of intraguild predation theory were generally not supported, my data revealed clear and unidirectional cross-gradient shifts in both the structure and interaction strengths of the food webs. My analyses suggested that adaptive and optimal foraging behavior, as well as competitive and facilitative interactions among basal prey species, may play an important role in structuring omnivorous food webs and that future theory may be able to account for these observed discrepancies by incorporating these empirical processes into modeling efforts.

Empirical food webs are complex, and incorporating additional interactions among basal species into core intraguild predation models will further increase model-complexity by orders of magnitude. In *Appendix E*, I outline an approach for reducing this complexity that uses Loop Analysis to generate testable qualitative hypotheses explaining empirical patterns.

In the future, I also hope to investigate the ability of optimal foraging theory to explain the cross-gradient changes observed in New Zealand's food webs. Petchey and colleagues (2008), for example, have recently suggested that much of the structural variation observed in food webs can be explained by optimal foraging theory. Their analyses, however, used interaction strengths as freely varying parameters, fitted to their model to maximize its concordance with observed web topologies. The data obtained in *Chapter IV* will provide a more direct empirical test of optimal foraging theory's predictive ability.

A key component of optimal foraging theory is the energetic benefit that predator's derive from consuming their prey. Two related variables – the biomass- and numeric conversion efficiencies by which predators respectively convert consumed prey into somatic growth and offspring production – are crucial components in the study of predator-prey dynamics and food webs as a whole (Sterner and Elser 2002). Despite this, I have come to realize over the course of my dissertation work that these key components are woefully understudied empirically. Though conversion efficiencies were considered more often by empirical ecologists in the past (e.g., Odum 1957, Paine 1965), and are implicit within the emerging subdiscipline of ecological stoichiometry (Sterner and Elser 2002), food web ecologists nevertheless still (i) typically use biomass conversion efficiencies to parameterize models where numeric conversion efficiencies are needed,

(ii) assume that conversion efficiencies are linear (see also Abrams and Ginzburg 2000), (iii) have little knowledge of how biomass- and numeric conversion efficiencies relate to each other (Lawton et al. 1975), and (iv) have little empirical data on what the more easily measured biomass conversion efficiencies are in all but the most simple of food webs and at the coarsest of taxonomic resolutions (e.g., Moore et al. 1993, Jennings and Blanchard 2004, parasitoid communities may be the best exception). For example, in *Chapter IV* I assumed that all prey-weight-corrected species conversion efficiencies were equal, and used the median value of biomass conversion estimates made by handful of other studies of predatory whelks as a proxy for their numeric conversion efficiency. I felt justified in doing so because in the New Zealand system this assumption was conservative with respect to the theoretical predictions I was testing; the two *Haustrum* species are unlikely to have radically different conversion efficiencies; and variation in relative carbon and nitrogen contents was minimal across prey species (Fig. 6.1).

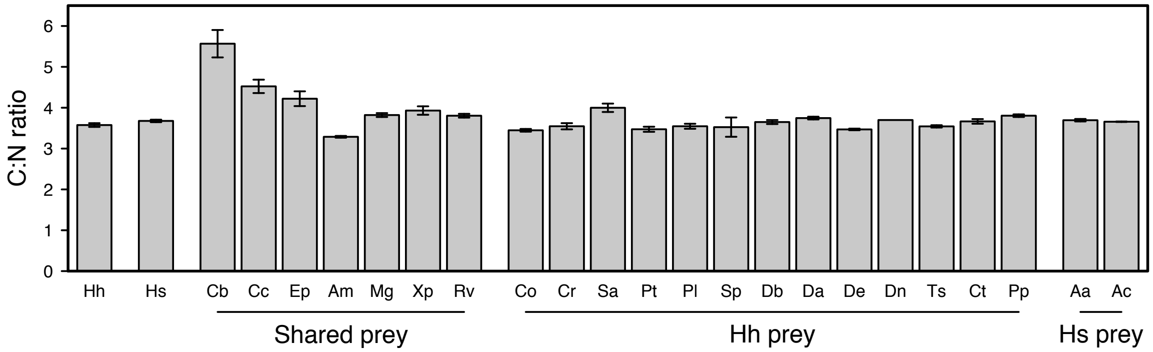

Figure 6.1. Mean ratio of carbon and nitrogen (± 95% CI) in tissues of species collected at Tauranga Head. See Table 4.3 for species-name abbreviations. Muscle tissue for all species, except mussels (Am, Mg, Xp; whole tissue) and barnacles (Cb, Cc, Ep; include cirri, which may have artificially raised C content). *n* = 5 - 8 for all but Hh (21), Hs (11), Dn (1), and Ac (2). Cb Cc, Rv, Aa, and Ac samples are of five pooled individuals each.

I believe, however, that our theory of species-rich food webs will require much better knowledge of empirical conversion efficiencies if it is to attain the predictive power we seek.

Furthermore, our inferences on the stability of predator-prey dynamics, which I addressed in *Chapter V*, are directly dependent upon the conversion efficiency values used to parameterize mathematical models. In this chapter, I used the attack rate, handling time, and prey abundance data from all six food webs studied in *Chapter IV* to determine the degree to which whelk feeding rates are saturated (i.e. nonlinear) with respect to the density of their prey. I showed that feeding rates are generally not strongly saturated and that most prey species contribute little to their predator's saturation. By extending the classic Rosenzweig-MacArthur model of predator-prey interactions (Rosenzweig and MacArthur 1963) and parameterizing this model with empirical estimates from *Chapters III* and *IV*, I then showed that the degree to which whelks are saturated is not nonlinear enough to cause their population dynamics to fluctuate in limit cycles. In doing so, however, I again assumed that conversion efficiency had linear functional forms, were equivalent to biomass conversion efficiencies, and assumed a fixed constant across all prey species with a value derived from the median observation of a handful of other whelk studies. Increased estimates of *H. scobina*'s conversion efficiency would have changed the inferred value of *H. scobina*'s death rate and may have concomitantly increased the likelihood of inferring limit cycles in its dynamics (see

Fig. 5.C.1). In the future, I intend to investigate how uncertainty in these and other parameter estimates may have affected this chapter's conclusions.

The mechanism by which generalist predators can stabilize the dynamics of their food webs (introduced in *Chapter V*) should nonetheless be generalizable. Specifically, I showed that increasing diet richness has a non-additive effect on a predator's saturation such that the addition of alternative prey has a stabilizing effect on predator-prey dynamics when predator's forage with multispecies Type II functional responses. This mechanism is interesting because it does not rely on density-dependent prey-switching (sensu Murdoch 1969) as is commonly assumed (Murdoch et al. 2002, Romanuk et al. 2006), or an extrinsically driven negative covariance in prey dynamics (Murdoch and Oaten 1975, McCann 2000). It thereby provides an alternative explanation for the empirical lack of consumer-resource driven cycles observed among generalist predators in nature (Murdoch et al. 2002, Romanuk et al. 2006), as well as the observation that most predators exhibit single-species Type II functional responses (Jeschke et al. 2004) despite these being otherwise destabilizing (Hassell and May 1973, Murdoch and Oaten 1975).

Many other patterns are also evident in the New Zealand data of interaction strengths but were not addressed in this dissertation. Predator:prey body size ratios, for example, are widely known to be important determinants of the structure and dynamics of food webs (Woodward et al. 2005), and are clearly important in determining the diets of whelk individuals (Fig. 6.2). Body size information is being used with increasingly

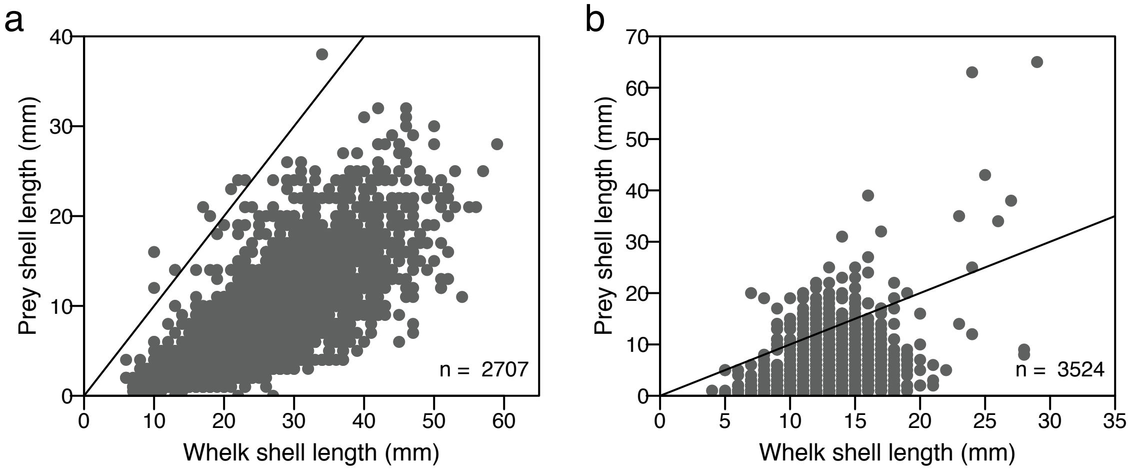

Figure 6.2. New Zealand-wide variation in predator:prey body size ratios for (a) *Haustrum haustorium* and (b) *H. scobina*. Lines indicate 1:1 ratio. Largest *H. scobina* prey are North Island oysters, *Crassostrea gigas*.

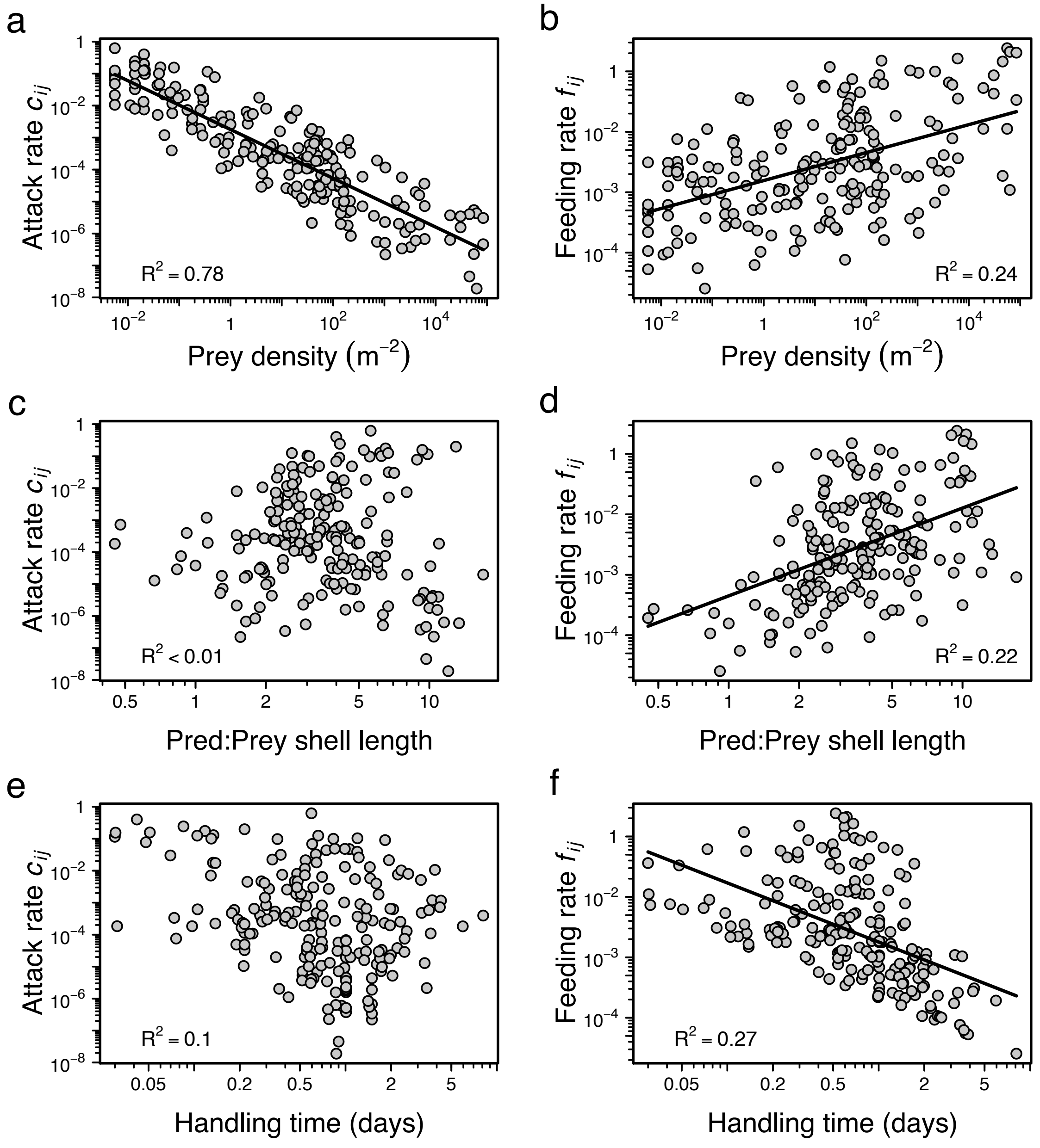

Figure 6.3. Relationships between species-specific per capita attack rates and feeding rates and (a-b) prey densities, (c-d) predator:prey body size ratios, and (e-f) prey handling times, as estimated across all focal study sites. Regression lines shown where significant, though these do not account for the lack of independence within sites and predator populations.

frequency to parameterize models of predator-prey interactions (e.g., Yodzis and Innes 1992, Emmerson and Raffaelli 2004), but the empirical relationships between body size, abundance, and interaction strengths remain poorly understood (Wootton and Emmerson 2005). My own data suggest a strong log-linear relationship between per capita attack rates and prey abundances, but no log-linear relationships between attack rates and body size ratios or handling times (Fig. 6.3). Further, they indicate significantly and equally predictive relationships between feeding rates and abundances, body sizes, and handling times (Fig. 6.3). In the future, I intend to explore these relationships in more detail to inform future food web parameterizations and better understand their implications.

In summary, I have introduced a new method with which to gain insight into the complexity of species-rich food webs and have used this method to link theory with empirical data to understand how omnivores and the nonlinear nature of predator-prey interactions can affect both the structure and dynamics of food webs. My dissertation thereby contributes to our growing understanding of the processes regulating ecological communities. I hope that such an understanding will actually make a difference under the coming U.S. administration of Barack Obama!

APPENDIX A

NEW ZEALAND-WIDE VARIATION IN WHELK BODY-SIZES

INTRODUCTION

In this appendix I provide summary statistics of the size of *Haustrum haustorium* and *H. scobina* individuals in populations located around New Zealand. Individual size measurements were obtained by a combination of systematic surveys and anecdotal observations made between 2004 and 20007 at the six focal study sites and during 2004 at a further 45 sites located primarily on the North Island..

Table A.1. Variation in the size (shell height, mm) of *Haustrum haustorium* individuals at sites located around New Zealand from systematic surveys and anecdotal observations made in 2004-7.

Coast	Region	Site	Northing*	Easting*	Mean	SD	Min	Max	n
North Island West	North Cape	Tapotupotu Bay West	6751887	2484669	26.2	7.2	13	45	72
North Island East	North Cape	Tapotupotu Bay East	6751826	2485006	40	9.5	24	52	23
North Island East	East Auckland	Leigh Goat Island Reserve	6546417	2672801	37.1	9.3	26	56	22
North Island East	East Auckland	Leigh Waterfall and Penny's Rocks[P]	6546417	2672801	30.7	10.2	9	62	1062
North Island East	East Auckland	Leigh Echinoderm Reef[P]	6546353	2671698	23.2	8.5	10	50	72
North Island East	East Auckland	Leigh Tabletop Rocks	6546278	2672484	26.1	8.2	12	52	268
North Island East	East Auckland	Leigh Shadow Rocks	6546108	2673073	31.3	6.7	17	53	102
North Island East	East Auckland	Tungutu Point	6520092	2664820	27.9	8.8	13	50	73
North Island East	East Auckland	Red Beach[P]	6509773	2663367	38.8	8.1	17	54	37
North Island East	East Auckland	Rangitoto Island White Beach[P]	6490161	2674072	33.5	12	9	59	131
North Island South	Southern Taranaki Bight	Opunake	6193622	2583053	35.2	11.9	14	59	72
North Island East	Wairarapara	Pourere Tuingara Point	6111500	2839250	13.1	8.2	5	49	244
North Island East	Wairarapara	Castle Point Cave	6029083	2782166	28.1	5	8	43	218
North Island East	Wairarapara	Castle Point Boulders	6028987	2782099	33.7	8.8	16	53	64
North Island South	Wellington	Pukerua Bay	6018152	2668575	24.4	8.2	8	45	53
North Island South	Wellington	Wairaka Point	6017849	2667259	36.1	9.7	22	60	11
North Island South	Wellington	Hongoeka Bay	6013352	2665796	34.2	7.5	20	46	16
North Island South	Wellington	Whitireia Park Point	6011392	2665284	31.4	9.5	17	45	10
North Island South	Wellington	Kau Point	5989259	2663603	27.6	7.7	19	43	14
North Island South	Wellington	Moa Point	5983009	2661399	36.7	13.3	9	56	31

* Site location coordinates provided in New Zealand Map Grid datum. Mapping and conversion utilities are available at http://www.nztopoonline.linz.govt.nz/ and http://www.linz.govt.nz/apps/coordinateconversions/index.html.

[P] Surveyed by R.T. Paine in 1968-9, *pers. comm.*

Table A.1. Variation in the size of *Haustrum haustorium* individuals, continued.

Coast	Region	Site	Northing*	Easting*	Mean	SD	Min	Max	n
North Island South	Wellington	Quarry Bay East	5982755	2656332	34	7.3	23	43	8
North Island South	Wellington	Island Bay Lab Rocks	5982714	2657671	38.4	9.5	8	58	88
North Island South	Wairarapara	Matakitakiakupe Cape Palliser	5952472	2699526	33	12.1	9	65	134
South Island West	Westland	Cape Foulwind NW Platform	5938940	2382452	35.7	8.7	19	51	27
South Island West	Westland	Cape Foulwind	5938210	2381793	31	7.7	10	58	2094
South Island West	Westland	Tauranga Bay North	5936796	2381603	38.5	5.3	26	48	25
South Island West	Westland	Tauranga Head	5935850	2381578	26	6.5	8	53	4747
South Island West	Westland	Tauranga Head West	5935555	2381244	30.7	9.8	9	52	192
South Island West	Westland	Tauranga Head South Boulders	5935526	2381404	35.1	11.2	22	48	8
South Island West	Westland	Tauranga Head SW	5935514	2381323	35.1	7.8	17	47	23
South Island West	Westland	Charleston Joyce Bay	5921552	2380143	23.8	10	11	53	110
South Island East	Cape Campbell	Ward Beach	5928089	2608283	33.7	5.2	25	41	12
South Island East	Kaikoura	Rakautara	5882637	2576996	29.2	10.2	1	59	3898
South Island East	Kaikoura	Memorial Garden Rocks	5866764	2566404	23.6	10.9	6	52	1071
South Island East	Kaikoura	Whakatu Point	5865651	2568129	31.1	11.5	15	46	19
South Island East	Kaikoura	EPFS Lab Rocks	5865540	2567382	28.2	9.2	13	64	99
South Island East	Kaikoura	Avoca Point North	5865446	2568244	32.1	12.1	12	52	53
South Island East	Kaikoura	Lighthouse Reef	5864581	2569000	34.5	11.7	20	58	15
South Island East	Kaikoura	First Bay	5864336	2568788	35.5	8.9	11	53	262
South Island East	Kaikoura	Limestone Bay Point	5864282	2566550	32.1	10.2	12	62	352
South Island East	Kaikoura	Intertunnel-North	5861690	2557071	40.7	10.7	18	56	35
South Island East	Kaikoura	Raramai	5860822	2555403	29.1	11	7	53	44
South Island East	Kaikoura	Duffs Knob North	5860341	2554859	28.2	10.3	9	55	40
South Island East	Kaikoura	Kie Kie	5859738	2554286	32.3	10.6	8	50	429
South Island East	Kaikoura	Paia Point	5859204	2554140	22.1	10.7	4	57	5349

Table A.1. Variation in the size of *Haustrum haustorium* individuals, continued.

Coast	Region	Site	Northing*	Easting*	Mean	SD	Min	Max	n
South Island East	Kaikoura	Paia Point	5859204	2554140	22.1	10.7	4	57	5349
South Island East	Kaikoura	Otumatu Rock	5858017	2553518	34.8	6.9	26	47	9
South Island East	Kaikoura	Oaro South	5853593	2551499	29.1	13.2	9	54	59
South Island Southwest	Haast	Jackson Head NW	5685027	2158339	36.5	2.9	32	40	6
South Island Southwest	Haast	Jackson Head	5684298	2157576	30.9	8.2	8	60	3194
South Island Southwest	Haast	Okahu Point	5684243	2157425	31	8	8	55	2987
South Island West	Westland	Smoothwater Bay South	5683285	2156287	38.3	7.1	28	48	7

Note: No surveys were conducted south of Oaro on the east coast, or south of Smoothwater Bay on the west coast.

Table A.2. Variation in the size (shell height, mm) of *Haustrum scobina* individuals at sites located around New Zealand from systematic surveys and anecdotal observations made in 2004-7.

Coast	Region	Site	Northing*	Easting*	Mean	SD	Min	Max	n
North Island West	North Cape	Tapotupotu Bay West	6751887	2484669	16.9	2.3	14	21	9
North Island West	North Cape	Te Werahi North	6751503	2481366	18.4	2.2	15	23	23
North Island East	East Auckland	Tungutu Point	6520092	2664820	27.1	3.1	23	31	12
North Island East	East Auckland	Rangitoto Island White Beach^{P}	6490161	2674072	21.0	6.2	11	27	6
North Island East	Wairarapara	Pourere Tuingara Point	6111500	2839250	14.4	3.1	7	20	23
North Island South	Wellington	Kau Point	5989259	2663603	26.8	1.7	23	30	16
North Island South	Wellington	Shelly Bay	5988098	2662151	26.6	4.8	20	37	14
North Island South	Wellington	Moa Point	5983009	2661399	16.9	2.8	10	22	32
North Island South	Wellington	Island Bay Lab Rocks	5982714	2657671	18.4	3.2	15	24	8
South Island West	Westland	Cape Foulwind NW Platform	5938940	2382452	17.2	4.7	9	21	5
South Island West	Westland	Cape Foulwind	5938210	2381793	12.5	2.7	2	24	3131
South Island West	Westland	Tauranga Head	5935850	2381578	12.5	2.7	3	28	2670
South Island East	Cape Campbell	Ward Beach	5928089	2608283	13.6	3.0	10	19	10
South Island East	Kaikoura	Rakautara	5882637	2576996	12.3	2.1	6	19	1748
South Island East	Kaikoura	Blue Duck	5880618	2573680	14.9	4.0	5	23	67
South Island East	Kaikoura	Whakatu Point	5865651	2568129	14.5	3.5	9	20	41
South Island East	Kaikoura	Avoca Point North	5865446	2568244	11.6	2.1	6	18	59
South Island East	Kaikoura	Lighthouse Reef	5864581	2569000	13.9	1.5	10	17	52
South Island East	Kaikoura	First Bay	5864336	2568788	12.5	1.6	9	15	21
South Island East	Kaikoura	Limestone Bay Point	5864282	2566550	16.8	1.1	15	19	13

Table A.2. Variation in the size of *Haustrum scobina* individuals, continued.

Coast	Region	Site	Northing*	Easting*	Mean	SD	Min	Max	n
South Island East	Kaikoura	Paia Point	5859204	2554140	12.3	2.4	5	25	4612
South Island East	Kaikoura	Oaro South	5853593	2551499	12.4	2.0	9	14	12
South Island Southwest	Haast	Jackson Head	5684298	2157576	12.1	2.2	3	21	2905
South Island Southwest	Haast	Okahu Point	5684243	2157425	12.5	2.5	5	20	2230

Note: A lack of *H. scobina* data at sites for which *H. haustorium* data are presented in Table A.1 does not indicate the absence of *H. scobina* from these sites.

APPENDIX B

SITE LOCATIONS, SURVEY DATES, AND MEAN MONTHLY TEMPERATURES

INTRODUCTION

In this appendix I provide location information for the six focal study sites and sites from which whelks and prey were collected for laboratory-based handling time experiments and for determining species-specific allometric relationships. I also provide summary information on the time periods during which abundance, size-frequency, and feeding surveys were conducted at the six focal study sites. Finally, I provide mean monthly temperatures that were measured using temperature loggers placed in the low shore zone of each focal site.

Table B.1. Locations of focal study and collection sites.

Site name	Abbreviation	Coast	Location
Tauranga Head	TH	Northwest	41°46′26″ S, 171°27′20″ E
Cape Foulwind	CF	Northwest	41°45′09″ S, 171°27′31″ E
Okahu Point	OP	Southwest	43°57′55″ S, 168°36′16″ E
Jackson Head	JH	Southwest	43°57′53″ S, 168°36′23″ E
Paia Point	PP	East	42°28′24″ S, 173°32′12″ E
Rakautara	Rk	East	42°15′38″ S, 173°48′43″ E
EPFS Rocks	ER	East	42°24′55″ S, 173°41′50″ E
Lighthouse Reef	LR	East	42°25′26″ S, 173°43′01″ E
Intertunnel	IT	East	42°27′07″ S, 173°34′08″ E
EPFS sea-table	ST	East	Open to natural recruitment

Table B.2. Time periods during which species abundance and size-frequency surveys were conducted at each site.

PP	Rk	OP	JH	TH	CF
5/30-5/31 & 8/16-8/20, 2005	7/25-7/26 & 8/6, 2005	-	-	5/22-5/25 & 7/22, 2005	6/23-6/24 & 7/21-7/23, 2005
2/5-2/6, 2006	2/4-2/6, 2006	2/25-3/2, 2006	2/27-3/3, 2006	1/29-2/2, 2006	1/30-2/3, 2006
6/16-6/23, 2006	6/18-6/24, 2006	7/12-7/17, 2006	7/11-7/17, 2006	5/26-5/30, 2006	5/24-5/29, 2006

Table B.3. Time periods during which systematic feeding surveys were conducted at each site.

PP	Rk	OP	JH	TH	CF
-	-	-	-	7/1, 2004	7/1, 2004
6/3-8/20, 2005	7/27-8/22, 2005	-	-	5/24-7/22, 2005	7/21-7/23, 2005
2/7-2/15, 2006	2/4-2/20, 2006	2/25-3/4, 2006	2/27-3/4, 2006	1/29-2/2, 2006	1/30-2/3, 2006
6/17-6/26, 2006	6/11-6/27, 2006	7/12-7/17, 2006	7/10-7/16, 2006	5/27-5/31, 2006	5/24-5/29, 2006
1/29-2/26, 2007	1/30-2/27, 2007	2/16-2/21, 2007	2/15-2/22, 2007	2/6, 2007	2/1-2/23, 2007
7/4-7/13, 2007	7/3-7/9, 2007	6/12-6/14, 2007	6/11-6/16, 2007	5/15, 2007	5/14 & 718, 2007

Table B.4. Monthly mean site-specific temperatures (°C, air and water combined) with standard deviation given in parentheses.

Year	Month	Site					
		PP	**Rk**	**OP**	**JH**	**TH**	**CF**
2005	July	-	-	-	-	12.2 (0.4)	12.2 (0.3)
2005	Aug.	12.7 (4.9)	13.8 (4.7)	-	-	12.1 (0.8)	12.2 (0.7)
2005	Sept.	10.5 (0.9)	10.7 (0.5)	-	-	13.0 (1.1)	12.9 (0.9)
2005	Oct.	12.0 (2.3)	11.9 (1.6)	-	-	13.9 (1.7)	13.7 (1.8)
2005	Nov.	14.5 (2.1)	14.3 (1.1)	-	-	14.9 (1.6)	14.4 (1.5)
2005	Dec.	15.6 (2.6)	15.5 (1.2)	-	-	17.2 (1.5)	16.9 (1.9)
2006	Jan.	16.4 (2.1)	16.2 (1.0)	-	-	15.3 (1.4)	14.8 (1.7)
2006	Feb.	16.3 (1.6)	16.5 (0.9)	13.1 (1.4)	16.4 (2.4)	16.2 (1.3)	15.7 (1.5)
2006	March	15.1 (1.2)	15.4 (0.9)	13.9 (1.6)	12.3 (2.1)	15.0 (1.0)	14.8 (1.1)
2006	April	14.2 (1.0)	14.9 (0.7)	15.4 (0.8)	13.7 (0.6)	16.1 (0.9)	16.1 (0.8)
2006	May	12.4 (0.9)	12.8 (1.0)	14.5 (1.3)	12.9 (0.9)	14.9 (0.9)	15.0 (0.9)
2006	June	10.2 (1.5)	10.7 (1.4)	13.0 (1.4)	11.4 (1.0)	13.0 (1.3)	13.5 (1.3)
2006	July	9.2 (0.8)	9.5 (0.4)	12.1 (1.3)	10.4 (1.0)	12.0 (0.7)	12.2 (0.7)
2006	Aug.	8.9 (1.0)	9.2 (0.7)	11.7 (1.4)	10.1 (0.9)	11.9 (0.9)	12.0 (1)
2006	Sept.	10.2 (1.7)	10.4 (1.0)	12.1 (0.9)	10.4 (0.8)	12.6 (0.7)	12.5 (0.7)
2006	Oct.	11.4 (1.9)	11.6 (0.8)	12.4 (1.2)	10.7 (0.9)	12.8 (0.9)	12.7 (0.9)
2006	Nov.	13.2 (1.7)	13.3 (1.2)	12.5 (1.3)	10.6 (1.2)	13.9 (1.3)	13.6 (1.7)
2006	Dec.	14.1 (1.9)	14.1 (1.3)	13.2 (1.3)	11.2 (1.0)	13.9 (1.4)	13.6 (1.7)
2007	Jan.	15.5 (2.3)	15.4 (1.3)	15.8 (1.4)	13.8 (1.2)	16.3 (1.5)	15.8 (1.7)
2007	Feb.	16.2 (2.4)	16.1 (1.5)	14.6 (2.0)	14.3 (2.0)	17.1 (1.5)	16.5 (1.8)
2007	March	16.2 (2.3)	16.4 (1.4)	12.5 (1.7)	14.9 (1.7)	15.7 (1.8)	15.4 (2.2)
2007	April	14.2 (1.5)	14.3 (1.1)	11.0 (1.4)	13.4 (1.4)	14.1 (1.0)	13.9 (1.1)
2007	May	12.3 (1.0)	12.8 (0.6)	10.9 (0.9)	13.5 (1.0)	14.0 (0.6)	13.7 (0.6)
2007	June	10.4 (1.0)	10.7 (0.9)	9.7 (1.3)	12.3 (1.6)	11.7 (1.4)	11.6 (1.4)
2007	July	9.4 (1.5)	9.6 (1.4)	-	-	10.5 (1.4)	10.2 (1.7)

APPENDIX C

PREDATOR DIETS AND HANDLING-TIME REGRESSION COEFFICIENTS

INTRODUCTION

In this appendix I provide a summary of the frequency by which prey species were observed in the diets of *Haustrum haustorium* and *H. scobina* whelks at each of the six focal study sites, summed across all systematic feeding surveys conducted at these sites. I also provide the weighted regression coefficients relating species-specific handling times to the size of whelk predators, the size of their prey, and temperature which I derived from laboratory experiments.

Table C.1. Frequency by which prey were observed in the diet of *Haustrum haustorium* at focal study sites.

Species	PP	Rk	OP	JH	TH	CF
Acanthochitona zelandica	2	2	-	-	-	-
Atalacmea fragilis	1	-	-	-	-	-
Austrolittorina antipodum	2	1	-	-	-	-
Austrolittorina cincta	6	2	-	-	-	-
Buccinulum sp.	-	-	-	1	-	-
Calantica spinosa	-	1	-	-	-	-
Cantharidella tesselata	4	-	2	-	13	5
Cellana denticulata	23	11	-	-	-	-
Cellana ornata	17	36	76	117	4	31
Cellana radians	3	4	4	2	1	2
Chamaesipho brunnea	10	-	-	-	-	-
Chamaesipho columna	179	37	5	3	113	16
Diloma aethiops	4	3	6	5	2	-
Diloma arida	-	-	2	-	2	-
Diloma bicanaliculata	-	-	4	-	4	3
Diloma nigerrima	1	-	1	-	2	1
Eatoniella sp.	9	-	-	-	-	-
Epopella plicata	5	1	-	1	2	2
Haustrum haustorium	7	1	-	-	-	-
Haustrum lacunosus	1	1	-	-	-	-
Haustrum scobina	4	4	7	7	146	60
Lasaea rubra hinemoa	3	-	-	-	-	-
Margarella sp.	-	-	-	1	7	2
Montfortula chathamensis	1	-	-	-	-	-
Mytilus galloprovincialis	3	-	-	1	1	2
Notoacmea sp. 2spokes	-	-	-	-	1	-
Notoacmea sp. Black	-	-	-	-	3	1
Notoacmea sp. Net	-	-	-	-	1	-
Notoacmea sp. Radialspokes	3	2	-	-	20	-
Notoacmea sp.	-	1	-	-	1	-
Notoacmea daedala	-	1	1	1	-	-
Onithochiton neglectus neglectus	3	4	-	-	-	-

Table C.1. Frequency by which prey were observed in the diet of *Haustrum haustorium*, continued.

Species	**PP**	**Rk**	**OP**	**JH**	**TH**	**CF**
Paratrophon patens	-	-	-	-	8	9
Patelloida corticata	35	105	134	94	70	24
Plaxiphora caelata	5	1	4	6	65	15
Plaxiphora obtecta	1	-	1	2	1	2
Risellopsis varia	80	13	3	1	4	-
Siphonaria australis	64	43	15	11	67	14
Sypharochiton pelliserpentis	2	7	2	-	10	-
Thoristella chathamensis	1	-	-	-	-	-
Trimusculus conicus	-	-	1	-	-	8
Turbo smaragdus	1	5	11	11	1	1
Xenostrobus pulex	4	-	3	1	51	10
Zeacumantus subcarinatus	2	2	-	-	-	-
Unidentified	2	3	1	-	7	-
Feeding	488	291	283	265	607	208
Not Feeding	4356	3532	2694	2892	3785	1627

Table C.2. Frequency by which prey were observed in the diet of *Haustrum scobina* at focal study sites.

Species	PP	Rk	OP	JH	TH	CF
Aulacomya atra maoriana	4	1	3	1	-	-
Austrolittorina antipodum	74	48	17	11	4	-
Austrolittorina cincta	59	107	23	24	3	3
Balanus sp.	1	-	-	-	-	-
Calantica spinosa	5	-	-	-	-	-
Calantica villosa	-	2	-	-	-	-
Cellana denticulata	-	1	-	-	-	-
Chamaesipho brunnea	326	194	-	-	-	1
Chamaesipho columna	300	48	193	377	321	394
Chiton glaucus	1	-	-	-	-	-
Epopella plicata	15	12	4	2	5	13
Lasaea rubra hinemoa	17	1	-	2	-	-
Mytilus galloprovincialis	3	2	7	-	5	5
Notoacmea sp. 2spokes	-	-	-	4	-	-
Notoacmea sp. Net	-	-	1	1	-	-
Notoacmea sp. Radialspokes	2	3	5	15	1	-
Risellopsis varia	12	4	4	2	2	2
Siphonaria australis	-	9	-	2	-	-
Xenostrobus pulex	17	7	199	191	213	191
Feeding	836	439	456	632	554	609
Not Feeding	3775	1308	1773	2273	2116	2522

Table C.3. Weighted multiple regression coefficients relating handling time (days) to whelk and prey size (mm) and temperature (°C)*. Log-transformed mean handling times and standard deviations (σ) are given for combinations with $n < 5$ observations. Collection sites: [1] ES, [2] LR, [3] PP, [4] TH, [5] IT,[6] Rk, [7] ST, [8] CF.

Predator	Prey	β_1	β_2	β_3	β_4	σ	n	R^2	P
Haustrum haustorium[1]	*Acanthochitona zelandica*[1,2]	2.560	-	-	-	0.870	2	-	-
H. haustorium[1]	*Austrolittorina cincta*[1,3]	8.311	-1.784	1.357	-1.143	1.155	68	0.54	<0.001
H. haustorium[1]	*Cantharidella tesselata*[4]	13.241	-2.189	1.056	-1.979	1.559	34	0.58	<0.001
H. haustorium[1]	*Cellana denticulata*[1,2]	9.496	-3.456	2.532	-0.888	1.453	45	0.72	<0.001
H. haustorium[1]	*Cellana ornata*[1,2,3]	8.002	-1.560	1.756	-1.689	1.537	93	0.53	<0.001
H. haustorium[1]	*Cellana radians*[1,2,3]	5.123	-1.518	2.364	-1.642	1.103	41	0.80	<0.001
H. haustorium[3]	*Chamaesipho spp*[5]	3.629	0.175	-0.201	-0.404	5.857	40	0.01	0.918
H. haustorium[1]	*Diloma aethiops*[1]	9.600	-2.458	2.344	-1.506	1.280	69	0.72	<0.001
H. haustorium[1]	*Haustrum scobina*[4]	8.225	-1.321	1.405	-1.381	0.799	77	0.44	<0.001
H. haustorium[1]	*Notoacmea* spp.[1,2,3,4,6]	9.136	-1.927	1.269	-1.535	2.076	73	0.49	<0.001
H. haustorium[1]	*Onithochiton neglectus neglectus*[7]	10.829	-2.583	1.576	-1.109	0.947	47	0.81	<0.001
H. haustorium[1]	*Patelloida corticata*[1,2,3]	8.963	-3.156	1.866	-0.235	2.144	66	0.38	<0.001
H. haustorium[1]	*Plaxiphora caelata*[4]	5.895	-2.283	1.961	0.071	1.507	25	0.42	0.009
H. haustorium[1]	*Risellopsis varia*[1,2,3]	3.949	-0.268	0.825	-0.456	1.143	78	0.09	0.085
H. haustorium[1,3]	*Siphonaria australis*[1,2,5]	6.362	-1.596	2.687	-1.860	1.913	54	0.68	<0.001
H. haustorium[1]	*Sypharochiton pelliserpentis*[1,2,3]	4.410	0.132	0.257	-0.700	1.128	32	0.13	0.248
H. haustorium[1]	*Turbo smaragdus*[1,2]	3.341	0.538	0.670	-0.954	1.350	43	0.15	0.084
H. haustorium[4]	*Xenostrobus pulex*[4]	3.579	-	-	-	0.177	4	-	-
H. scobina[3]	*Austrolittorina cincta*[3]	5.135	-0.423	0.859	-0.850	0.853	37	0.48	<0.001
H. scobina[3]	*Chamaesipho* spp.[5]	8.667	-0.755	1.110	-1.759	2.768	37	0.69	<0.001
H. scobina[3]	*Epopella plicata*[5]	3.186	-	-	-	-	1	-	-
H. scobina[3]	*Lasaea rubra hinemoa*[3]	1.643	-	-	-	-	1	-	-
H. scobina[3]	*Mytilus galloprovincialis*[4]	2.657	-0.539	0.955	0.079	0.421	17	0.67	0.002
H. scobina[3]	*Notoacmea* spp.[3,6]	1.294	-1.228	2.925	-0.162	0.967	30	0.39	0.004
H. scobina[3]	*Risellopsis varia*[2,3,6]	1.791	0.113	0.428	0.068	1.319	40	0.07	0.428
H. scobina[3]	*Xenostrobus pulex*[4]	6.351	-1.106	1.326	-1.152	0.680	45	0.70	<0.001

* $\ln\ h_{ij} = \beta_1 + \beta_2\ \ln L_j + \beta_3\ \ln L_i + \beta_4\ \ln T + \epsilon$

Table C.4. Unmeasured predator-prey combinations to which the handling time regression coefficients of measured predator-prey combinations were matched.

Unmeasured		**Matched to**	
Predator	**Prey**	**Predator**	**Prey**
Haustrum haustorium	*Atalacmea fragilis*	*H. haustorium*	*Cellana radians*
H. haustorium	*Austrolittorina antipodum*	*H. haustorium*	*Austrolittorina cincta*
H. haustorium	*Buccinulum* sp.	*H. haustorium*	*Haustrum scobina*
H. haustorium	*Calantica spinosa*	*H. scobina*	*Xenostrobus pulex*
H. haustorium	*Diloma arida*	*H. haustorium*	*Diloma aethiops*
H. haustorium	*Diloma bicanaliculata*	*H. haustorium*	*Diloma aethiops*
H. haustorium	*Diloma nigerrima*	*H. haustorium*	*Diloma aethiops*
H. haustorium	*Eatoniella* sp.	*H. haustorium*	*Austrolittorina cincta*
H. haustorium	*Epopella plicata*	*H. scobina*	*Epopella plicata*
H. haustorium	*Haustrum haustorium*	*H. haustorium*	*Haustrum scobina*
H. haustorium	*Haustrum lacunosus*	*H. haustorium*	*Haustrum scobina*
H. haustorium	*Lasaea rubra hinemoa*	*H. scobina*	*Lasaea rubra hinemoa*
H. haustorium	*Margarella* sp.	*H. haustorium*	*Diloma aethiops*
H. haustorium	*Montfortula chathamensis*	*H. haustorium*	*Cellana ornata*
H. haustorium	*Mytilus galloprovincialis*	*H. scobina*	*Mytilus galloprovincialis*
H. haustorium	*Notoacmea daedala*	*H. haustorium*	*Cellana radians*
H. haustorium	*Paratrophon patens*	*H. haustorium*	*Haustrum scobina*
H. haustorium	*Plaxiphora obtecta*	*H. haustorium*	*Plaxiphora caelata*
H. haustorium	*Thoristella chathamensis*	*H. haustorium*	*Diloma aethiops*
H. haustorium	*Trimusculus conicus*	*H. haustorium*	*Cellana ornata*
H. haustorium	*Zeacumantus subcarinatus*	*H. haustorium*	*Austrolittorina cincta*
H. scobina	*Aulacomya atra maoriana*	*H. scobina*	*Mytilus galloprovincialis*
H. scobina	*Austrolittorina antipodum*	*H. scobina*	*Austrolittorina cincta*
H. scobina	*Balanus* sp.	*H. scobina*	*Chamaesipho* spp.
H. scobina	*Calantica spinosa*	*H. scobina*	*Xenostrobus pulex*
H. scobina	*Calantica villosa*	*H. scobina*	*Xenostrobus pulex*
H. scobina	*Cellana denticulata*	*H. haustorium*	*Cellana denticulata*
H. scobina	*Chamaesipho brunnea*	*H. scobina*	*Chamaesipho* spp.
H. scobina	*Chamaesipho columna*	*H. scobina*	*Chamaesipho* spp.
H. scobina	*Chiton glaucus*	*H. haustorium*	*Onithochiton neglectus neglectus*
H. scobina	*Siphonaria australis*	*H. haustorium*	*Siphonaria australis*

APPENDIX D

SPECIES-SPECIFIC ALLOMETRY MEASUREMENTS AND PERCENT-COVER TO COUNT CONVERSIONS

INTRODUCTION

In this appendix I provide the species-specific allometric regression coefficients relating estimates of individual body size (shell length) to their whole-, shell-, and tissue-weight. I used these relationships to infer each species' biomass and to estimate each prey species' energetic impact (i.e. bottom-up interaction strength) on their two whelk predators (*Chapter IV*). I also provide the site-specific regression coefficients relating a species' abundance as estimated by percent cover to an estimate of its density (#/m^2) for the species whose abundance was assessed by percent cover in the quadrat surveys.

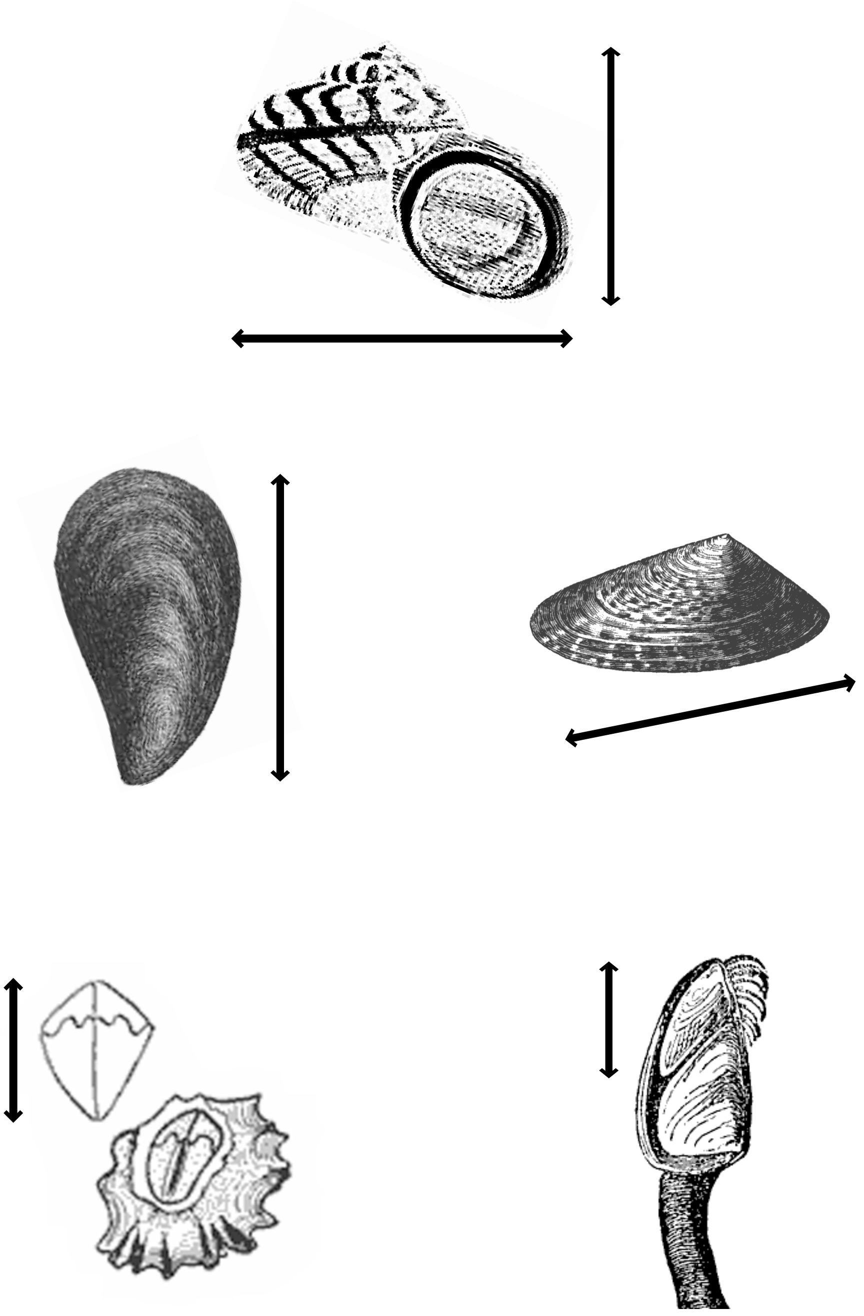

Figure D.1. Shell length measures used in Table D.1.

Table D.1. Allometric regression coefficients and sample sizes (n) relating total length (L) to total wet weight, dry shell weight, and dry tissue weight (W, in grams), corresponding to $W = i\,L^e$.

Species	**Total wet weight**			**Dry shell weight**			**Dry tissue weight**		
	i	***e***	***n***	***i***	***e***	***n***	***i***	***e***	***n***
Acanthochitona zelandica	8.877 x 10^{-5}	3.117	45	5.375 x 10^{-5}	2.889	44	1.168 x 10^{-5}	2.808	37
Amourichiton sp.	5.293 x 10^{-4}	2.517	4	-	-	-	-	-	-
Aulacomya atra maoriana	8.661 x 10^{-5}	3.029	44	9.118 x 10^{-5}	2.876	30	1.146 x 10^{-5}	2.823	16
Austrolittorina antipodum	5.725 x 10^{-4}	2.561	154	4.308 x 10^{-3}	1.416	36	-	-	-
Austrolittorina cincta	1.191 x 10^{-4}	3.265	138	9.817 x 10^{-5}	3.194	94	9.041 x 10^{-5}	2.261	69
Benhamina obliquata	1.573 x 10^{-4}	2.963	29	9.673 x 10^{-5}	2.799	20	1.558 x 10^{-5}	3.031	20
Buccinulum sp.	8.618 x 10^{-5}	3.057	11	6.506 x 10^{-5}	3.020	11	4.223 x 10^{-6}	3.196	11
Calantica villosa[1]	6.218 x 10^{-4}	3.325	47	5.621 x 10^{-4}	2.916	47	3.188 x 10^{-5}	3.491	45
Cantharidella tesselata	1.364 x 10^{-3}	2.549	113	1.061 x 10^{-3}	2.442	49	1.495 x 10^{-4}	2.466	15
Cellana denticulata	3.277 x 10^{-5}	3.353	46	1.446 x 10^{-5}	3.422	36	4.541 x 10^{-6}	3.217	26
Cellana flava	4.080 x 10^{-5}	3.377	6	5.087 x 10^{-5}	3.169	6	2.339 x 10^{-5}	2.621	6
Cellana ornata	4.788 x 10^{-5}	3.346	64	2.491 x 10^{-5}	3.352	49	9.041 x 10^{-6}	3.137	34
Cellana radians	3.976 x 10^{-5}	3.230	62	1.650 x 10^{-5}	3.300	47	6.600 x 10^{-6}	3.080	32
Chamaesipho brunnea[2]	2.349 x 10^{-3}	2.776	102	9.040 x 10^{-5}	4.315	85	8.041 x 10^{-4}	1.449	29
Cominella maculosa	1.416 x 10^{-4}	3.007	64	8.544 x 10^{-5}	3.027	46	1.005 x 10^{-5}	3.093	33
Diloma aethiops	8.871 x 10^{-4}	2.807	108	4.415 x 10^{-4}	2.910	76	1.063 x 10^{-4}	2.519	36
Diloma arida	4.980 x 10^{-3}	2.136	27	4.238 x 10^{-3}	2.048	17	4.225 x 10^{-3}	1.147	7
Diloma bicanaliculata	2.133 x 10^{-3}	2.442	41	1.282 x 10^{-3}	2.498	31	1.089 x 10^{-4}	2.554	19
Diloma nigerrima	2.648 x 10^{-3}	2.394	36	2.344 x 10^{-3}	2.283	30	8.872 x 10^{-5}	2.758	24
Epopella plicata[2]	6.612 x 10^{-3}	2.383	46	4.327 x 10^{-3}	2.461	37	3.766 x 10^{-4}	2.355	21
Haustrum haustorium	1.616 x 10^{-4}	2.954	343	1.499 x 10^{-4}	2.870	141	1.988 x 10^{-6}	3.466	60
Haustrum scobina	1.214 x 10^{-4}	3.210	252	6.105 x 10^{-5}	3.279	108	5.909 x 10^{-6}	3.417	37

[1] Tergum length. Weight includes cirri.

[2] Aperture length. Weight includes cirri.

Table D.1. Allometric regression coefficients and sample sizes (*n*) relating total length (*L*) to total wet weight, dry shell weight, and dry tissue weight (*W*, in grams), continued.

Species	Total wet weight			Dry shell weight			Dry tissue weight		
	i	***e***	***n***	***i***	***e***	***n***	***i***	***e***	***n***
Margarella sp.	2.002 x 10^{-3}	2.338	8	6.195 x 10^{-4}	2.819	8	3.709 x 10^{-4}	1.992	8
Montfortula chathamensis	1.932 x 10^{-4}	3.009	5	8.050 x 10^{-5}	3.056	5	4.429 x 10^{-4}	1.633	5
Mytilus galloprovincialis	1.648 x 10^{-4}	2.809	98	1.104 x 10^{-4}	2.801	67	6.803 x 10^{-6}	2.806	47
Notoacmea spp.	2.156 x 10^{-5}	3.973	39	3.567 x 10^{-5}	3.475	37	1.419 x 10^{-5}	3.026	32
Notoacmea pileopsis	2.723 x 10^{-3}	1.860	16	5.504 x 10^{-5}	3.072	5	4.765 x 10^{-3}	0.777	4
Onchidella nigricans	4.857 x 10^{-4}	2.453	13	-	-	-	8.614 x 10^{-5}	2.637	13
Onithochiton neglectus neglectus	1.951 x 10^{-4}	2.726	40	2.973 x 10^{-4}	2.218	40	2.915 x 10^{-5}	2.385	37
Paratrophon patens	6.256 x 10^{-5}	3.407	28	3.089 x 10^{-5}	3.550	22	5.897 x 10^{-6}	3.272	18
Patelloida corticata	5.579 x 10^{-5}	3.283	112	4.708 x 10^{-5}	3.160	78	4.542 x 10^{-6}	3.267	45
Perna canaliculus	1.728 x 10^{-4}	2.765	73	9.812 x 10^{-5}	2.814	61	1.242 x 10^{-5}	2.635	59
Plaxiphora caelata	4.737 x 10^{-5}	3.239	27	8.785 x 10^{-5}	2.633	20	2.571 x 10^{-5}	2.334	13
Risellopsis varia[3]	3.427 x 10^{-4}	2.782	109	2.201 x 10^{-4}	2.772	40	3.254 x 10^{-5}	2.759	33
Siphonaria australis	1.533 x 10^{-4}	2.792	85	9.705 x 10^{-5}	2.732	85	8.363 x 10^{-6}	3.036	52
Sypharochiton pelliserpentis	3.660 x 10^{-5}	3.294	55	2.607 x 10^{-5}	3.169	37	7.024 x 10^{-6}	2.896	22
Trimusculus conicus	6.721 x 10^{-5}	3.246	38	4.340 x 10^{-5}	3.175	38	1.035 x 10^{-5}	3.094	37
Turbo smaragdus	1.192 x 10^{-3}	2.717	103	1.154 x 10^{-3}	2.554	63	5.444 x 10^{-5}	2.912	26
Xenostrobus pulex	1.188 x 10^{-4}	2.855	98	1.032 x 10^{-4}	2.766	73	1.636 x 10^{-5}	2.454	59
Zeacumantus subcarinatus	3.948 x 10^{-4}	2.385	147	1.895 x 10^{-2}	0.454	4	5.126 x 10^{-5}	1.834	29

[3] Shell width

Table D.2. Unmeasured species to which the allometric regression coefficients of measured species were matched.

Unmeasured Species	**Matched to**
Atalacmea fragilis	*Cellana radians*
Austrolittorina antipodum	*Austrolittorina cincta*
Balanus sp.	*Chamaesipho brunnea*
Calantica spinosa	*Calantica villosa*
Chamaesipho columna	*Chamaesipho brunnea*
Chiton glaucus	*Sypharochiton pelliserpentis*
Dicathais orbita	*Haustrum haustorium*
Eatoniella sp.	*Austrolittorina cincta*
Haustrum lacunosus	*Haustrum scobina*
Lasaea rubra hinemoa	*Xenostrobus pulex*
Montfortula chathamensis	*Diloma aethiops*
Notoacmea daedala	*Cellana radians*
Plaxiphora obtecta	*Plaxiphora caelata*
Thoristella chathamensis	*Diloma aethiops*
Zeacumantus subcarinatus	*Austrolittorina cincta*
Unidentified	*Diloma aethiops*

Table D.3. The mean site-specific number of individuals contained in 1% of the area of a 0.25 m^2 quadrat as estimated by linear least squares regression ($y = 0 + \beta\ x$) between the number and percent-cover of individuals occupying 0.0025 m^2 quadrats.

Species	**Site**	**Count**	**SE**	**t-value**	***n***	***P***
Aulacomya atra maoriana	Cape Foulwind	15.91	1.88	8.45	15	< 0.001
Aulacomya atra maoriana	Okahu Point	25.74	3.24	7.94	15	< 0.001
Aulacomya atra maoriana	Paia Point	27.10	1.79	15.16	15	< 0.001
Aulacomya atra maoriana	Rakautara	19.98	1.72	11.59	15	< 0.001
Aulacomya atra maoriana	Tauranga Head	7.74	0.88	8.79	15	< 0.001
Calantica spp	Cape Foulwind	10.41	0.92	11.37	15	< 0.001
Calantica spp	Jackson Head	7.37	1.07	6.92	15	< 0.001
Calantica spp	Okahu Point	9.58	0.44	21.69	15	< 0.001
Calantica spp	Paia Point	6.40	0.73	8.79	15	< 0.001
Calantica spp	Rakautara	8.58	0.53	16.16	15	< 0.001
Calantica spp	Tauranga Head	13.07	1.43	9.12	15	< 0.001
Chamaesipho brunnea	Paia Point	120.14	12.53	9.59	30	< 0.001
Chamaesipho brunnea	Rakautara	124.86	9.90	12.61	30	< 0.001
Chamaesipho columna	Cape Foulwind	313.97	8.82	35.61	40	< 0.001
Chamaesipho columna	Jackson Head	400.34	17.44	22.96	30	< 0.001
Chamaesipho columna	Okahu Point	375.08	8.53	43.98	30	< 0.001
Chamaesipho columna	Paia Point	348.31	15.33	22.71	30	< 0.001
Chamaesipho columna	Rakautara	322.85	22.22	14.53	30	< 0.001
Chamaesipho columna	Tauranga Head	418.50	19.72	21.22	40	< 0.001
Epopella plicata	Cape Foulwind	63.26	2.79	22.64	30	< 0.001
Epopella plicata	Jackson Head	51.04	4.59	11.13	30	< 0.001
Epopella plicata	Okahu Point	41.05	3.00	13.68	30	< 0.001
Epopella plicata	Paia Point	41.07	2.21	18.59	30	< 0.001
Epopella plicata	Rakautara	29.47	2.21	13.31	30	< 0.001
Epopella plicata	Tauranga Head	68.38	3.07	22.25	30	< 0.001
Lasaea rubra hinemoa	Paia Point	709.62	50.13	14.16	5	< 0.001
Mytilus galloprovincialis	Cape Foulwind	8.58	0.68	12.63	30	< 0.001
Mytilus galloprovincialis	Jackson Head	20.02	3.44	5.81	15	< 0.001
Mytilus galloprovincialis	Okahu Point	15.80	2.77	5.70	15	< 0.001
Mytilus galloprovincialis	Paia Point	11.57	1.93	6.01	15	< 0.001
Mytilus galloprovincialis	Rakautara	10.33	0.88	11.73	15	< 0.001
Mytilus galloprovincialis	Tauranga Head	9.06	0.48	18.94	30	< 0.001
Xenostrobus pulex	Cape Foulwind	66.15	3.12	21.19	49	< 0.001
Xenostrobus pulex	Jackson Head	100.93	8.94	11.28	30	< 0.001
Xenostrobus pulex	Okahu Point	145.55	16.37	8.89	30	< 0.001
Xenostrobus pulex	Paia Point	247.15	26.44	9.35	30	< 0.001
Xenostrobus pulex	Rakautara	171.57	13.78	12.45	30	< 0.001
Xenostrobus pulex	Tauranga Head	78.81	3.61	21.85	50	< 0.001

APPENDIX E

UNDERSTANDING CROSS-GRADIENT CHANGES IN SPECIES ABUNDANCE USING LOOP ANALYSIS

INTRODUCTION

In *Chapter IV*, I suggested that two key predictions of current intraguild predation theory are not supported by the empirical evidence of New Zealand's intertidal. Counter to theory, I showed that it is the omnivorous whelk, *H. haustorium*, that is the superior competitor to the intermediate predator, *H. scobina*, when all prey are considered, and that *H. scobina*'s abundance increases with increasing productivity along New Zealand's shores.

A likely reason for these discrepancies is that most intraguild predation models have considered only tightly-coupled three-species systems. The models of Daugherty et al. (2007) and Holt and Huxel (2007) have begun to address this issue (see also Kondoh 2008), but have shown that the addition of alternative prey should not change the focal predictions of three-species models. In *Chapter IV*, I therefore suggest that future modeling efforts should incorporate the potential of non-trophic interactions occurring between basal prey species (see also Polis and Strong 1996). Basal interactions will, of course, be challenging to incorporate in models explicitly, for there are 3^{18} ($3^{(28-10)}$ = 387,420,489) possible ways to configure a core IGP interaction web where predators each have their own exclusive prey and direct and indirect interactions between basal species may either be absent, competitive or facilitative (Fig. E.1). In this appendix, I outline an approach that uses Loop Analysis to begin tackling this challenge.

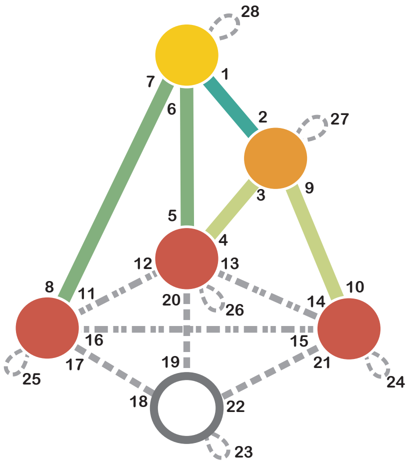

Figure E.1. Adding interactions among basal prey species to models of intraguild predation is made challenging by the many ways that species may be connected to one-another. Solid links indicate the core IGP food web (#1-10) which must, by definition, be of paired +/- signs. (Prey have positive direct effects on predators, while predators have negative direct effects on prey.) Dashed links between basal prey species may be present as direct interactions between species (#11-16) or be mediated indirectly (#17-22) by spatial heterogeneity (open circle), for example. The nature of these interactions may be competitive (-), facilitative (+), or absent (0). All interaction web components may similarly exhibit negative, positive, or no intraspecific density-dependence (#23-28).

QUALITATIVE RESPONSES IN NEW ZEALAND FOOD WEBS

The addition of interactions among basal prey species renders too many possible interaction web structures and interaction strength values for quantitative estimates of trophic interaction strengths alone to be of immediate use. Qualitative modeling approaches, such as Loop Analysis (Levins 1974, Dambacher et al. 2002, Justus 2006), may on the other hand, be useful to begin surmounting the added complexity. Loop analysis uses minimal information (just the existence and sign of species interactions) to make predictions for how communities should respond to species-specific population change. In essence, loop analysis predictions take into account all the connections linking species together that, via feedback, either positively or negatively affect the response of one or more species to changes in the growth or death rate of another (see more detailed description below). In the context of the observed cross-gradient changes in the abundance of New Zealand's species, these predictions regard how different interaction web configurations between basal species may be expected to shape the qualitative response of the system to changes in basal productivity. By allowing comparisons between observed and predicted changes on a simple qualitative basis, loop analysis could reduce the world of possible interaction web configurations to a smaller, more manageable subset of competing hypotheses.

As a preliminary application of this proposed approach, I have considered two sets of possible interaction web configurations to superimpose on the core IGP food web with alternative prey: basal species with self-limitation and direct interactions only, and basal species with or without self-limitation interacting only indirectly via a sixth, self-limited interaction web component (Fig. E.2). For both configuration sets, I allowed for predators to feed upon each other's "exclusive" prey and experience intraspecific density-dependence (since cannibalism and such feeding links were observed at the low and intermediate productivity sites of the New Zealand system, see *Chapter III*).

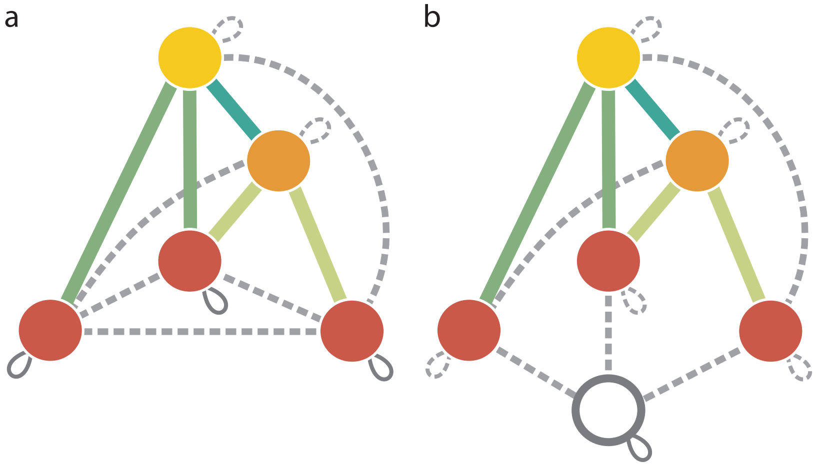

Figure E.2. The two sets of possible interaction web configurations superimposed on the core IGP food web with alternative prey that I have begun to investigate: (a) basal species with self-limitation and direct interactions only, and (b) basal species with or without self-limitation interacting only indirectly via a sixth, self-limited interaction web component. Predators may feed upon each other's "exclusive" prey and experience intraspecific density-dependence. Solid links indicate core interactions present in all configurations, while dashed links indicate hypothesized variations (+, - or 0) on which loop analysis was performed.

The total number of possible interaction web configurations for which qualitative predictions were made therefore totaled 3^8 x 2^2 (= 24,244) and 3^{11} x 2^2 (= 708,588) for the two configuration sets, respectively. In comparing observed and predicted cross-gradient changes in species abundance, I considered predictions regarding an increase in the growth rate of both shared and non-shared prey, the latter of which could hypothetically correspond to the empirical gradient of mussel and barnacle growth and recruitment rates in a latently inverse manner.

Results suggest that some interaction web configurations do produce qualitative predictions that match the observed cross-gradient patterns in species-group abundances. Loop analysis, furthermore, reduced the number of likely configurations by multiple orders of magnitude to 48 and 3,247 for the two investigated configuration sets, respectively. Only few of these configurations appear consistent with the natural history of intertidal systems (results not shown), but general patterns do emerge. For example, while none of the 48 configurations imposing only direct effects among basal species appears consistent with natural history, all require density-dependence in the intermediate predator. When this density-dependence is negative, the omnivore must exhibit positive density-dependence; when it is positive, the omnivore may exhibit positive or no density-dependence, but may not exhibit negative density-dependence.

Further, a specific interaction web from the second set of configurations is partially consistent with that hypothesized in *Chapter IV*. In *Chapter IV*, I suggested that an increase in the productivity of mussels and barnacles is likely to have an indirect facilitative effect on small littorine snails (*H. scobina*'s alternative prey) via the formation of increased structural substrate complexity. Increased structure, however, may have an indirect negative effect on *H. haustorium*'s alternative prey (larger limpets and snails) which typically prefer less complex surfaces on which to graze (mechanisms reviewed by

Menge 1995). Loop analysis predicts that such a configuration among basal prey may also require positive density-dependence within the intermediate predator and that the intermediate predator also feeds on the omnivore's alternative prey (Fig. E.3). Loop analysis thereby provides testable hypotheses for future modeling efforts and manipulative empirical experiments to explore.

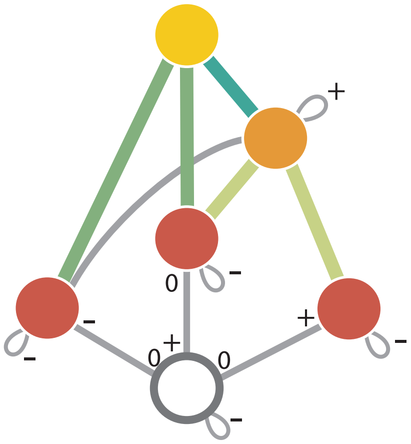

Figure E.3. An example on an interaction web that is predicted, by loop analysis, to be qualitatively consistent with the cross-gradient changes in species abundances observed in New Zealand and the configuration of basal species interactions hypothesized in *Chapter IV*. The signs of trophic interactions are omitted for clarity.

MAKING PREDICTIONS USING LOOP ANALYSIS

Making predictions with loop analysis proceeds as follows: consider a four-species interaction web in which an omnivorous predator preys upon three species: an intermediate predator species with whom it competes for a shared prey species, and an alternate prey species on which the intermediate predator does not feed (Fig. E.4). The two basal prey species are assumed to experience self-limitation (in the form of density dependent logistic growth, for example).

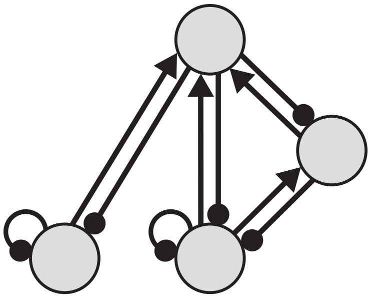

Figure E.4. The four-species interaction web used to describe loop analysis as illustrated by a signed digraph. Arrows indicate positive effects, solid points indicate negative effects.

All the direct interactions between the species of this system can be organized into what has been termed the *community matrix*

$$\mathbf{A} = \begin{bmatrix} -a_{1,1} & -a_{1,2} & -a_{1,3} & 0 \\ a_{2,1} & 0 & -a_{2,3} & 0 \\ a_{3,1} & a_{3,2} & 0 & -a_{3,4} \\ -0 & 0 & a_{4,3} & -a_{4,4} \end{bmatrix}.$$

This matrix is read as the direct effect of the species in column *j* on the species of row *i*. This community matrix has frequently been equated to the *Jacobian matrix*. In the context of making community response predictions, however, the elements of the community matrix represent *per capita interaction strengths* – the average effect of an individual of one species on one individual of another species, denoted by α_{ij}. In the empirical context of Lotka-Volterra trophic interactions, interspecific top-down per capita interaction strengths, α_{ij}, are the number of prey eaten per predator per prey available per unit time assuming a linear functional response, bottom-up per capita interaction strengths $\alpha_{ji} = e_{ij}\ \alpha_{ij}$, where e_{ij} are numeric efficiencies with which prey are converted to predators, and intraspecific $\alpha_{ii} = 1/K_i$ where K is a species' carrying capacity in the absence of predation and competition. In the theoretical prediction context the community matrix is therefore equivalent to what has been termed the *interaction matrix*. Thus $a_{ij} = \alpha_{ij}$ and *not* the elements of the Jacobian matrix (Laska and Wootton 1998) which specify the effect that a single individual of species *j* has on the population growth rate of species *i* when all species are at equilibrium (i.e. $a_{ij} \neq \alpha_{ij}N_i^*$, where N_i^* are the equilibrial abundances). A tremendous amount of confusion exists in the literature regarding these matrices because the stability properties of the interaction matrix are equivalent to those of the Jacobian matrix at equilibrium (Stefano Allesina, *pers. comm.*).

Quantitative predictions for how equilibrium abundances will be changed by a perturbation can be made when all per capita interaction strengths are known by calculating the inverse of the *negative community matrix* $-\mathbf{A}^{-1}$ (Nakajima 1992, Bender, 1984 #1109), also known as the *prediction matrix*. Calculating the negative inverse of the Jacobian matrix does not provide the prediction matrix. (For subsequent clarity I denote the inverse of the negative community matrix by $-^{\#}\mathbf{A}^{-1}$ when it pertains to the quantitative interaction matrix.) Each element of $-^{\#}\mathbf{A}^{-1}$ specifies the expected direction and magnitude by which the equilibrium abundance of each i^{th} species will respond to a *sustained* addition to the population of species *j* (a press change, sensu Bender et al. 1984). Such press perturbations could be an increased birth or decreased death rate of species *j*, but notably not a one time change (pulse or removal) in species *j*'s abundance as is typically done in field experiments (but see Flake 1980). Changes in the equilibrium abundance of species *i* are the result of all the direct and indirect interactions between it and species *j* that cause both positive and negative feedback between the species.

Typically, however, detailed knowledge of per capita interaction strengths is not available and only the existence and sign of species interaction is known. The community matrix is therefore specified qualitatively as

$$^\circ\mathbf{A} = \begin{bmatrix} -1 & -1 & -1 & 0 \\ 1 & 0 & -1 & 0 \\ 1 & 1 & 0 & -1 \\ 0 & 0 & 1 & -1 \end{bmatrix}.$$

In what he originally termed loop analysis, Levins (1974) developed an algorithm for the computation of predictions from °**A**. The computation of this qualitative prediction matrix, termed the *classical adjoint matrix* (a.k.a. the adjugate matrix), was practically limited to very small matrices however. Dambacher and colleagues illustrated the correspondence of qualitative and quantitative prediction matrices, showing that the classical adjoint of °**A** is scaled to $-^\circ\mathbf{A}^{-1}$ by the *matrix determinant* of °**A** (Dambacher et al. 2002). Generalizing to both qualitative and quantitative community matrices, Dambacher et. al termed the generalized *adjoint matrix*, $adj\ -\mathbf{A} = -\mathbf{A}^{-1}\ \det(-\mathbf{A})$. The adjoint matrix (a.k.a. the conjugate transpose) is the prediction matrix of either a quantified or qualitatively specified interaction matrix. This insight permits the use of the same matrix algebra used in calculating $-^{\#}\mathbf{A}^{-1}$ to make predictions for larger qualitatively specified systems than had been possible using Levins' algorithm as both $-\mathbf{A}^{-1}$ and det($-\mathbf{A}$) can be computed rapidly. The adjoint matrix of the example interaction web (Fig. E.4) would be

$$adj\ -^{\circ}\ \mathbf{A} = (-^{\circ}\mathbf{A}^{-1})(det^{\circ}\mathbf{A}) = \begin{bmatrix} 1 & -2 & 1 & 1 \\ 0 & 2 & -2 & -2 \\ 1 & 0 & 1 & 1 \\ -1 & 0 & -1 & 1 \end{bmatrix}.$$

Thus a sustained input to the shared prey is predicted to cause a one-fold increase in the abundance of the omnivore, a one-fold decrease in the abundance of the omnivore's alternate prey, and no change in the abundance of the intermediary predator. The response of the intermediary predator is indeterminate (sensu Yodzis 1988) because it is affected by two counteracting feedback loops: one having a positive effect via the increased abundance of the shared prey, and a second having a negative effect via the increased abundance of the omnivore (i.e., $a_{2,1}\, a_{3,4}\, a_{4,3} - a_{3,1}\, a_{2,3}\, a_{4,4} = 0$ when all $a = -1$ or 1). In such situations where the number of incoming positive and negative feedback loops is exactly equal, the direction of a species' response depends on the relative per capita interaction strengths.

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