

Estimating interaction strengths in nature: experimental support for an observational approach

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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 strengths of trophic species interactions offer a means to identify keystone species and bridge mathematical models and data to synthesize our knowledge of population dynamics and predator feeding behaviors. Many such methods have been proposed, but few have seen independent validation of their estimates or underlying assumptions. This is particularly so with respect to the nonlinear functional responses by which predators often respond to their prey. 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 predatory intertidal whelk, *Haustrum scobina*, I estimated its per capita attack rates on all nine of its observed prey species. These spanned two orders of magnitude in per capita strength. Concurrent experimental manipulations of the two predator populations provided population time series for the response of a mussel prey species, *Xenostrobus pulex*. I obtained independent interaction strength estimates for this focal interaction by fitting a sequence of hypothesized predator–prey models to these time series. Overall, site-specific models assuming linear functional responses performed better than all others. A direct comparison of the attack-rate estimates from the observational method with those of the best-performing nonlinear model nevertheless revealed high concordance between the two methods. The results of this study therefore support the use of the observational method in larger and more complex food webs and suggest that trophic interactions in the range of mean prey densities observed in nature are approximately linear.

Key words: attack rates; food webs; functional response; *Haustrum scobina*; New Zealand intertidal; parameter estimation; per capita interaction strengths; species interactions; whelks; *Xenostrobus pulex*.

INTRODUCTION

Efforts to quantify the strengths of species interactions have become an important focus of community ecology, particularly in the context of predator–prey interactions. Trophic interaction strength estimates offer insights into how communities are structured by describing the channels by which energy and elements move through food webs (Baird and Ulanowicz 1989) and have played a central role in our growing understanding of the ecological processes governing diversity, species coexistence, and community stability (McCann 2000, Duffy 2002). They are often offered as a means to more accurately predict the community consequences of changing species abundances and extinctions (Agrawal et al. 2007).

Many methods have been proposed to estimate trophic interaction strengths (reviewed in Berlow et al. 2004, Wootton and Emmerson 2005). Of particular interest are methods that do so on a per capita (or per biomass) basis because these underlie all other metrics of interaction strength (Laska and Wootton 1998). Per capita interaction strengths are directly comparable between all the species of a food web because they scale out differences in population size (Wootton 1997), allowing keystone species with disproportionately strong effects to be identified (Power et al. 1996). Per capita interaction strengths also 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. This is surprising given that all methods must make a variety of potentially critical assumptions regarding the properties of species interactions in nature. Shared among most methods, for example, are assumptions that (1) population abundances are near equilib-

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rium or a mass-balanced state (e.g., Bender et al. 1984, Paine 1992, Moore et al. 1993, Hall et al. 2000, Bascompte et al. 2005), (2) that predators and predator–prey size ratios used in experiments exhibit behaviors and feeding rates consistent with those exhibited in nature (Sala and Graham 2002, Emmerson and Raffaelli 2004), (3) that pairwise interactions are unchanged in multispecies contexts (Sala and Graham 2002, Emmerson and Raffaelli 2004), and (4) 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, 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).

These assumptions may be unjustified. (1) The existence of equilibrium conditions is difficult to ascertain, if not contentious (Connell and Sousa 1983). (2) Feeding rates are often sensitive to experimental design and conditions (Ruesink 2000). (3) Predator–prey interactions typically exhibit dynamics that are different in multispecies situations than when species pairs are studied in isolation (Peacor and Werner 2004). (4) The most frequently observed functional responses are of a nonlinear saturating form (Murdoch and Oaten 1975, Hassell et al. 1977, Seitz et al. 2001, Jeschke et al. 2004). Thus, there is room for improving methods to quantify interaction strengths (Abrams 2001).

The functional form by which predator feeding rates relate to the density of their prey is of particular interest in food web ecology. Whether the strength of a predator–prey interaction exhibits positive, negative, or no density dependence to the prey's or the predator's abundance has marked consequences for food web dynamics and the degree to which predation will affect prey suppression (Murdoch and Oaten 1975, Gascoigne and Lipcius 2004). Numerous experiments have shown how the density dependence of feeding rates can vary across predator species, prey species, and environmental conditions in marine and terrestrial systems alike (Seitz et al. 2001, Jeschke et al. 2004). We remain largely ignorant, however, of how these experiments may be scaled to the interactions of whole food webs (Abrams and Ginzburg 2000).

Here I describe an empirical test of a method for estimating the per capita strength of trophic 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 quantifying interaction strengths in the field (see also Wootton 1997, Woodward et al. 2005). Requiring data on prey abundances, handling times, and information from predator-specific feeding surveys (see *Methods*), 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. More specif-

ically, it assumes that predators (P) exhibit multispecies Type II functional responses to changes in all their prey's abundances (N_i), such that

$$\frac{dN_i}{dt} = g(N_i) - \frac{c_i N_i P}{1 + \sum_{j \in \text{prey}} c_j N_j} \quad (1)$$

(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 per capita attack rates, equivalent to prey preferences; Chesson [1983]) and h (the handling times) describe the density-dependent form of the predator's feeding rate on prey i (Novak and Wootton 2008). The method therefore assumes that all per capita attack rates are constant (i.e., no prey refuges, prey switching, or predator learning; Holling [1959], Murdoch [1969]) and independent of predator density (i.e., no ratio dependence; Abrams and Ginzburg [2000]). It also assumes that a predator's feeding rates are of the same functional form across all prey species (but see Murdoch and Oaten 1975). For clarity, note that the c parameters are not themselves the per capita interaction strengths between a predator and its prey. Rather, they are parameters that contribute to the species pairs' per capita interaction strength functions (i.e., $c_i N_i / (1 + \sum_j h_j N_j)$) (Novak and Wootton, *in press*).

I tested this observational 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 on one of its prey species experimentally. I did this by assessing the performance of a series of hypothesized predator–prey models fit to the population dynamics of the mussel *Xenostrobus pulex* in year-long replicated manipulations of *Haustrum*. While model-comparisons revealed that models with linear functional responses performed better than all others in describing the prey's dynamics in the experiments, a direct comparison of the observational attack-rate estimates with those of the best-performing nonlinear model revealed high concordance. This study therefore supports the use of the observational method in more complex food webs, and contributes to a growing literature suggesting that trophic interactions may be approximately linear in the range of mean prey densities observed in nature.

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 (TH; 41°46'26" S, 171°27'20" E) and Cape Foulwind (CF; 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 consists variably of *Perna canaliculus* mussels and a *Gigartina*-dominated algal community.

The focal predator of this study, *Haustrum* (*Lepsiella*) *scobina*, is a muricid whelk not unlike the *Nucella* species of the northern hemisphere. *Haustrum*'s diet consists primarily of acorn barnacles and mussels (Morton and Miller 1968, Luckens 1975b, Menge et al. 1999) but may also include oysters, limpets, snails, and tubeworms (Luckens 1975b). Muricid whelks like *Haustrum* typically drill through the shells of their prey to feed (Carriker 1981). Handling times, the time needed to drill and ingest a prey item, may vary on the order of hours to days, and in a Type II functional response fashion, can limit feeding rates at experimentally manipulated high prey densities (Murdoch 1969, Katz 1985, Moran 1985). 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 (Jeschke et al. 2002, Novak 2008). *Haustrum* is abundant at both study sites where it attains a maximum size of ~22 mm shell height (Novak 2008) 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* forms dense monospecific mats within the high zone that harbor few other species. It reproduces by broadcast spawning with larvae recruiting to settle on barnacles, in cracks, or between conspecifics (Luckens 1975a; M. Novak, *personal observation*). Individuals attain a maximum shell length of ~28 mm at the study sites, which is not large enough to escape predation by *Haustrum* whelks (M. Novak, *personal observation*).

Observational attack-rate estimation

The observational method for estimating the per capita attack rates of a predator assumed to exhibit a multispecies Type II functional response requires information on (1) prey-specific handling times (h_i), (2) prey abundances (N_i), and (3) 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 prey species (A_i); and second, the proportion of the population's feeding individuals that are observed to be feeding on each prey species (F_i). With these data, per capita attack rates (c_i) for each i th prey are calculated as

$$c_i = \frac{F_i A_i}{(F_x - A_x) h_i N_i} \quad (2)$$

where x denotes an arbitrarily chosen prey species used throughout the calculation of all attack rates (Novak and Wootton 2008). I obtained this information to estimate *Haustrum scobina*'s prey-specific attack rates as follows:

Feeding surveys.—I estimated A_i and F_i 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, approximately half hour long low-tide searches of the high zone during which each encountered 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 species' densities using 10–15 quadrats of 0.25 m² distributed randomly among three 20-m transects at each site. 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 ($\sqrt{0.5}$ m) and the mean 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 (Novak 2008). Surveys were repeated three times at each site (May–July 2005, January–February 2006, May 2006).

Handling-time estimation.—In theory, handling times could be estimated by a variety of methods (see Novak and Wootton 2008). I measured the time needed for a whelk to drill and ingest prey in the laboratory. For example, whelks (7–18 mm) and *Xenostrobus* mussels (3–22 mm) were collected at Tauranga Head and transported to the Edward Percival Field Station, Kaikoura, New Zealand. There, mussels were maintained with flowing sea water (~9–11°C) filtered to 40 μ m, while whelks were sorted into aerated aquaria in three temperature-controlled rooms maintained at ~10°, 14°, and 18°C ($\pm 0.4^\circ$ C SD; monitored using iButton temperature loggers; Maxim Integrated Products, California, USA) and a 12 h:12 h day:night cycle. After an acclimation period ≥ 3 days and a starvation period ≥ 5 days, individual whelks were measured (± 0.1 mm), placed into aerated 4 L semi-translucent plastic aquaria (17 cm diameter, 18.5 cm height) 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 1/10 day window or a maximum possible start to end time difference being $\leq 80\%$ 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 typically obtained whelks and prey from east coast locations nearer the laboratory. The only prey species for which this 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 (15 × 9 × 8 cm) with independent and continually flowing filtered sea water, the temperature of which varied over the course of the year (9°–17.5°C). 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 (± 0.1 mm) under a dissecting microscope.

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, Massachusetts, USA) positioned in the low midlittoral of each site to record low-tide air and high-tide water temperatures at half-hour 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. 2 to estimate attack-rate means and calculated 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 prey most frequently observed in a draw as species *x*. I estimated attack rates in two ways: 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 to account for the spatial variability of environmental conditions (e.g., slope, wave exposure). Mussel densities within cages reflected the natural variation in densities observed along the shore but were more similar across treatments within a block than between blocks. 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. Mussels were removed individually using forceps, leaving other species and the underlying barnacle cover intact. This reduction was performed to aid in model-fitting by increasing variation in mussel densities. Minimum within-cage densities remained within the spatial variation of mussel abundances observed at the site.

Each cage consisted of a 22 × 20 × 5 cm stainless steel mesh perimeter (2.5 mm opening diameter, 0.075 mm mesh size) with a polyethylene Vexar lid (5.1 mm opening diameter, 1.3 mm mesh size; Conwed Plastics, Minneapolis, Minnesota, USA) and was secured to the bedrock with eight stainless steel screws. At the start of the experiment (August 2006), each whelk-enclosure cage was stocked with enough whelks to match ambient high-zone densities (Tauranga Head, New Zealand [TH], 3 whelks/cage vs. the target of 2.6 whelks/cage based on 60.4 ± 7.2 whelks/m² [mean \pm SE] ambient density; Cape Foulwind, New Zealand [CF], 4 whelks/cage vs. 4.1 whelks/cage based on 92.9 ± 8.4 whelks/m² [mean \pm SE] ambient density). Whelks were stocked at an initial size of 12–14 mm (ambient size, 12.6 ± 2.7 mm [mean \pm SD] at both sites) but grew to 14.7 ± 4.9 mm (mean \pm SD) by the end of the experiment.

At the start and during each of three subsequent censuses of the experiment (conducted after 178, 280, and 338 elapsed days; Appendix B: Fig. B1) I counted and removed all non-stocked *Haustrum* individuals that had either invaded or hatched within the cages, counted all dead *Xenostrobus* and barnacle individuals, counted all other live prey and non-prey species, 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 the analyses.

Attack-rate estimation.—While all prey species were counted in the experiments, I focused my analyses on *Xenostrobus* mussels alone because (1) they were present

in all cages throughout the experiment, (2) their abundance was high and could be estimated reliably, (3) their response to *Haustrum* predation was least likely to be obscured by the indirect effects among prey species because of their dominance in *Haustrum*'s diet and the habitat-forming nature of their interactions with other prey species. The effects of caging and *Haustrum* predation on the mobile and less abundant prey species would similarly have confounded method comparisons.

I first used linear mixed-effects models to test for the effects of caging and *Haustrum* predation on *Xenostrobus* counts. This approach allowed me to accommodate the nested and storm-induced unbalanced design of the experiment (Pinheiro and Bates 2000, Zuur et al. 2009). As the two sites differed in their treatments and the number of whelks their *Haustrum* enclosures contained, I performed the analyses separately for each site. I designated treatment(s) and time (non-categorical) as fixed effects, and blocks and plots as nested random effects, assumed homoscedastic within-group errors and no within-group correlations, and used the restricted maximum-likelihood method to produce unbiased estimates of variance and covariance parameters (Pinheiro et al. 2009).

I then used the time series from the *Haustrum*-enclosure and predator-exclusion treatments to fit a nested set of competing models hypothesized to describe the dynamics of *Xenostrobus* in the presence and absence of *Haustrum* predation. Alternative experimental index methods for estimating attack rates (e.g., Paine 1992, Wootton 1997) are either inappropriate given the open-recruitment biology of *Xenostrobus* mussels or produce interaction strength estimates not comparable to those of the observational method (Novak and Wootton 2008, *in press*). 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

$$\frac{dN}{dt} = I - g(N) - f(N, P). \quad (3a)$$

Whelk-independent contributions to mussel population growth were described as

$$g(N) = \begin{cases} mM \\ nNN \\ mN + nNN \end{cases} \quad (3b)$$

where m modeled the density-independent mortality (or growth) rate of the mussel 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

$$f(N) = \begin{cases} 0 \\ \alpha NP \\ cNP/(1 + chN) \end{cases} \quad (3c)$$

with whelks (P) having either no effect, or preying on mussels with either a linear Type I or a nonlinear Type II functional response.

Assuming log-normally distributed process noise, I used a one-step-ahead prediction procedure to obtain 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 the corrected Akaike's information criterion (AIC_c) to compare their performance. AIC_c is the most appropriate criterion 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 caging experiments to those of the observational method, I rescaled the model-fit estimates from the area of a cage to a per meter basis. Since the high collinearity between the attack-rate and handling-time parameters may have influenced parameter estimation, I (1) refit the best-performing nonlinear model after replacing ch with a single parameter, and (2) 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 2008) using the nlme package for the mixed-effects analysis (Pinheiro et al. 2009), the general purpose optimization functions nlminb and optim for model fitting, and the bbmle package for model comparisons (Bolker 2007).

RESULTS

Observational attack-rate estimation

In a total of 33 high-zone feeding surveys of the two *Haustrum scobina* populations I examined a total of 4093 whelks. The proportion of individuals found feeding in a given survey was $23\% \pm 2\%$ (mean \pm SE) at Tauranga Head, New Zealand (TH) and $22\% \pm 2\%$ at Cape Foulwind, New Zealand (CF). I observed *Haustrum* feeding on eight species at TH and six species at CF (Appendix A: Fig. A2). These prey were the snails *Austrolittorina antipodum*, *A. cincta*, and *Risellopsis varia*, the barnacles *Chamaesipho brunea*, *C. columna*, and *Epopella plicata*, the mussels *Mytilus galloprovincialis* and *Xenostrobus pulex*, and a *Notoacmea* sp. limpet. However, *Haustrum*'s diet was dominated by only two

species: *C. columna* and *Xenostrobus* together represented 98% and 97% of the feeding observations made at TH and CF, respectively (Appendix A: Table A1). *Xenostrobus* by itself represented 40% of the observations made at TH, and 29% of the observations made at CF.

The proportion of feeding individuals was higher at both sites during summers ($27\% \pm 2\%$; all subsequent values reported are mean \pm SE) than in the fall–winter seasons ($18\% \pm 1\%$), commensurate with increased summer temperatures (Appendix A: Fig. A1). Mean prey abundance ranged across five orders of magnitude within a site (9–110 000 individuals/m² for *Mytilus* and *C. columna*, respectively; Appendix A: Table A2). *Xenostrobus* densities averaged 3500 ± 640 individuals/m² at TH and 3500 ± 670 individuals/m² at CF, and *H. scobina* densities averaged 60.4 ± 7.2 individuals/m² at TH and 92.9 ± 8.4 individuals/m² at CF. No species densities exhibited strong or consistent seasonal patterns.

Haustrum exhibited no diel variation in feeding activity and consumed laboratory prey both above and below the water's surface. The time required for individuals to handle prey items in the laboratory 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 by temperature (Appendix A: Fig. A3). As the range across which these factors were varied in the laboratory was greater than that observed in the field, field-estimated handling times exhibited less variation (Appendix A: Table A3)

Estimates of *Haustrum*'s per capita attack rates varied across two orders of magnitude between prey species when averaged across the two years of the study (Fig. 1). Attack rates on *Xenostrobus* mussels were estimated to be higher at TH than at CF, and were three times higher during the summer than during the fall–winter seasons (Table 1). With the mean back-calculated *Xenostrobus* handling times being 1.24 ± 0.05 days at TH and 1.63 ± 0.08 days at CF, mean estimated feeding rates on *Xenostrobus* were also higher at TH (0.071 mussels·whelk⁻¹·m⁻² d⁻¹) than at CF (0.037 mussels·whelk⁻¹·m⁻²·d⁻¹).

Experimental attack-rate estimation

Mussel population sizes exhibited more growth in the predator-exclusion treatments than in the *Haustrum*-enclosure treatments (Fig. 2; Appendix B). This was true at TH ($t_{42} = 3.07$, $P = 0.004$, $P_{\text{adj}} = 0.01$) and marginally so at CF ($t_{80} = 1.96$, $P = 0.054$, $P_{\text{adj}} = 0.28$), where a model including time as a polynomial term fit significantly better than a model with only a linear time term (maximum-likelihood ratio test = 24.2, $P < 0.001$). Mussel dynamics were not significantly different be-

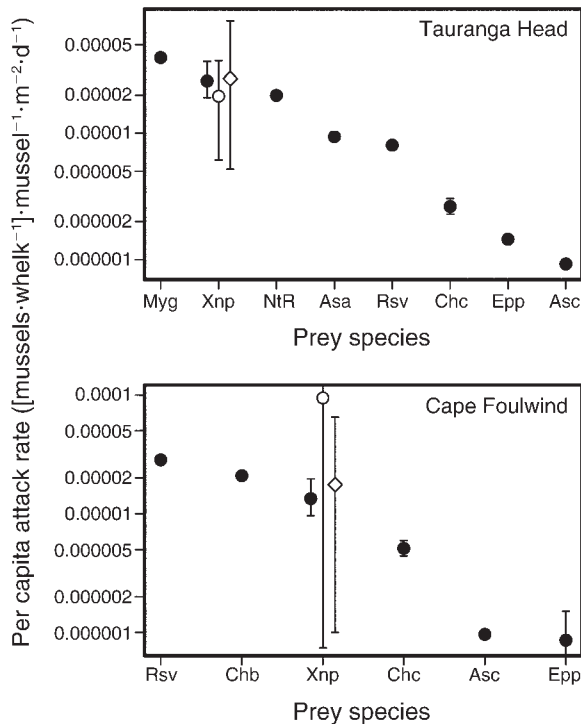


FIG. 1. Per capita attack rates (mussels eaten per whelk per mussel per square meter per day) by the intertidal whelk *Haustrum scobina* on each of its prey as estimated by the observational approach (solid symbols) at two experimental sites in New Zealand. Confidence intervals (90%) are shown only for prey observed more than five times. Open symbols indicate maximum-likelihood estimates from the best-performing nonlinear model fit to the caging experiment's mussel dynamics, with handling times unconstrained (circle) or constrained (diamond). Species abbreviations are Asa, *Austro-littorina antipodum*; Asc, *A. cincta*; Chb, *Chamaesipho brumnea*; Chc, *C. columna*; Epp, *Epopella plicata*; Myg, *Mytilus galloprovincialis*; NtR, *Notoacmea* sp.; Rsv, *Risellopsis varia*; Xnp, *Xenostrobus pulex*.

tween the *Haustrum*-enclosure cages and the cage-free reference plots at TH ($t_{42} = 1.13$, $P = 0.264$, $P_{\text{adj}} = 0.746$), but densities did increase in enclosure cages relative to the reference plots at CF ($t_{80} = 5.44$, $P < 0.001$, $P_{\text{adj}} < 0.001$). 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 due to their small size (mean = 7 mm).

In model fitting, nine of the twelve hypothesized models that included predation terms performed better in describing prey dynamics than did the remaining six models that did not (Table 2). The three best-performing models performed equally well ($\Delta\text{AIC}_i < 4$; 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 and self-limitation terms. This model suggested higher mussel immigration and self-limitation rates, and lower *Haustrum* attack rates, at

TABLE 1. Mean attack rates, c (mussels eaten per whelk per mussel per square meter per day), of *Haustrum scobina* whelks on *Xenostrobus pulex* mussels as estimated by the observational method.

Site and year or season	Estimate	90% confidence limits	
		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}

CF than at TH (Table 3). The best-performing nonlinear model also included only mussel immigration and self-limitation rates on a site-specific basis (Table 2). It too suggested higher immigration and self-limitation rates and lower feeding rates at CF than at TH (Table 4).

Comparison of methods

The best-performing nonlinear model’s per capita attack-rate estimate from the caging experiments closely matched the estimate obtained by the observational method at TH (Fig. 1). This site’s experimental 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. Increased variation across cages resulted in substantially wider confidence intervals at CF (Table 4). Agreement between the point estimates of the two methods nonetheless remained high at CF (<31%) when handling time was constrained. Despite the attack-rate point estimate of the unconstrained model being substantially higher than that of the observational method at CF, estimates remained within an order of magnitude (<610%) and did not differ significantly from one another. Congruence between the two methods for CF increased to <23% when cages with manipulated *Xenostrobus* treatments were omitted from the analysis (Table 4).

DISCUSSION

Estimates of species interaction strengths offer important insights into the structure and dynamics of food webs. Interaction strengths are difficult to measure however, and all methods suffer from simplifying assumptions that are rarely tested. This study used manipulative experiments to independently test the observational method for estimating interaction strengths proposed by Novak and Wootton (2008). Model-fit point estimates of per capita attack rates from these experiments were in close agreement with estimates of the observational method (within 23–610%). In fact, when handling times were constrained to their most likely empirical values, the best-performing nonlinear model produced point estimates that were within 5–31%

of the observational method’s estimates. Species-specific feeding-rate estimates were therefore similar to those observed in other studies of whelk–prey interactions for both methods (e.g., Navarrete and Castilla 2003, Aschaffenburg 2008). Yodzis (1988) has suggested that much of the indeterminacy inherent in food webs could be alleviated by an ability to estimate interaction

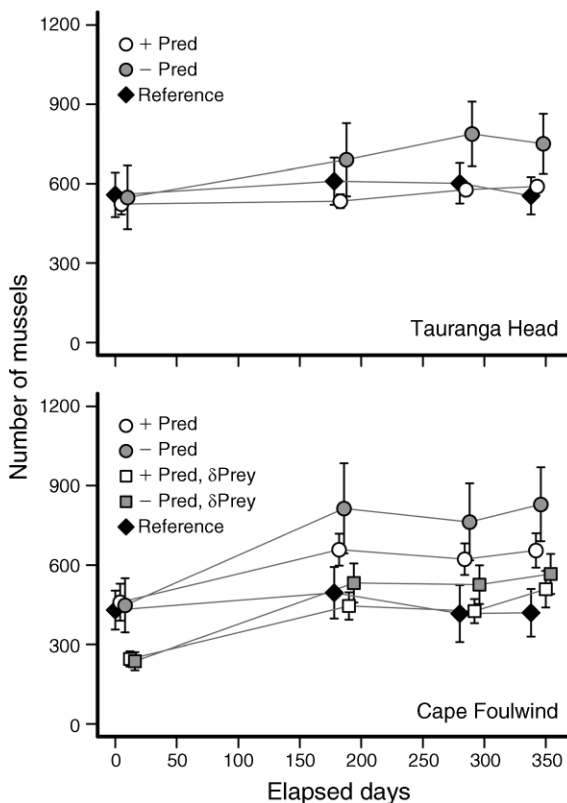


FIG. 2. Change in *Xenostrobus pulex* mussel population counts over time (mean \pm SE) observed in the experimentally manipulated presence (+Pred) and absence (–Pred) of *Haustrum* predation. At Cape Foulwind, starting mussel abundances were either reduced (δ Prey) or left unmanipulated. The reference treatment served as a control for the potential effects of the cages, which were $22 \times 20 \times 5$ cm in size. Points are staggered for clarity.

TABLE 2. AIC_c comparisons of competing models fit to the time-series dynamics of *Xenostrobus* mussels (prey) in the experimental presence or absence of *Haustrum* whelks (predator), without and with site-specific parameters.

Predator functional response	Density-independent prey mortality	Prey population self-limitation	k	L	AIC _c	Δ_i	w_i
No site-specific parameters							
No predator effect							
	no	yes	3	592.2	1190.7	11.9	0.001
	yes	no	3	592.1	1190.4	11.5	0.002
	yes	yes	4	592.0	1192.5	13.7	<0.001
Type I							
	no	yes	4	587.7	1183.8	5.0	0.041
	yes	no	4	588.3	1185.0	6.1	0.023
	yes	yes	5	587.6	1185.8	7.0	0.015
Type II							
	no	yes	5	587.7	1186.1	7.2	0.014
	yes	no	5	588.3	1187.2	8.4	0.008
	yes	yes	6	587.6	1188.1	9.2	0.005
Site-specific parameters							
No predator effect							
	no	yes	6	587.0	1186.9	8.1	0.009
	yes	no	6	587.2	1187.3	8.5	0.007
	yes	yes	8	586.6	1190.9	12.0	0.001
Type I							
	no	yes	8	580.6	1178.8	†	0.501
	yes	no	8	581.4	1180.5	1.7	0.214
	yes	yes	10	580.0	1182.6	3.7	0.078
Type II							
	no	yes	10	580.4	1183.4	4.6	0.050
	yes	no	10	581.2	1185.0	6.1	0.023
	yes	yes	12	580.0	1187.7	8.8	0.006

Notes: Symbols and variables are as follows: 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; and w_i , AIC_c weight. For information about Type I and Type II responses, see text following Eq. 3.

† Lowest AIC_c value.

strengths to an accuracy of within an order of magnitude (1000%). The results of this study therefore suggest that the observational method is robust and that it may be a productive approach for gaining insight into the species-rich and complex food webs of nature.

The agreement of the two approaches in estimating *Haustrum*'s attack rates on *Xenostrobus* mussels is notable for several reasons. *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. 1). 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 (TH) than at Cape Foulwind (CF) despite the fact that the two populations exhibited equivalent feeding activity levels as a whole (22–23% of individuals observed feeding). In fact, at TH the per capita attack rate was estimated to be an order of magnitude larger on *Xenostrobus* than on *Chamaesipho columna* (Fig. 1), the prey observed most frequently in *Haustrum*'s diet (Table A2). These results underscore the utility of

TABLE 3. Maximum-likelihood parameter estimates for the best-performing model.

Parameter and site	Estimate	90% confidence limits	
		Lower	Upper
Immigration, I (mussels·m ⁻² ·d ⁻¹)			
TH	4.621×10^{-2}	2.510×10^{-2}	9.667×10^{-2}
CF	7.832×10^{-2}	5.126×10^{-2}	1.241×10^{-1}
Self-limitation, n (mussels·mussel ⁻¹ ·m ⁻² ·d ⁻¹)			
TH	2.750×10^{-8}	3.666×10^{-9}	1.061×10^{-7}
CF	7.644×10^{-8}	5.717×10^{-8}	1.713×10^{-7}
Attack rate, α (mussels eaten·whelk ⁻¹ ·mussel ⁻¹ ·m ⁻² ·d ⁻¹)			
TH	1.964×10^{-5}	5.299×10^{-6}	3.504×10^{-5}
CF	1.242×10^{-5}	1.246×10^{-6}	2.554×10^{-5}

Note: Site abbreviations are Tauranga Head, New Zealand (TH), and Cape Foulwind, New Zealand (CF).

TABLE 4. Maximum-likelihood attack-rate estimates, c (mussels eaten·whelk⁻¹·mussel⁻¹·m⁻²·d⁻¹), for the best-performing Type II functional response model.

Site	Handling time constrained	Estimate	90% confidence limit	
			Lower	Upper
TH	yes†	2.700×10^{-5}	5.198×10^{-6}	7.725×10^{-5}
CF	yes†	1.757×10^{-5}	1.002×10^{-6}	6.500×10^{-5}
TH	no‡	1.964×10^{-5}	6.134×10^{-6}	3.743×10^{-5}
CF	no‡	9.463×10^{-5}	7.405×10^{-7}	4.184×10^{-1}
CF§	no	1.642×10^{-5}	1.557×10^{-6}	5.094×10^{-3}

Note: Site abbreviations are Tauranga Head, New Zealand (TH), and Cape Foulwind, New Zealand (CF).

† Handling time constrained to $h_{\text{TH}} = 1.24$ and $h_{\text{CF}} = 1.63$.

‡ Maximum-likelihood handling-time estimates were $h_{\text{TH}} = 0$ and $h_{\text{CF}} = 5.53$.

§ Includes only cages with ambient *Xenostrobus* starting density. Maximum-likelihood handling time estimate was $h_{\text{CF}} = 0$.

measuring interaction strengths on a per capita basis when pairs of species are compared (Novak and Wootton, *in press*).

The agreement between the two methods is also interesting because observational and experimental approaches did assume a subtle difference in functional responses: a multispecies vs. a single-species Type II functional response, respectively. Thus the fitted models assumed a predator responding only to *Xenostrobus* densities and ignored *Haustrum*'s feeding on other prey species, most importantly *Chamaesipho columna*. While technically feasible, the inclusion of *Haustrum*'s feeding on *C. 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) and the presence of live individuals beneath the *Xenostrobus* cover. (2) Models incorporating *C. 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 (Luckens 1975a; M. Novak, *personal observation*). (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 congruence between methods despite this difference in functional response assumptions suggests that alternative prey had relatively weak effects on the degree to which *Haustrum*'s feeding rates on *Xenostrobus* were saturated.

The nonlinearity of species interactions.—A second result of this study was that model selection favored models that described predation by a linear Type I functional response (Table 2). This result seems surprising given that whelks have repeatedly exhibited saturating functional responses under experimental manipulations of prey density (Murdoch 1969, Katz 1985, Moran 1985, Novak 2008). In fact, the *Haustrum*–*Xenostrobus* interaction was expected to be among the most nonlinear interactions of the system because

Xenostrobus' abundance, attack rates, and handling times were high relative to those of *Haustrum*'s other prey species. 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 CF, 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 4). The density reductions of these additional caging treatments at CF clearly influenced the performance of the nonlinear models.

Rather than being a problem of insufficient replication, this result may corroborate the idea that trophic interactions are approximately linear in the range of mean prey densities actually observed in nature, especially in multispecies settings (Abrams 1980, 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. 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.

It was also flexible to varied model formulations, including both linear and nonlinear functional responses. Paine's interaction strength index (Paine 1992), for example, is inappropriate to the open-recruitment biology of this study's focal prey (Novak and Wootton, *in press*). Other experimental indices avoiding these assumptions can also be derived but either produce biased attack-rate estimates or do not provide sufficient sensitivity when applied to this study's experiments (Appendix C; Novak 2008; Novak and Wootton, *in press*).

The observational method does itself assume a particular model and interpretation of the predator-dependent component of prey dynamics: a multispecies Type II functional response that assumes nontrivial handling times but trivial capture and post-handling digestion times (Novak and Wootton 2008). While the method appears flexible to near-linear interaction forms, many other functional response forms have also been proposed to describe predator-prey interactions (Abrams and Ginzburg 2000, Jeschke et al. 2002). The observational method would be ill suited for predicting long-term predator effects if predators exhibit strong positive density dependence in their feeding rates when prey abundances are low, as typified by Type III and ratio-dependent functional responses. Cross-habitat or prey-specific variation in the density-dependent form of a predator's feeding rates (e.g., Lipcius and Hines 1986, Seitz et al. 2001) would also complicate predictions and render the simple application of the observational method inappropriate (but see Novak and Wootton 2008). Nevertheless, Type II functional responses are among the most common nonlinear forms assumed by theoreticians and empiricists alike because they can be derived from first principles and have seen a wealth of empirical evidence to support their use (Murdoch and Oaten 1975, Jeschke et al. 2004). More experiments varying the density of multiple prey in factorial designs are needed to assess how well this largely single-prey-focused literature applies to the multispecies conditions of nature (e.g., Tschanz et al. 2007).

Further assumptions were also made by applying the observational approach in this study. Size and temperature-dependent handling times measured in the laboratory, for example, were assumed to correspond to those experienced by whelks in the field. An alternative approach would have monitored tagged individuals in the field (e.g., West 1986, 1988). I also assumed that feeding observations made during low tide periods accurately reflected the overall feeding rates of whelks across all tidal periods. In regions of the world where whelks exhibit pronounced behavioral responses to aerial exposure (Fairweather 1988), this assumption would not be appropriate. In this study the high agreement between observational and experimental attack-rate estimates for *Xenostrobus* suggests that these assumptions had minimal effect, though further inves-

tigations would be needed to assess potential biases across prey species.

The appeal of the observational approach is that it avoids many of the potentially confounding physical (Miller and Gaylord 2007), behavioral (Hall et al. 1990), and multi-predator (Menge et al. 2003) effects inherent in experimental species 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 CF, but not at TH (Fig. 2). The sources of between-cage variation that resulted in the high uncertainty of experimental attack-rate estimates at CF are similarly unclear; the observational method produced estimates with substantially smaller confidence intervals at both sites (Fig. 1).

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, but other, nonexperimental 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 were observed being fed upon so infrequently (Appendix A: Table A1), or had densities so low (Appendix A: Table A2), that feeding rates would have been too low to detect effects in any predator-exclusion experiment (Hall et al. 1990). Simulations have suggested that the method's estimates are unbiased by prey-specific differences in abundances, handling times, or attack rates, and that its accuracy is only weakly affected by the magnitude of the attack rates being estimated (Novak and Wootton 2008). Prey species experiencing weak per capita attack rates (e.g., *Epopella plicata*) would therefore require more feeding surveys than prey experiencing strong per capita attack rates (e.g., *Xenostrobus*) for equivalent precision to be achieved.

Employing the observational method at seasonal scales also revealed considerable temporal variation in attack rates. This variation was likely a function of both the metabolic effects of temperature (Largen 1967) and the behavioral changes in *Haustrum* associated with seasonal reproductive activity (M. Novak, *personal observation*). 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). 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 A

Seasonal temperatures, survey frequency, prey counts and accumulation curves, species abundances, and prey handling times (*Ecological Archives* E091-171-A1).

APPENDIX B

Mixed effects model summary tables (*Ecological Archives* E091-171-A2).

APPENDIX C

Performance of experimental interaction strength indices (*Ecological Archives* E091-171-A3).