Quantifying predator dependence in the functional response of generalist predators.

Supporting Information

Mark Novak, Christopher Wolf, Kyle Coblentz, Isaac Shepard

A. Intuition for the observational approach.

B. Derivation, applications, and future extensions of the observational approach.

C. Supplementary figures.

D. Functional response parameter estimates.

E. Data tables.

A   Intuition for the observational approach

Holling type II prey dependence

Novak & Wootton (2008) introduced an observational method for estimating the prey-specific per capita attack rates of a generalist predator population using estimates of prey abundance (N_i), handling times (h_i), and the number of feeding (n_i) and non-feeding (n_0) individuals observed during snapshot surveys of a focal predator population. Their analytical estimator for the attack rate on the ith prey (a_i) assumes a multispecies Holling type II functional response,

$$f_i(\vec{N}) = \frac{a_i N_i}{1 + \sum_k a_k h_k N_k},$$

(S1)

and is equivalent to

$$\hat{a}_i = \frac{n_i}{n_0} \frac{1}{h_i N_i}$$

(S2)

(Wolf *et al.*, in press). The next section of the SOM provides a derivation based on a statistical argument that is simpler, and hence more easily generalized, than the non-statistical 'first-principles' argument used by Novak & Wootton (2008).

As described in the main text, intuition for the method may be built by using the estimator to reformulate the type II functional response model in terms of the fraction of predator individuals expected to be observed feeding at any given time. For example, when the predator is a specialist feeding on only one prey species,

$$\frac{n_1}{n_0 + n_1} = \frac{\hat{a}_1 h_1 N_1}{1 + \hat{a}_1 h_1 N_1},$$

(S3)

which tends to 1 as a_1, h_1, or N_1 increase. The fraction of individuals observed to be feeding on a particular prey species during a snapshot survey will therefore increase the higher the predator's attack rate, the longer its handling time, or the more abundant the prey species is (Fig. 1A). Assumptions implicit in applying the approach are discussed in Novak & Wootton (2008). This approach has seen independent empirical support in a New Zealand intertidal study system (Novak, 2010; Yeakel *et al.*, 2011) and has been successfully applied in contexts logistically inaccessible to experimentation (Novak, 2013).

Note that many other prey-dependent functional response models also exist, including ones for which the attack rates and handling times are not assumed constant (see *Future extensions* below).

Ratio dependence

A multi-prey extension to the ratio-dependent model of Arditi & Ginzburg (1989) is

$$f_i(\vec{N}, P) = \frac{\alpha_i N_i}{P + \sum_k \alpha_k h_k N_k},$$

(S4)

where P is the focal predator's abundance (Abrams, 1997; Arditi & Michalski, 1995). The attack rate α_i is often interpreted as the rate at which prey become available to the predator, which differs from the interpretation of a_i (Abrams, 2015; Arditi & Ginzburg, 2012). In the next section of the SOM we show that the analytical estimator for this parameter is

$$\hat{\alpha}_i = \frac{n_i}{n_0} \frac{P}{h_i N_i}.$$

(S5)

When a specialist predator feeds on only one prey species, for example, the fraction of predators that are expected to be feeding at any given time is

$$\frac{n_1}{n_0 + n_1} = \frac{\hat{\alpha}_1 h_1 N_1}{P + \hat{\alpha}_1 h_1 N_1}. \tag{S6}$$

How quickly the predator population's feeding rate saturates thus depends on its own abundance. Equivalently, the greater the predator's abundance, the higher its attack rate must be to maintain a constant feeding rate when prey abundances and handling times remain unchanged.

Predator dependence

In the Beddington-DeAngelis model,

$$f_i(\vec{N}, P) = \frac{a_i N_i}{1 + \sum_k a_k h_k N_k + \gamma P}, \tag{S7}$$

parameter γ reflects the per capita strength of intraspecific effects among predators (Beddington, 1975; DeAngelis *et al.*, 1975). The model represents interference between predators associated with a reduction in the time a predator individual has available to search for prey. Note that a_i has the same interpretation as in the type II model and that predators can conceivably have facilitative effects on feeding rates, increasing available time for searching, when $\gamma < 0$. This single-predator functional response may be extended to consider multiple interacting predator species by describing the focal predator j's feeding rate on the ith prey by

$$f_{ij}(\vec{N}, \vec{P}) = \frac{a_{ij} N_i}{1 + \sum_k a_{kj} h_{kj} N_k + \sum_p \gamma_{jp} P_p}, \tag{S8}$$

where γ_{jp} reflects the intra- or interspecific effect of predator species p on the focal predator j's feeding rate.

In the next section of the SOM we show how the observational framework may be used to derive

$$\frac{\hat{a}_{ij}}{1 + \sum_p \hat{\gamma}_{jp} P_p} = \frac{n_i}{n_0} \frac{1}{h_i N_i}, \tag{S9}$$

relating the unknown terms of interest, $\hat{a}_{ij}$ and $\hat{\gamma}_{jp}$, to the observed number of feeding and non-feeding individuals, the prey and predator abundances, and the handling times. Note that in the absence of mutual predator effects this equation reduces to the estimator for $\hat{a}_i$ of the type II model (eqn. S2). Intuitively, the greater the number or per capita effects of interfering predators, the larger the per capita attack rate must be to maintain the same proportion of feeding individuals when handling times and species abundances remain unchanged. For a specialist predator, for example, the fraction of individuals expected to be feeding at any point in time (Fig. 1B) is

$$\frac{n_1}{n_0 + n_1} = \frac{\hat{a}_1 h_1 N_1}{1 + \hat{a}_1 h_1 N_1 + \sum_p \hat{\gamma}_{jp} P_p}. \tag{S10}$$

The simultaneous estimation of $\hat{a}_{ij}$ and $\hat{\gamma}_{jp}$ terms is not possible with only one snapshot survey. Rather, this requires surveys replicated in space or in time that differ in predator densities. Specifically, we require at least one more survey than the number of predator species. With such information the $\hat{a}_{ij}$ and $\hat{\gamma}_{jp}$ terms may be statistically estimated for any number of prey and predator species.

In fact, with a sufficient number of surveys, the unknown terms of many other functional response model may be estimated as well. This is made possible by noting that for a generalist predator the fractions not-feeding versus feeding on a particular prey species correspond to the probabilities of a multinomial distribution, just as the fraction feeding corresponds to the probability of a binomial distribution for a specialist predator. Here we thereby also consider a multi-prey extension to the predator-dependent Hassell-Varley style model of (Arditi & Akçakaya, 1990):

$$f_i(\vec{N}, P) = \frac{\alpha_i N_i}{P^m + \sum_k \alpha_k h_k N_k}. \tag{S11}$$

This model exponentiates the predator density of the ratio-dependent model (eqn. S4) with parameter m to represent a degree of intraspecific interference among predators whenever $m > 0$ (Hassell & Varley, 1969). Exponent m describes how fast feeding rates decline with predator density due to a reduction in the predator's search effectiveness (DeLong, 2014). The Hassell-Varley model reduces to the type II model when $m = 0$ and corresponds to the ratio-dependent model when $m = 1$.

Many other predator-dependent functional response forms are also possible (e.g., Abrams, 2010; Crowley & Martin, 1989; Jeschke *et al.*, 2002) (see *Future Extensions* below).

B Derivation, applications, and future extensions of observational approach

Function-free (density-independent) feeding rates

Consider a generalist predator whose diet includes $i = 1, ..., S$ different prey species but that can feed on only one prey item at a time. Let $i = 0$ denote the state of not feeding. The predator's feeding status at any point in time will follow a categorical distribution with probability p_i of being in the ith state.

Let f_i be the feeding rate of the predator on the ith prey species and let d_i be the detection time during which a feeding event is detectable to an observer. Over the course of some time T the predator will, on average, consume $f_i T$ individuals of prey i. This will amount to $f_i T d_i$ total time that the predator will be observable feeding on prey i. The proportion of time that the predator will be observable feeding on prey i will be $f_i d_i$, while the proportion of time it will be observable not feeding on any prey species will be $1 - \sum_{k=1}^{S} f_k d_k$.

It follows that if we observe n independent and equivalent predator individuals, the numbers of individuals observed in each state (denoted by subscripts) at any given time will reflect a multinomial distribution,

$$(n_0, n_1, ..., n_S) \sim Mult_n(1 - \sum_{k=1}^{S} f_k d_k, f_1 d_1, ..., f_S d_S). \tag{S12}$$

Noting that $0 \leq \sum_{k=1}^{S} f_k d_k \leq 1$, this permits us to use snapshot surveys of a predator population to estimate prey-specific feeding rates when detection times are known, regardless of the predator's underlying functional response. That is,

$$\hat{f}_i = \frac{\hat{p}_i}{d_i} = \frac{n_i}{n} \frac{1}{d_i}, \tag{S13}$$

where the notation $\hat{p}_i$ denotes a sample estimate for the proportion of individuals feeding on prey i. Equation S13 is the same as eqn. 3 of the main text and corresponds to the 'density-independent' (non-functional) model to which we refer. The model represents the hypothesis that the patch-to-patch variation in feeding rates is best explains by their overall mean feeding rate (i.e. an intercept-only model), with variation in the proportion of individuals observed feeding being driven by detection times (due to variation in predator size, prey size and identity, and temperature) alone, and not by variation in species abundances.

Equating detection and handling times

The ability to infer a predator population's feeding rates using eqn. 3 (eqn. S13) does not rest on the assumption that a predator's handling times (h_i) are equivalent to the time over which a feeding event is observable (its detection time, d_i). Indeed, the observable time of any aspect of the feeding process (e.g., capture, mastication, ingestion, digestion) may be used as long as this time period corresponds to the manner in which feeding versus not-feeding individuals are distinguished during feeding surveys. Furthermore, feeding rates may be estimated from a single snapshot survey. In principal, therefore, given a

sufficient number of surveys across a range of prey densities, the handling times relevant to the rate-limiting step of feeding rates and population dynamics (i.e. the 'effective' rather than just the 'observable' handling time) could be estimated by allowing these to be free parameters of a given functional response model, just like in the traditional functional response model-fitting framework.

In contrast, the derivations of the analytical attack rate estimators of the type II functional response (eqns. 1 & S2) and the ratio-dependent functional response (eqn. S5) do equate handling and detection times. The detection time is therefore assumed to correspond to the rate-limiting step of the feeding process. This is not apparent in the derivation of eqn. 1 presented by Novak & Wootton (2008) and highlights how many behavioral studies using direct measurements of handling times (Novak, 2010; Okuyama, 2012) may not be measuring a dynamically-relevant variable. Hence, in applications of the observational approach where handling times are to be estimated by model-fitting (see also *Future extensions* below), the analytical attack rate estimators and 'observable' handling times serve primarily to provide useful starting values for model-fitting optimization algorithms.

In our analyses of the *Nucella* data, we considered detection times and handling times to by equivalent. This allowed us to reduce the number of free parameters to be estimated (i.e. $\hat{a}$, $\hat{\alpha}$, $\hat{\gamma}$ and $\hat{m}$) and permitted the fitting of all models for even the most rarely observed prey species (in many cases a single observation in a single patch). For whelks, for which observable handling times range from hours to days (Novak, 2013), this assumption was deemed appropriate because the time it takes an individual to chase and capture an encountered prey item is minuscule compared to the time it takes to handle the prey item, and because handling entails both the drilling and digestion of the prey item such that the post-handling digestion time is also minuscule (Novak, 2008).

Handling (detection) times were calculated on the basis of each observed individual's size (shell length L_j in mm), prey identity and size (shell length L_i in mm) and temperature (T in °C) as

$$\ln h_i = \beta_0 + \beta_1 \ln L_j + \beta_2 \ln L_i + \beta_3 T, \tag{S14}$$

using regression coefficients (β_0 to β_3) estimated using laboratory experiments involving New Zealand's *Haustrum* whelks (see Table S29, Novak, 2010, 2013). Potential overestimates (underestimates) of *Nucella ostrina*'s true handling (detection) times incurred by poor matches between the whelk species will have resulted in underestimates (overestimates) of *Nucella*'s feeding rates, but should not have affected the relationship between its feedings rates and species densities or the relative performance of alternative functional response models.

Prey dependence

Suppose that both handling times (h_i) and prey abundances (N_i) are known and that predators feed according to a multispecies type II functional response, $f_i(\vec{N}) = \frac{a_i N_i}{1 + \sum a_k h_k N_k}$. If a random sample of n independently foraging predators are surveyed at the same time we expect the number of not-feeding and feeding individuals to be distributed as

$$(n_0, ..., n_S) \sim Mult_n \left(1 - \frac{\sum\limits_{k=1}^{S} a_k h_k N_k}{1 + \sum\limits_{k=1}^{S} a_k h_k N_k}, ..., \frac{a_i h_i N_i}{1 + \sum\limits_{k=1}^{S} a_k h_k N_k}, ... \right). \tag{S15}$$

Since we have assumed handling and detection times to be equivalent, the only unknown parameters are the a_i per capita attack rates. The Novak & Wootton (2008) estimator for these may be derived using the method of moments as follows:

From the probability that individuals are not feeding, $p_0 = 1 - \dfrac{\sum\limits_{k=1}^{S} a_k h_k N_k}{1 + \sum\limits_{k=1}^{S} a_k h_k N_k}$, we get $\dfrac{1}{p_0} =$

$1 + \sum\limits_{k=1}^{S} a_k h_k N_k$. Substituting this into the expression for p_i gives $p_i = \dfrac{a_i h_i N_i}{\frac{1}{p_0}}$, which implies $a_i = \dfrac{p_i}{p_0} \dfrac{1}{h_i N_i}$. Letting the sample estimate $\hat{p}_i = \dfrac{n_i}{n}$, it follows that $\hat{a}_i = \dfrac{n_i}{n_0} \dfrac{1}{h_i N_i}$ corresponding to the Novak & Wootton (2008) estimator (eqn. 1) as reformulated by Wolf *et al.* (in press).

Ratio dependence

The method of moments estimator for multispecies ratio-dependent functional response, $f_i(\vec{N}, P) = \dfrac{\alpha_i N_i / P}{1 + \sum \alpha_k h_k N_k / P} = \dfrac{\alpha_i N_i}{P + \sum \alpha_k h_k N_k}$, is obtained in the same way as it is in the multispecies type II functional response except that the predator's abundance must also be known. That is, for a single random survey of independently foraging predators we expect that the number of not-feeding and feeding individuals to be distributed as

$$(n_0, ..., n_S) \sim Mult_n \left(1 - \dfrac{\sum\limits_{k=1}^{S} \alpha_k h_k N_k}{P + \sum\limits_{k=1}^{S} \alpha_k h_k N_k}, ..., \dfrac{\alpha_i h_i N_i}{P + \sum\limits_{k=1}^{S} \alpha_k h_k N_k}, ... \right). \tag{S16}$$

Here the only unknown parameters are the α_i attack rates. From the probability that individuals are not feeding we get $\dfrac{1}{p_0} = P + \sum\limits_{k=1}^{S} \alpha_k h_k N_k$. Substituting this into the expression for p_i gives $p_i = \dfrac{\alpha_i h_i N_i}{\frac{P}{p_0}}$, which implies $\alpha_i = \dfrac{p_i}{p_0} \dfrac{P}{h_i N_i}$. Letting the sample estimate $\hat{p}_i = \dfrac{n_i}{n}$, it follows that $\hat{\alpha}_i = \dfrac{n_i}{n_0} \dfrac{P}{h_i N_i}$ corresponding to eqn. S5.

Predator dependence

The method of moments used above involves solving a system of S independent equations for S unknowns using data from a single survey. In each case the equation for p_0 is 1 minus the sum of the prey-specific probabilities since the population and sample proportions must each sum to 1. For functional responses having additional parameters we would generally need to perform additional surveys of populations having different species abundances in order to estimate all parameters. (This ignores issues of identifiability and the possibility of additional solutions due to non-linearities. For example, no amount of surveys would allow both attack rates and detection times to be estimated since only their product appears in the likelihood.)

For example, the single-predator single-prey Beddington-DeAngelis response, $f(N, P) = \dfrac{aN}{1 + ahN + \gamma P}$, involves such an additional parameter in the form of γ, denoting mutual predator effects. Here the probability of observing n_i feeding events in a single survey of n predators is distributed binomially. The method of moments estimator $\hat{p} = \dfrac{aNh}{1 + ahN + \gamma P}$ for the binomial cannot be solved with both a and γ unknown. However, a solution does exist and may be estimated (by maximum likelihood, for example) when two populations differing in predator abundance are surveyed.

Future extensions: Additional functional response models

The assumptions implicit in applying the observational approach to individual (or aggregated) surveys are discussed in Novak & Wootton (2008) and Novak (2010, 2013). Applications of the approach for the estimation and fitting of functional response models across multiple surveys repeated in space (or in time), as performed in the main text, introduces the additional assumption that per capita rates – e.g., interference rates and attack rates – are constant across these surveys. In principle this assumption could be relaxed by using flexible-preference functional response models (e.g., Abrams, 1990) given data from a sufficient number of surveys to fit these more complex models. Hierarchical models (Cressie *et al.*, 2009) that blend the two extremes of the case-wide versus patch-specific models used in manipulative patches will likely offer a useful approach for investigating such models while accounting for variation in sample sizes across surveys.

The fitting of many other functional response models should also be possible with additional surveys and co-variates. For example, with our data we were unable to obtain convergence in all three cases when attempting to fit the more complicated Crowley-Martin predator-dependent functional response which allows mutual predator effects to occur during both searching and handling behaviors, unlike the Beddington-DeAngelis model which assumes mutual predator effects occur only during searching (Crowley & Martin, 1989; Skalski & Gilliam, 2001). Likewise, a fast-growing literature based on theory and experiments using isolated predator-prey pairs evidences significant explanatory power in the allometric relationships the predator-prey body sizes and some functional response parameters (e.g., attack rates and handling times; Rall *et al.*, 2012; Pawar *et al.*, 2012; Weterings *et al.*, 2015) but not others (e.g., interference rates; DeLong, 2014). These relationships are in sore need of field-based investigations given the potential of other prey traits, intraspecific variation, and a generalist's prey preferences to reduce their utility (e.g., Kalinoski & DeLong, 2016; Nakazawa, 2017; Wootton & Emmerson, 2005). In our study, sample sizes (the number of surveys) and the range of relative body sizes were insufficient to rigorously do so (but see Fig. S6). That said, the observational approach is particularly useful for investigating the explanatory power of intraspecific allometric relationships given the ease with which the feeding observations of a focal predator population may be categorized into predator and prey size classes (Wolf *et al.*, in press; Novak, 2008).

Future extensions: Additional study systems, individual-level inferences, estimates of energy flow, and matters of 'instantism'

Organisms such as snakes, spiders and seastars whose detection times are long are obvious candidates for additional applications of the observational framework for inferring feeding rates from snapshot surveys of a predator population (see also Novak & Wootton, 2008). However, the framework may also be used when the duration of only some aspect of an individual's feeding process is observable, regardless of how short it is. Doing so necessitates the corresponding categorization of individuals into feeding versus not-feeding during feeding surveys. That is, the focal aspect of the feeding process need not be its rate-limiting step. The framework is therefore applicable to many other organisms as well, albeit with methods that may differ from common practices. For example, photographs of a fish school, a petri dish of protozoans, or an intertidal bench of foraging gulls (Wootton, 1997) may be used if studies of the associated detection times are also performed. Extensions of the framework to predators that are observed feeding on multiple prey simultaneously, as is needed for the use of gut contents surveys, for example, are also possible with additional

assumptions (*unpubl. ms*).

Inferences made using the observational framework as it is presented and used in this manuscript are at the population level. However, the approach may also be used to characterize individual-level feeding rates and functional responses by repeatedly surveying the same individual over time. That is, just as we apply the approach at the population by treating all individuals as (conditionally) independent and identically distributed, surveys of a single individual over (conditionally) independent and identically distributed time points spanning variation in prey and predator densities may be used to infer individual-level functional response parameters. In both cases, the more individuals (time points) that are surveyed, the better the estimates of the prey-specific feeding proportions ($\hat{p}_i$) will become. The approach may therefore be particularly useful in the context of assessing individual diet specialization (Bolnick *et al.*, 2003; Coblentz *et al.*, in press) where inferences have implicitly assumed that prey detection times are the same for all predator individuals.

It is also worth noting that potential applications of the framework to estimate rates of prey to predator energy flow would assume that all observed feeding events are successful (e.g., Novak, 2013). Without independent estimates of success rate, estimates of feeding and attack rates are better interpreted in a context of prey encounter rate and preference. For example, in our study we did not observe *Nucella ostrina* successfully drilling through the shells of *Mytilus californianus* mussels (cf. Sanford *et al.*, 2003).

Finally, a further and contentious issue in the debate over functional responses that future uses of the observational framework should help to overcome is the issue of 'instantism' when quantifying functional responses for use in models of predator-prey population dynamics (Abrams, 2015; Arditi & Ginzburg, 2012; Barraquand, 2014; Fussmann *et al.*, 2007; Jensen *et al.*, 2007). The crux of the issue is that predator reproduction unfolds on longer time-scales than the behavioral functional responses of predator individuals. The parameters of population models should therefore reflect these longer time-scales. The issue is equally germane to most experimental interaction strength estimates where the continuous-time models implicitly describing species interactions do not coincide with the discrete-time nature of population size counts (Novak & Wootton, 2010). Integro-differential equations and the use of coupled models reflecting the dynamics of both behavioral and population scales have been offered as ways forward (Barraquand, 2014; Jensen *et al.*, 2007), but here too logistical limitations have impeded empirical progress. More so than alternative approaches (see *Introduction*), the logistical feasibility and snapshot nature of the observational framework should make the appropriate parameterization of such models accessible by permitting the repeated estimation of parameters at higher frequencies over the duration of the biologically-appropriate time-scale of a focal predator population. More generally, these issues reflect the importance of distinguishing between functional (behavioral) and numerical (population dynamical) responses.

References

Abrams, P. (1997). Anomalous predictions of ratio-dependent models of predation. *Oikos*, 80, 163–171.

Abrams, P. A. (1990). The effects of adaptive-behavior on the type-2 functional-response. *Ecology*, 71, 877–885.

Abrams, P. A. (2010). Implications of flexible foraging for interspecific interactions: lessons from simple models. *Functional Ecology*, 24, 7–17.

Abrams, P. A. (2015). Why ratio dependence is (still) a bad model of predation. *Biological Reviews*, 90, 794–814.

Arditi, R. & Akçakaya, H. R. (1990). Underestimation of mutual interference of predators. *Oecologia*, 83, 358–361.

Arditi, R. & Ginzburg, L. R. (1989). Coupling in predator-prey dynamics: Ratio-dependence. *Journal of Theoretical Biology*, 139, 311–326.

Arditi, R. & Ginzburg, L. R. (2012). *How species interact: altering the standard view of trophic ecology*. Oxford University Press, Oxford.

Arditi, R. & Michalski, J. (1995). Nonlinear food web models and their responses to increased basal productivity. In: *Food Webs* (eds. Polis, G. & Winemiller, K. O.), book section 2.11. Springer, pp. 122–133.

Barraquand, F. (2014). Functional responses and predator–prey models: a critique of ratio dependence. *Theoretical Ecology*, 7, 3–20.

Beddington, J. R. (1975). Mutual interference between parasites or predators and its effect on searching efficiency. *The Journal of Animal Ecology*, 44, 331–340.

Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D. & Forister, M. L. (2003). The ecology of individuals: Incidence and implications of individual specialization. *American Naturalist*, 161, 1–28.

Coblentz, K. E., Rosenblatt, A. E. & Novak, M. (in press). The application of bayesian hierarchical models to quantify individual diet specialization. *Ecology*.

Cressie, N., Calder, C. A., Clark, J. S., Hoef, J. M. V. & Wikle, C. K. (2009). Accounting for uncertainty in ecological analysis: the strengths and limitations of hierarchical statistical modeling. *Ecological Applications*, 19, 553–570.

Crowley, P. H. & Martin, E. K. (1989). Functional responses and interference within and between year classes of a dragonfly population. *Journal of the North American Benthological Society*, 8, 211–221.

DeAngelis, D. L., Goldstein, R. A. & O'Neill, R. V. (1975). A model for tropic interaction. *Ecology*, 56, 881–892.

DeLong, J. P. (2014). The body-size dependence of mutual interference. *Biology Letters*, 10, 20140261.

Fussmann, G. F., Weithoff, G. & Yoshida, T. (2007). A direct, experimental test of resource vs. consumer dependence: Reply. *Ecology*, 88, 1603–1604.

Hassell, M. P. & Varley, G. C. (1969). New inductive population model for insect parasites and its bearing on biological control. *Nature*, 223, 1133–1137.

Jensen, C. X. J., Jeschke, J. M. & Ginzburg, L. R. (2007). A direct, experimental test of resource vs. consumer dependence: Comment. *Ecology*, 88, 1600–1602.

Jeschke, J. M., Kopp, M. & Tollrian, R. (2002). Predator functional responses: Discriminating between handling and digesting prey. *Ecological Monographs*, 72, 95–112.

Kalinoski, R. M. & DeLong, J. P. (2016). Beyond body mass: how prey traits improve predictions of functional response parameters. *Oecologia*, 180, 543–550.

Nakazawa, T. (2017). Individual interaction data are required in community ecology: a conceptual review of the predator–prey mass ratio and more. *Ecological Research*, 32, 5–12.

Novak, M. (2008). *Trophic omnivory and the structure, strength, and nonlinear nature of species interactions across a productivity gradient.* Ph.d., University of Chicago.

Novak, M. (2010). Estimating interaction strengths in nature: experimental support for an observational approach. *Ecology*, 91, 2394–2405.

Novak, M. (2013). Trophic omnivory across a productivity gradient: intraguild predation theory and the structure and strength of species interactions. *Proceedings of the Royal Society B: Biological Sciences*, 280.

Novak, M. & Wootton, J. T. (2008). Estimating nonlinear interaction strengths: an observation-based method for species-rich food webs. *Ecology*, 89, 2083–2089.

Novak, M. & Wootton, J. T. (2010). Using experimental indices to quantify the strength of species interactions. *Oikos*, 119, 1057–1063.

Okuyama, T. (2012). Flexible components of functional responses. *Journal of Animal Ecology*, 81, 185–189.

Pawar, S., Dell, A. I. & Van, M. S. (2012). Dimensionality of consumer search space drives trophic interaction strengths. *Nature*, advance online publication.

Rall, B. C., Brose, U., Hartvig, M., Kalinkat, G., Schwarzmüller, F., Vucic-Pestic, O. & Petchey, O. L. (2012). Universal temperature and body-mass scaling of feeding rates. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367, 2923–2934.

Sanford, E., Roth, M. S., Johns, G. C., Wares, J. P. & Somero, G. N. (2003). Local selection and latitudinal variation in a marine predator-prey interaction. *Science*, 300, 1135–1137.

Skalski, G. T. & Gilliam, J. F. (2001). Functional responses with predator interference: Viable alternatives to the holling type ii model. *Ecology*, 82, 3083–3092.

Weterings, R., Umponstira, C. & Buckley, H. L. (2015). Density-dependent allometric functional response models. *Ecological Modelling*, 303, 12–18.

Wolf, C., Novak, M. & Gitelman, A. I. (in press). Bayesian characterization of uncertainty in species interaction strengths. *Oecologia*.

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

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

Yeakel, J. D., Novak, M., Guimarães, Paulo R., J., Dominy, N. J., Koch, P. L., Ward, E. J., Moore, J. W. & Semmens, B. X. (2011). Merging resource availability with isotope mixing models: The role of neutral interaction assumptions. *PLoS ONE*, 6, e22015.

C   Supplementary figures
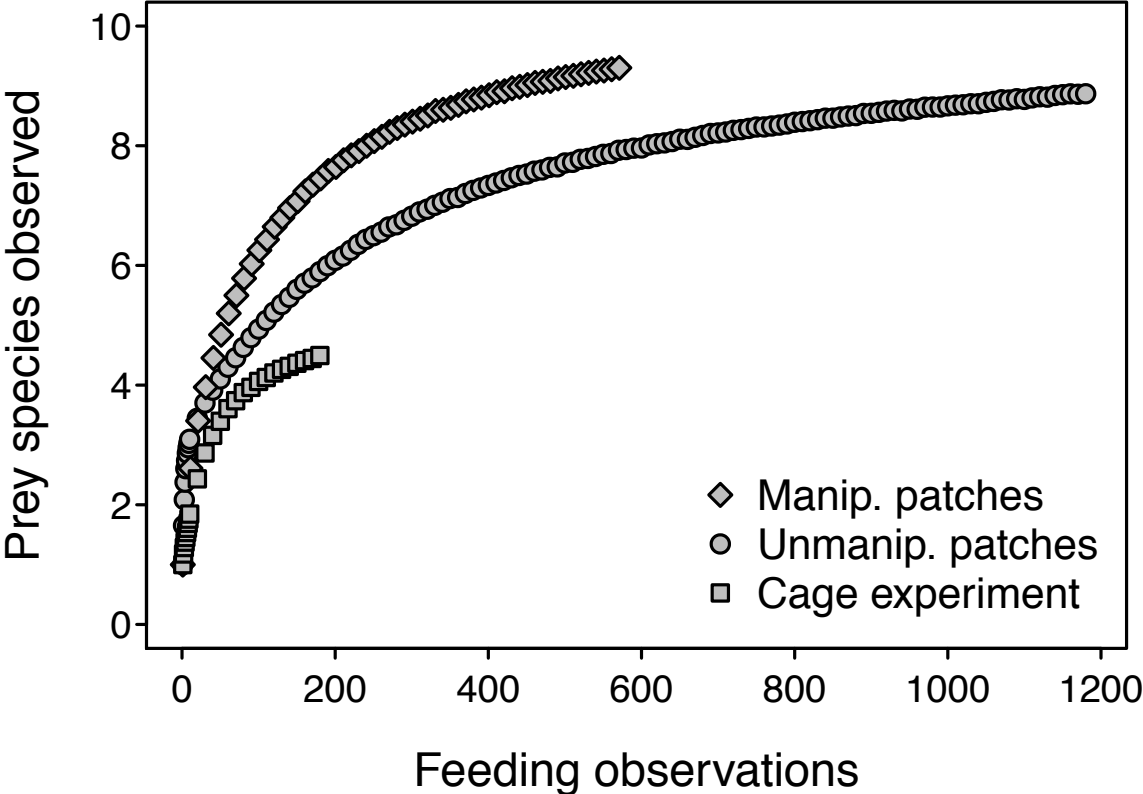
Figure S1: Species accumulation curves reflecting the mean number of prey species documented in *Nucella ostrina*'s diet as a function sampling effort (feeding observations). Note that the burrowing mussel *Adula californiensis*, on which two whelks were observed feeding in the unmanipulated patches, is excluded from these data.
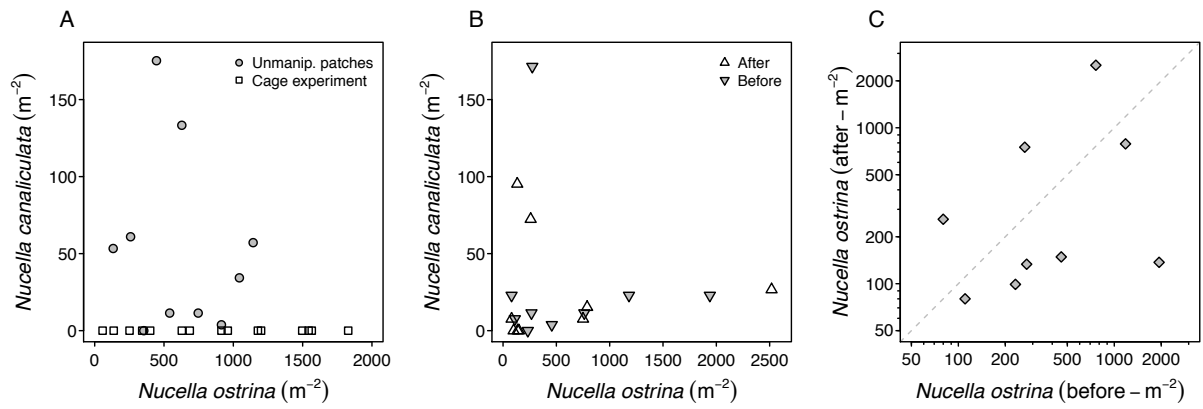
Figure S2: The density of *Nucella ostrina* and *N. canaliculata* in the (A) unmanipulated patches and experimental cages, and (B) the manipulated patches. (C) The density of *N. ostrina* before versus after manipulation.
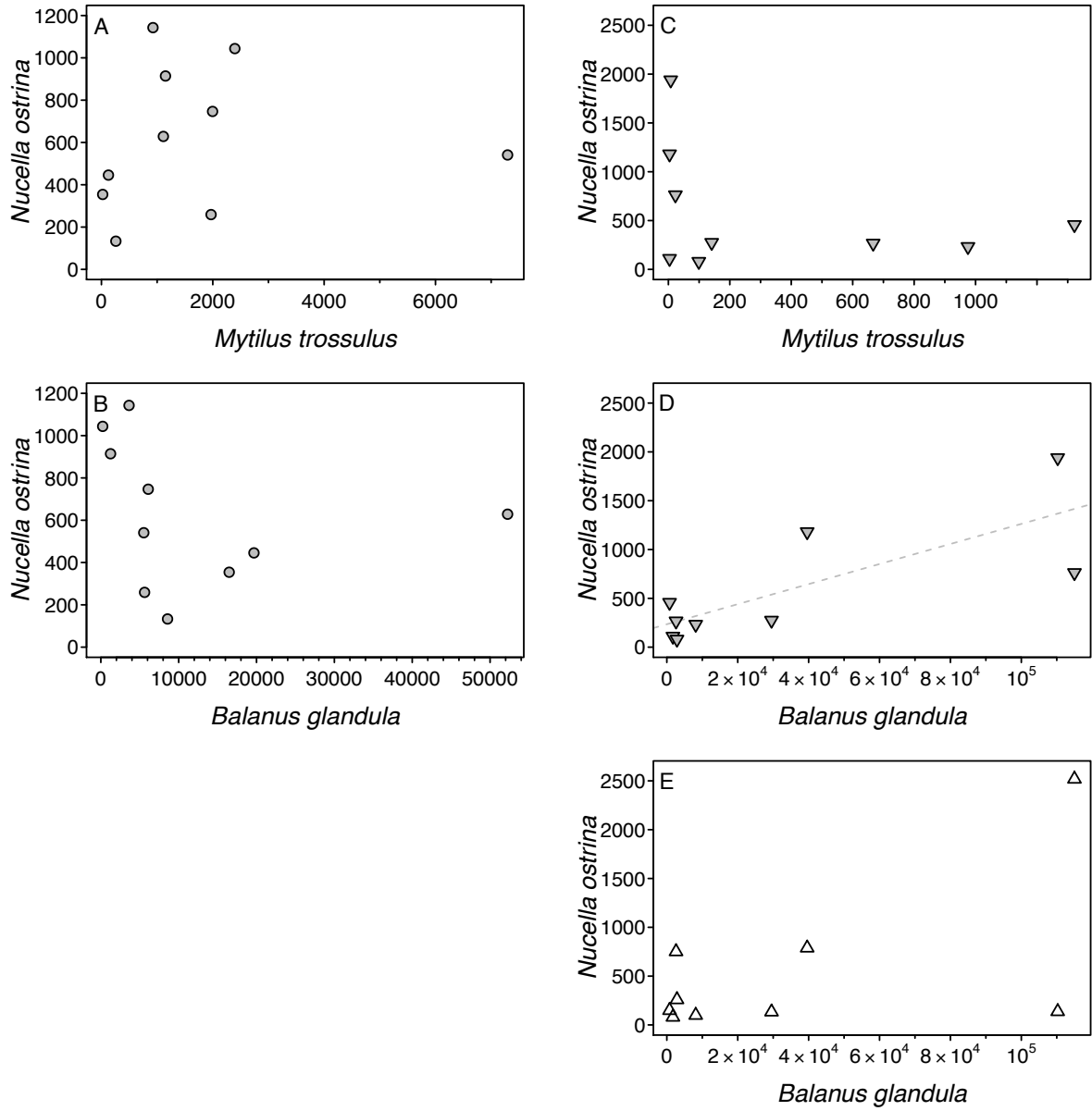
Figure S3: The relationships between the density of *Nucella ostrina* and its two primary prey species, *Mytilus trossulus* and *Balanus glandula*, in the (A-B) unmanipulated and (C-E) manipulated patches. The correlation between *N. ostrina* and *B. glandula* seen in (D) the manipulated patches prior to the manipulation of whelk densities ($R^2 = 0.60, p = 0.015$) was (E) absent after the manipulation.
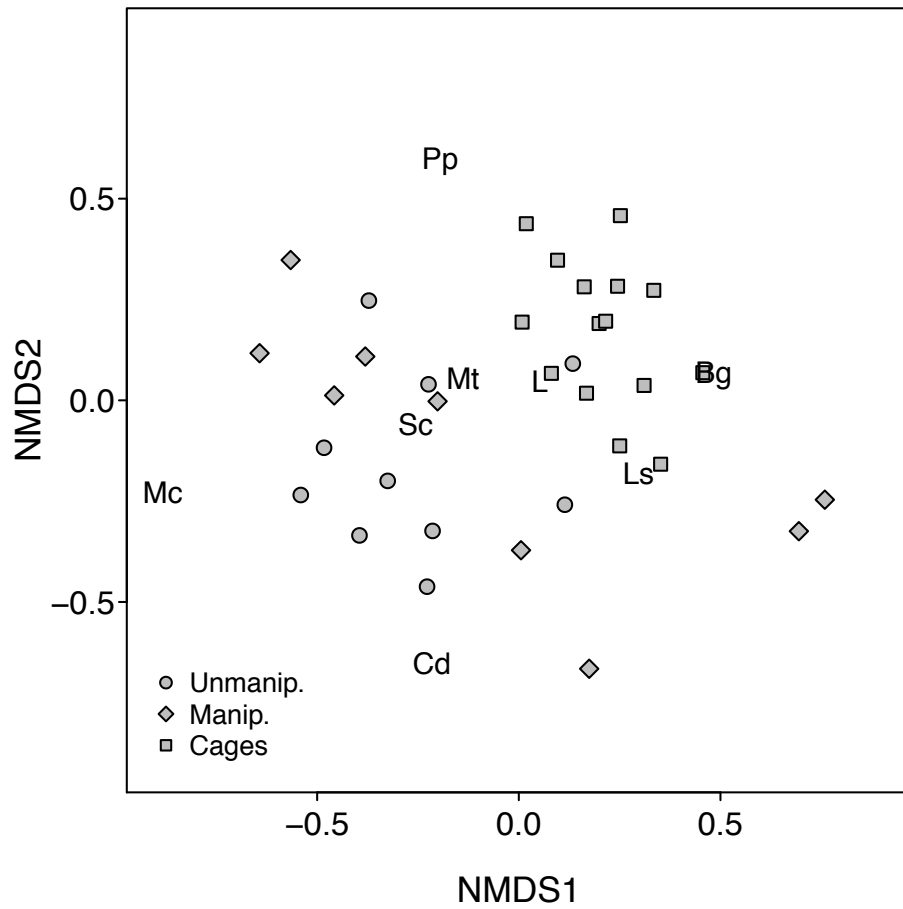
Figure S4: Prey composition of the two sets of patches and the caging experiment as visualized by non-metric multidimensional scaling using default settings of the Vegan:metaMDS function (incl. Bray-Curtis dissimilarities on square-root transformed species densities). See Table S1 for species codes. Code *L* refers to the sum of all three *Lottia* limpet species.
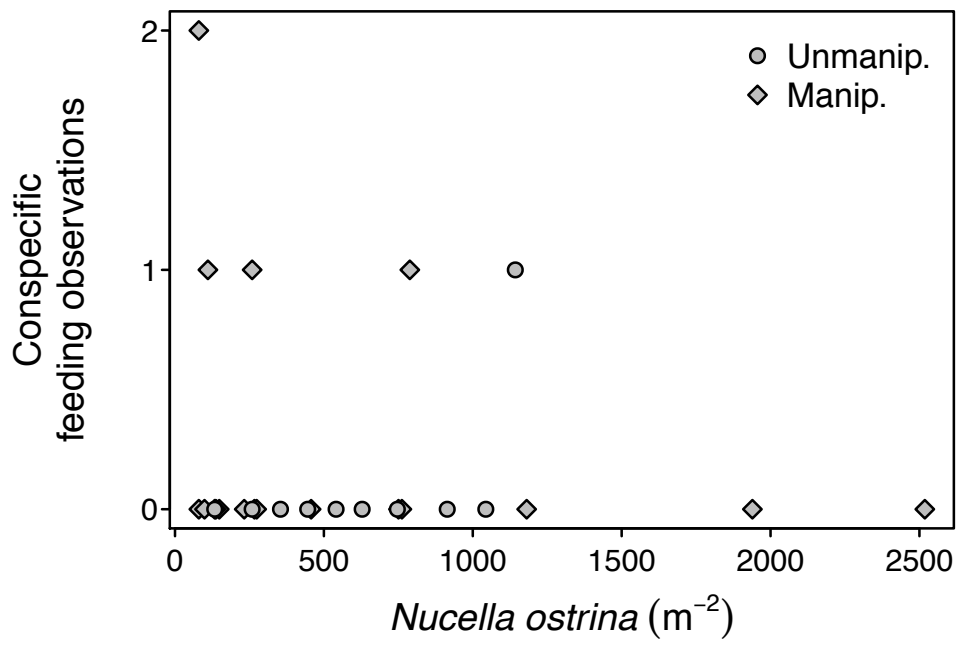
Figure S5: The incidence of conspecific feeding observations as a function of *Nucella ost-rina*'s density in the two sets of patch surveys.
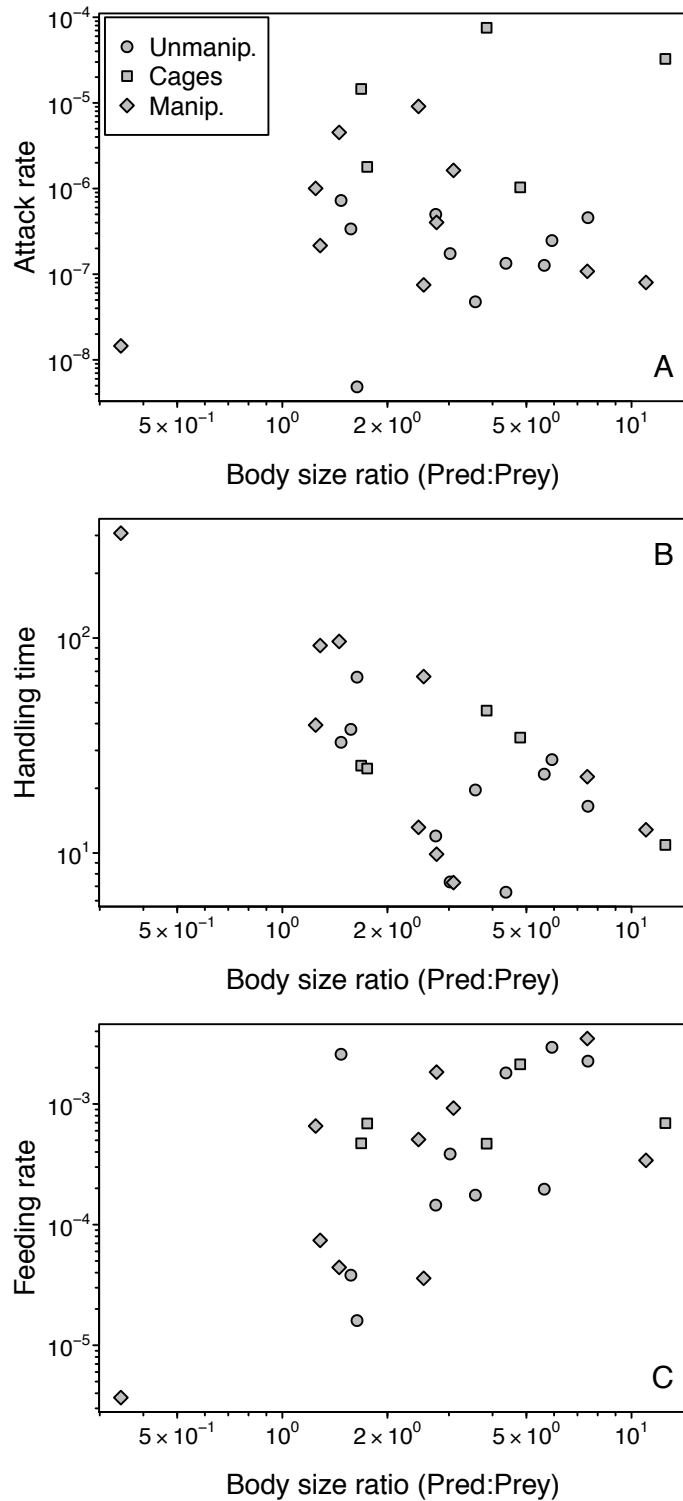
Figure S6: The relationships between relative predator and prey sizes (shell lengths) and *Nucella ostrina*'s (A) attack rates (as estimated assuming the Beddington-DeAngelis model), (B) handling times, and (C) feeding rates. Note that the negative relationship in (C) is to be expected given the assumed regression model relating predator size, prey size, and temperature to handling times as measured in laboratory experiments (see Novak (2010)).

D   Functional response parameter estimates

Table S1: Species abbreviations used throughout the appendices.

Species	Code
Not feeding	NF
Adula californiensis	Ac
Balanus glandula	Bg
Chthamalus dalli	Cd
Littorina sitkana	Ls
Lottia asmi	La
Lottia digitalis	Ld
Lottia pelta	Lp
Mytilus californianus	Mc
Mytilus trossulus	Mt
Nucella canaliculata	Nc
Nucella ostrina	No
Pollicipes polymerus	Pp
Semibalanus cariosus	Sc

Table S2: Maximum likelihood point estimates for models applied to the unmanipulated patches.

	Dens..indep.	Type.II	Ratio	BD..intra.	BD..intra.inter.	HV
Bg	$2.95x10^{-3}$	$4.53x10^{-7}$	$2.50x10^{-7}$	$2.47x10^{-7}$	$2.85x10^{-7}$	$4.53x10^{-7}$
Cd	$2.27x10^{-3}$	$1.06x10^{-6}$	$7.81x10^{-7}$	$4.57x10^{-7}$	$4.38x10^{-7}$	$1.06x10^{-6}$
Ls	$1.76x10^{-4}$	$1.64x10^{-7}$	$1.76x10^{-7}$	$4.76x10^{-8}$	$5.13x10^{-8}$	$1.64x10^{-7}$
La	$3.85x10^{-4}$	$4.70x10^{-7}$	$2.49x10^{-7}$	$1.74x10^{-7}$	$1.78x10^{-7}$	$4.70x10^{-7}$
Lp	$3.81x10^{-5}$	$8.05x10^{-7}$	$6.97x10^{-7}$	$3.38x10^{-7}$	$2.94x10^{-7}$	$8.05x10^{-7}$
Mc	$1.45x10^{-4}$	$9.71x10^{-7}$	$7.05x10^{-7}$	$4.99x10^{-7}$	$4.73x10^{-7}$	$9.71x10^{-7}$
Mt	$2.58x10^{-3}$	$1.56x10^{-6}$	$1.01x10^{-6}$	$7.26x10^{-7}$	$7.10x10^{-7}$	$1.56x10^{-6}$
No	$1.60x10^{-5}$	$1.67x10^{-8}$	$1.81x10^{-8}$	$4.84x10^{-9}$	$5.21x10^{-9}$	$1.67x10^{-8}$
Pp	$1.81x10^{-3}$	$1.76x10^{-7}$	$5.89x10^{-8}$	$1.34x10^{-7}$	$1.49x10^{-7}$	$1.76x10^{-7}$
Sc	$1.97x10^{-4}$	$2.68x10^{-7}$	$1.64x10^{-7}$	$1.27x10^{-7}$	$1.15x10^{-7}$	$2.68x10^{-7}$
No	-	-	-	$-6.44x10^{-4}$	$-7.25x10^{-4}$	$3.28x10^{-5}$
Nc	-	-	-	-	$2.01x10^{-3}$	-

Table S3: Maximum likelihood point estimates for models applied to the caging experiment.

Species	Dens..indep.	Type.II	Ratio	BD..intra.	HV
Bg	$2.13x10^{-3}$	$7.13x10^{-7}$	$7.10x10^{-7}$	$1.03x10^{-6}$	$7.13x10^{-7}$
Cd	$6.94x10^{-4}$	$1.68x10^{-6}$	$3.08x10^{-6}$	$3.26x10^{-5}$	$5.96x10^{-5}$
Mt	$4.72x10^{-4}$	$9.15x10^{-6}$	$1.42x10^{-5}$	$1.45x10^{-5}$	$9.15x10^{-6}$
Pp	$6.90x10^{-4}$	$1.43x10^{-6}$	$9.38x10^{-7}$	$1.79x10^{-6}$	$1.43x10^{-6}$
Sc	$4.69x10^{-4}$	$5.63x10^{-5}$	$4.31x10^{-5}$	$7.53x10^{-5}$	$5.63x10^{-5}$
No	-	-	-	$3.75x10^{-4}$	$6.13x10^{-6}$

Table S4: Maximum likelihood point estimates for models applied to the manipulated patches.

Species	Dens..indep.	Type.II	Ratio	BD..intra.	BD..intra.inter.	HV
Bg	$3.49x10^{-3}$	$1.06x10^{-7}$	$8.46x10^{-8}$	$1.08x10^{-7}$	$9.21x10^{-8}$	$1.06x10^{-7}$
Cd	$3.41x10^{-4}$	$7.89x10^{-8}$	$4.88x10^{-8}$	$8.01x10^{-8}$	$6.86x10^{-8}$	$7.89x10^{-8}$
La	$9.25x10^{-4}$	$1.61x10^{-6}$	$7.39x10^{-7}$	$1.63x10^{-6}$	$1.41x10^{-6}$	$1.61x10^{-6}$
Ld	$5.08x10^{-4}$	$9.07x10^{-6}$	$1.51x10^{-6}$	$9.11x10^{-6}$	$8.86x10^{-6}$	$9.07x10^{-6}$
Lp	$4.42x10^{-5}$	$4.51x10^{-6}$	$6.23x10^{-7}$	$4.52x10^{-6}$	$3.95x10^{-6}$	$4.51x10^{-6}$
Mc	$3.68x10^{-6}$	$1.44x10^{-8}$	$1.06x10^{-8}$	$1.45x10^{-8}$	$1.38x10^{-8}$	$1.44x10^{-8}$
Mt	$6.57x10^{-4}$	$9.97x10^{-7}$	$4.08x10^{-7}$	$1.00x10^{-6}$	$9.40x10^{-7}$	$9.97x10^{-7}$
No	$7.41x10^{-5}$	$2.14x10^{-7}$	$7.98x10^{-8}$	$2.16x10^{-7}$	$1.79x10^{-7}$	$2.14x10^{-7}$
Pp	$1.84x10^{-3}$	$4.02x10^{-7}$	$4.08x10^{-8}$	$4.02x10^{-7}$	$3.60x10^{-7}$	$4.02x10^{-7}$
Sc	$3.59x10^{-5}$	$7.42x10^{-8}$	$4.31x10^{-8}$	$7.50x10^{-8}$	$7.09x10^{-8}$	$7.43x10^{-8}$
No	-	-	-	$1.56x10^{-5}$	$-1.67x10^{-5}$	$1.75x10^{-13}$
Nc	-	-	-	-	$-3.91x10^{-3}$	-

Table S5: Maximum likelihood patch-specific feeding rate point estimates for the manipulated patches.

Species	AA4	AA6	AA7	BV1	IS1	MN1	MN2	SH1	SH2
Bg	$4.36x10^{-4}$	$1.65x10^{-4}$	$5.47x10^{-4}$	$5.99x10^{-3}$	$5.37x10^{-4}$	$1.41x10^{-2}$	$4.06x10^{-3}$	$6.43x10^{-3}$	$2.03x10^{-3}$
Cd	$1.21x10^{-4}$	-	-	$2.50x10^{-4}$	-	$4.53x10^{-4}$	$5.54x10^{-4}$	-	$2.69x10^{-3}$
La	$1.88x10^{-3}$	-	$3.43x10^{-3}$	$3.53x10^{-4}$	-	-	-	-	-
Ld	-	$1.51x10^{-3}$	-	-	-	$2.71x10^{-4}$	-	-	-
Lp	-	$1.42x10^{-4}$	$2.79x10^{-5}$	-	-	-	-	-	-
Mc	$4.13x10^{-6}$	-	-	-	-	-	-	-	-
Mt	$5.02x10^{-4}$	$2.56x10^{-3}$	$7.96x10^{-4}$	-	$8.49x10^{-4}$	-	$6.75x10^{-4}$	-	$1.16x10^{-3}$
No	-	$1.66x10^{-4}$	$7.12x10^{-5}$	$5.74x10^{-5}$	-	-	-	-	-
Pp	-	$2.59x10^{-3}$	$2.71x10^{-3}$	$3.86x10^{-4}$	-	-	-	-	-
Sc	$4.02x10^{-5}$	-	-	-	-	-	-	-	-
No	-	-	-	-	-	-	-	-	-

Table S6: Maximum likelihood patch-specific Type II attack rate point estimates for the manipulated patches.

Species	AA4	AA6	AA7	BV1	IS1	MN1	MN2	SH1	SH2
Bg	$1.76x10^{-7}$	$1.04x10^{-7}$	$2.03x10^{-7}$	$1.72x10^{-7}$	$7.69x10^{-7}$	$1.53x10^{-7}$	$1.50x10^{-7}$	$7.66x10^{-8}$	$2.86x10^{-7}$
Cd	$5.84x10^{-8}$	-	-	$1.36x10^{-8}$	-	$5.74x10^{-7}$	$2.74x10^{-7}$	-	$6.30x10^{-7}$
La	$1.51x10^{-6}$	-	$4.48x10^{-6}$	$8.85x10^{-7}$	-	-	-	-	-
Ld	-	$1.30x10^{-5}$	-	-	-	$7.46x10^{-6}$	-	-	-
Lp	-	$3.25x10^{-6}$	$7.88x10^{-6}$	-	-	-	-	-	-
Mc	$1.43x10^{-8}$	-	-	-	-	-	-	-	-
Mt	$7.93x10^{-7}$	$7.46x10^{-4}$	$8.63x10^{-6}$	-	$6.98x10^{-7}$	-	$5.22x10^{-6}$	-	$1.43x10^{-6}$
No	-	$1.57x10^{-6}$	$3.37x10^{-7}$	$7.51x10^{-8}$	-	-	-	-	-
Pp	-	$5.90x10^{-7}$	$1.87x10^{-7}$	$1.07x10^{-5}$	-	-	-	-	-
Sc	$7.41x10^{-8}$	-	-	-	-	-	-	-	-
No	-	-	-	-	-	-	-	-	-

Table S7: Maximum likelihood patch-specific ratio-dependent point estimates for the manipulated patches.

Species	AA4	AA6	AA7	BV1	IS1	MN1	MN2	SH1	SH2
Bg	$9.57x10^{-8}$	$9.47x10^{-9}$	$3.61x10^{-8}$	$1.82x10^{-7}$	$3.13x10^{-7}$	$7.78x10^{-8}$	$2.73x10^{-8}$	$9.71x10^{-8}$	$4.47x10^{-8}$
Cd	$3.18x10^{-8}$	-	-	$1.58x10^{-8}$	-	$1.15x10^{-7}$	$4.58x10^{-8}$	-	$1.43x10^{-7}$
La	$4.17x10^{-7}$	-	$1.15x10^{-6}$	$1.03x10^{-6}$	-	-	-	-	-
Ld	-	$1.42x10^{-6}$	-	-	-	$1.49x10^{-6}$	-	-	-
Lp	-	$3.57x10^{-7}$	$2.03x10^{-6}$	-	-	-	-	-	-
Mc	$1.07x10^{-8}$	-	-	-	-	-	-	-	-
Mt	$4.62x10^{-7}$	$6.01x10^{-5}$	$2.22x10^{-6}$	-	$2.56x10^{-7}$	-	$9.52x10^{-7}$	-	$3.24x10^{-7}$
No	-	$1.72x10^{-7}$	$7.55x10^{-8}$	$6.08x10^{-8}$	-	-	-	-	-
Pp	-	$5.29x10^{-8}$	$1.95x10^{-8}$	$1.25x10^{-5}$	-	-	-	-	-
Sc	$4.31x10^{-8}$	-	-	-	-	-	-	-	-
No	-	-	-	-	-	-	-	-	-

Table S8: Maximum likelihood patch-specific Beddington-DeAngelis point estimates for the manipulated patches.

Species	AA4	AA6	AA7	BV1	IS1	MN1	MN2	SH1	SH2
Bg	$1.89x10^{-5}$	$2.91x10^{-8}$	$5.23x10^{-6}$	$1.28x10^{-5}$	$2.91x10^{-5}$	$1.26x10^{-7}$	$6.55x10^{-8}$	$3.71x10^{-8}$	$3.08x10^{-7}$
Cd	$6.29x10^{-6}$	-	-	$1.11x10^{-6}$	-	$5.48x10^{-7}$	$1.31x10^{-7}$	-	$6.90x10^{-7}$
La	$8.31x10^{-5}$	-	$1.63x10^{-4}$	$7.26x10^{-5}$	-	-	-	-	-
Ld	-	$2.53x10^{-6}$	-	-	-	$7.13x10^{-6}$	-	-	-
Lp	-	$6.34x10^{-7}$	$2.86x10^{-4}$	-	-	-	-	-	-
Mc	$2.10x10^{-6}$	-	-	-	-	-	-	-	-
Mt	$9.14x10^{-5}$	$3.04x10^{-4}$	$3.13x10^{-4}$	-	$2.39x10^{-5}$	-	$2.28x10^{-6}$	-	$1.57x10^{-6}$
No	-	$3.06x10^{-7}$	$1.08x10^{-5}$	$4.29x10^{-6}$	-	-	-	-	-
Pp	-	$1.70x10^{-7}$	$2.89x10^{-6}$	$8.80x10^{-4}$	-	-	-	-	-
Sc	$8.53x10^{-6}$	-	-	-	-	-	-	-	-
No	$1.96x10^{-1}$	$-7.32x10^{-3}$	$1.37x10^{-1}$	$6.94x10^{-2}$	$9.00x10^{-2}$	$-1.24x10^{-4}$	$-2.48x10^{-3}$	$-2.60x10^{-4}$	$4.18x10^{-4}$

Table S9: Maximum likelihood patch-specific Hassel-Varley point estimates for the manipulated patches.

Species	AA4	AA6	AA7	BV1	IS1	MN1	MN2	SH1	SH2
Bg	$4.85x10^{-8}$	$1.04x10^{-7}$	$1.98x10^{-8}$	$1.87x10^{-7}$	$2.82x10^{-7}$	$1.53x10^{-7}$	$1.50x10^{-7}$	$7.66x10^{-8}$	$2.58x10^{-7}$
Cd	$1.61x10^{-8}$	-	-	$1.80x10^{-8}$	-	$5.74x10^{-7}$	$2.74x10^{-7}$	-	$5.77x10^{-7}$
La	$1.44x10^{-7}$	-	$7.54x10^{-7}$	$1.18x10^{-6}$	-	-	-	-	-
Ld	-	$1.30x10^{-5}$	-	-	-	$7.46x10^{-6}$	-	-	-
Lp	-	$3.25x10^{-6}$	$1.33x10^{-6}$	-	-	-	-	-	-
Mc	$8.29x10^{-9}$	-	-	-	-	-	-	-	-
Mt	$2.52x10^{-7}$	$7.46x10^{-4}$	$1.45x10^{-6}$	-	$2.27x10^{-7}$	-	$5.22x10^{-6}$	-	$1.31x10^{-6}$
No	-	$1.57x10^{-6}$	$4.57x10^{-8}$	$5.11x10^{-8}$	-	-	-	-	-
Pp	-	$5.90x10^{-7}$	$9.28x10^{-9}$	$1.43x10^{-5}$	-	-	-	-	-
Sc	$2.35x10^{-8}$	-	-	-	-	-	-	-	-
No	$1.83x10^{+00}$	$8.73x10^{-5}$	$1.31x10^{+00}$	$1.84x10^{+00}$	$1.11x10^{+00}$	$9.32x10^{-5}$	$8.24x10^{-5}$	$3.16x10^{-5}$	$5.91x10^{-2}$

Table S10: Pairwise comparisons of the prey-specific feeding rates and per capita attack rates across the three cases using Spearman's rank order correlation under the alternative hypothesis that a correlation is greater than zero. Feeding rates estimated by the density-independent model. Attack rates estimated by the single-predator Beddington-DeAngelis model.

Estimates	Comparison	Rank correlation	p-value
Feeding rates	Unmanipulated - Manipulated	0.717	0.018
	Unmanipulated - Cages	0.700	0.117
	Manipulated - Cages	0.700	0.117
Attack rates	Unmanipulated - Manipulated	0.000	0.509
	Unmanipulated - Cages	-0.200	0.658
	Manipulated - Cages	-0.600	0.883

Table S11: Comparison by AIC of all functional response models applied to (A) the unmanipulated patches, (B) the caging experiment, and (C) the manipulated patches (for which asterisks indicate models with patch-specific parameters). Note that it was not possible to fit the Beddington-DeAngelis model including both intra- and inter-specific effects to the cages or to the manipulated patches on a patch-specific basis.

Model	AIC	ΔAIC	df	weight
A. Unmanipulated Patches				
BD (intra+inter)	850.9	0.0	12	0.9967
BD (intra)	862.3	11.4	11	0.0033
Type II	968.8	117.9	10	<0.001
HV	970.8	119.9	11	<0.001
Dens. indep.	1198.4	347.5	10	<0.001
Ratio	1308.0	457.1	10	<0.001
B. Caging Experiment				
BD (intra)	144.7	0.0	6	0.45
Type II	144.9	0.2	5	0.40
HV	146.9	2.2	6	0.15
Dens. indep.	172.0	27.3	5	<0.001
Ratio	176.1	31.5	5	<0.001
C. Manipulated Patches				
BD (intra)*	271.1	0	44	>0.999
HV*	301.3	30.3	44	<0.001
Dens indep.*	333.2	62.1	35	<0.001
Type II*	335.3	64.2	35	<0.001
BD (intra+inter)	478.7	207.6	12	<0.001
Type II	490.7	219.6	10	<0.001
BD (intra)	492.6	221.5	11	<0.001
HV	492.7	221.6	11	<0.001
Ratio*	614.9	343.9	35	<0.001
Ratio	751.3	480.2	10	<0.001
Dens. indep.	900.9	629.9	10	<0.001

Table S12: Maximum likelihood point estimates and standard errors for the intraspecific-only Beddington-DeAngelis model in the unmanipulated patches.

Species	Estimate	Std..Error	z.value	Pr.z.
Bg	2.47e-07	6.58e-05	-126.19	0.00e+00
Cd	4.57e-07	9.38e-05	-82.03	0.00e+00
Ls	4.76e-08	4.59e-04	-21.69	2.69e-104
La	1.74e-07	4.16e-04	-20.79	5.34e-96
Lp	3.38e-07	1.00e-03	-7.97	1.53e-15
Mc	4.99e-07	1.00e-03	-7.59	3.19e-14
Mt	7.26e-07	7.36e-05	-98.15	0.00e+00
No	4.84e-09	1.01e-03	-12.17	4.30e-34
Pp	1.34e-07	4.50e-04	-19.80	3.07e-87
Sc	1.27e-07	3.07e-04	-29.20	1.78e-187
No	-6.44e-04	2.51e-05	-25.65	4.70e-145

Table S13: Maximum likelihood point estimates and standard errors for the intraspecific-only Beddington-DeAngelis model in the caging experiment.

Species	Estimate	Std..Error	z.value	Pr.z.
Bg	1.03e-06	2.86e-04	-2.41e+01	6.26e-128
Cd	3.26e-05	2.35e-18	-1.46e+15	0.00e+00
Mt	1.45e-05	5.08e-04	-8.32e+00	8.52e-17
Pp	1.79e-06	1.03e-03	-6.17e+00	6.92e-10
Sc	7.53e-05	4.43e-04	-5.84e+00	5.23e-09
No	3.75e-04	3.41e-04	1.10e+00	2.71e-01

Table S14: Maximum likelihood point estimates and standard errors for the intraspecific-only Beddington-DeAngelis model in the manipulated patches. Standard errors could not be estimated for the patch-specific point estimates as only two surveys were performed on each patch.

Species	Estimate	Std..Error	z.value	Pr.z.
Bg	1.08e-07	0.000109	-83.538	0.00e+00
Cd	8.01e-08	0.000324	-29.135	1.28e-186
La	1.63e-06	0.000383	-16.758	4.93e-63
Ld	9.11e-06	0.000710	-6.620	3.58e-11
Lp	4.52e-06	0.000710	-7.604	2.87e-14
Mc	1.45e-08	0.001002	-11.117	1.03e-28
Mt	1.00e-06	0.000123	-56.200	0.00e+00
No	2.16e-07	0.000452	-18.689	6.12e-78
Pp	4.02e-07	0.000247	-31.613	2.44e-219
Sc	7.50e-08	0.000580	-16.375	2.90e-60
No	1.56e-05	0.000068	0.229	8.19e-01

E   Data tables

Table S15: Mean prey densities (m^{-2}) of the unmanipulated patches.

Species	AA1	AA2	AA3	AA4	AA5	AA6	AA7	AA8	AA9	AA10
Ac	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Bg	1249.5	5619.0	8571.4	5516.2	3622.9	52251.4	19668.6	240.0	6087.6	16487.6
Cd	6979.0	1177.1	472.4	5504.8	2125.7	68.6	2129.5	361.9	2342.9	2727.6
Ls	358.1	61.0	251.4	491.4	1661.0	61.0	30.5	152.4	1257.1	133.3
La	1668.6	2525.7	1897.1	1211.4	1131.4	807.6	1485.7	624.8	1291.4	670.5
Lp	57.1	95.2	53.3	34.3	15.2	301.0	377.1	110.5	41.9	34.3
Mc	361.9	61.0	22.9	26.7	15.2	0.0	0.0	34.3	175.2	19.0
Mt	1150.5	1969.5	259.0	7295.2	925.7	1112.4	125.7	2396.2	1996.2	22.9
No	914.3	259.0	133.3	541.0	1142.9	628.6	445.7	1043.8	746.7	354.3
Pp	301.0	14426.7	1680.0	243.8	64.8	152.4	0.0	156.2	99.0	0.0
Sc	979.0	731.4	872.4	232.4	1782.9	312.4	434.3	190.5	449.5	1165.7

Table S16: Mean predator densities (m^{-2}) of the unmanipulated patches.

Species	AA1	AA2	AA3	AA4	AA5	AA6	AA7	AA8	AA9	AA10
No	914.3	259	133.3	541.0	1142.9	628.6	445.7	1043.8	746.7	354.3
Nc	3.8	61	53.3	11.4	57.1	133.3	175.2	34.3	11.4	0.0

Table S17: Feeding observations of the unmanipulated patches.

Species	AA1	AA2	AA3	AA4	AA5	AA6	AA7	AA8	AA9	AA10
NF	502	305	84	528	751	412	347	690	460	169
Ac	-	1	-	1	-	-	-	-	-	-
Bg	39	50	11	21	27	147	93	22	14	48
Cd	111	4	1	30	48	1	1	6	8	-
Ls	-	-	-	-	4	-	1	-	-	-
La	-	-	1	-	1	-	-	2	2	-
Lp	1	-	-	-	-	-	-	-	-	-
Mc	-	-	-	-	-	-	-	-	1	-
Mt	77	17	3	35	78	11	3	143	107	-
No	-	-	-	-	1	-	-	-	-	-
Pp	-	5	-	-	-	-	-	-	-	-
Sc	4	1	2	-	-	-	1	-	-	3

Table S18: Mean expected handling times (in hours) of the unmanipulated patches.

Species	AA1	AA2	AA3	AA4	AA5	AA6	AA7	AA8	AA9	AA10
Ac	-	64	-	16.8	-	-	-	-	-	-
Bg	33	28.1	15.9	38.9	30.6	26	23.9	24.9	31.2	19.5
Cd	19.9	17.8	11.2	20.9	20.4	12	10.6	15.7	20.1	-
Ls	-	-	-	-	22.9	-	16.3	-	-	-
La	-	-	12.7	-	5.6	-	-	9	2	-
Lp	37.6	-	-	-	-	-	-	-	-	-
Mc	-	-	-	-	-	-	-	-	12	-
Mt	48.6	52.3	15.2	45.8	24.9	25.4	19.9	40.1	22.5	-
No	-	-	-	-	65.8	-	-	-	-	-
Pp	-	6.6	-	-	-	-	-	-	-	-
Sc	53.8	18.7	15.8	-	-	-	17.2	-	-	10.9

Table S19: Feeding observations of the unmanipulated patches for Nucella canaliculata.

Species	AA1	AA2	AA3	AA4	AA5	AA6	AA7	AA8	AA9
NF	12	38	56	19	88	82	100	58	22
Bg	-	8	1	-	1	36	16	-	-
Cd	3	-	-	-	1	-	2	-	-
Mt	-	3	-	7	4	-	-	10	3
Sc	-	-	3	-	-	-	-	-	-

Table S20: Mean expected handling times (in hours) of the unmanipulated patches for Nucella canaliculata.

Species	AA1	AA3	AA4	AA5	AA6	AA7	AA8	AA9	AA2
Bg	-	9.5	-	32.2	25.1	23.7	-	-	27.7
Cd	14.1	-	-	19.6	-	17.9	-	-	-
Mt	-	-	44.3	27.5	-	-	33.2	53.3	76.9
Sc	-	16	-	-	-	-	-	-	-

Table S21: Mean predator and prey sizes (shell length, mm) in the unmanipulated patches.

Pred	Prey	PredSize	PreySize
Nucella canaliculata	Balanus glandula	14.3	2.3
Nucella canaliculata	Chthamalus dalli	9.3	1.2
Nucella canaliculata	Mytilus trossulus	13.7	10.8
Nucella canaliculata	Not Feeding	12.7	0.0
Nucella canaliculata	Semibalanus cariosus	12.3	1.3
Nucella ostrina	Adula californiensis	12.0	9.5
Nucella ostrina	Balanus glandula	14.2	2.4
Nucella ostrina	Chthamalus dalli	12.0	1.6
Nucella ostrina	Littorina sitkana	15.0	4.2
Nucella ostrina	Lottia asmi	13.0	4.3
Nucella ostrina	Lottia pelta	11.0	7.0
Nucella ostrina	Mytilus californianus	11.0	4.0
Nucella ostrina	Mytilus trossulus	13.7	9.3
Nucella ostrina	Not Feeding	13.8	0.0
Nucella ostrina	Nucella ostrina	18.0	11.0
Nucella ostrina	Pollicipes polymerus	16.6	3.8
Nucella ostrina	Semibalanus cariosus	13.5	2.4

Table S22: Mean prey densities (m^{-2}) of the caging experiment.

Survey	Bg	Cd	Mt	Pp	Sc
Cage01	3210	21	0	0	28
Cage02	3374	0	47	9	47
Cage03	2752	30	33	83	23
Cage04	3652	0	65	141	2
Cage05	2921	0	15	108	9
Cage06	2891	0	36	304	7
Cage07	2653	0	36	489	4
Cage08	3919	0	15	204	1
Cage09	3444	4	21	81	5
Cage10	1926	0	32	576	11
Cage11	2764	0	47	280	60
Cage12	2806	0	57	541	6
Cage13	3214	11	164	0	25
Cage14	3815	19	23	2	10
Cage15	4352	0	60	0	2

Table S23: Mean predator densities (m^{-2}) of the caging experiment.

Survey	No
Cage01	1177.1
Cage02	1828.6
Cage03	400.0
Cage04	1497.1
Cage05	251.4
Cage06	960.0
Cage07	685.7
Cage08	137.1
Cage09	1200.0
Cage10	628.6
Cage11	57.1
Cage12	1565.7
Cage13	342.9
Cage14	914.3
Cage15	1542.9

Table S24: Feeding observations of the caging experiment (first survey).

Survey	NF	Bg	Cd	Mt	Pp	Sc
Cage01	98	3	1	1	-	-
Cage02	145	14	1	-	-	-
Cage03	32	2	-	-	-	1
Cage04	114	16	-	1	-	-
Cage05	21	1	-	-	-	-
Cage06	78	6	-	-	-	-
Cage07	53	7	-	-	-	-
Cage08	12	-	-	-	-	-
Cage09	95	10	-	-	-	-
Cage10	50	3	-	-	1	1
Cage11	5	-	-	-	-	-
Cage12	128	8	-	1	-	-
Cage13	26	4	-	-	-	-
Cage14	73	3	-	-	-	4
Cage15	119	13	-	3	-	-

Table S25: Feeding observations of the caging experiment (second survey).

Survey	NF	Bg	Cd	Mt	Pp	Sc
Cage01	103	6	-	-	-	-
Cage02	153	7	-	-	-	-
Cage03	32	3	-	-	-	-
Cage04	115	14	-	-	-	-
Cage05	20	2	-	-	-	-
Cage06	80	4	-	-	-	-
Cage07	55	4	-	-	-	-
Cage08	9	1	-	-	-	-
Cage09	97	8	-	-	-	-
Cage10	53	2	-	-	-	-
Cage11	4	1	-	-	-	-
Cage12	123	8	-	-	-	1
Cage13	28	2	-	-	-	-
Cage14	71	6	-	-	-	-
Cage15	144	8	-	2	-	-

Table S26: Mean expected handling times (in hours) of the caging experiment (first survey).

Survey	Bg	Cd	Mt	Pp	Sc
Cage01	34.3	10.6	28.1	-	-
Cage02	25.5	11.2	-	-	-
Cage03	44.4	-	-	-	42.2
Cage04	33.5	-	24.6	-	-
Cage05	44.3	-	-	-	-
Cage06	36	-	-	-	-
Cage07	33.5	-	-	-	-
Cage08	-	-	-	-	-
Cage09	38.1	-	-	-	-
Cage10	51.2	-	-	24.7	46.7
Cage11	-	-	-	-	-
Cage12	33.9	-	4.6	-	-
Cage13	27.8	-	-	-	-
Cage14	20.7	-	-	-	40.7
Cage15	30.2	-	33.2	-	-

Table S27: Mean expected handling times (in hours) of the caging experiment (second survey).

Survey	Bg	Cd	Mt	Pp	Sc
Cage01	25.2	-	-	-	-
Cage02	28.4	-	-	-	-
Cage03	26	-	-	-	-
Cage04	32.7	-	-	-	-
Cage05	31.4	-	-	-	-
Cage06	44.5	-	-	-	-
Cage07	44.3	-	-	-	-
Cage08	44.3	-	-	-	-
Cage09	37.7	-	-	-	-
Cage10	33.6	-	-	-	-
Cage11	42.2	-	-	-	-
Cage12	39.7	-	-	-	54.1
Cage13	9.5	-	-	-	-
Cage14	32.3	-	-	-	-
Cage15	38.3	-	36.9	-	-

Table S28: Mean predator and prey sizes (shell length, mm) in the experimental cages.

Pred	Prey	PredSize	PreySize
Nucella ostrina	Balanus glandula	14.4	3.0
Nucella ostrina	Chthamalus dalli	12.5	1.0
Nucella ostrina	Mytilus trossulus	14.8	8.8
Nucella ostrina	Not Feeding	14.2	
Nucella ostrina	Pollicipes polymerus	14.0	8.0
Nucella ostrina	Semibalanus cariosus	15.0	3.9

Table S29: The handling times of *Nucella* feeding observations were inferred on the basis of an individual predator's size, its prey's identity and size, and temperature using regression coefficients obtained for *Haustrum* whelks of New Zealand (Novak, 2013)).

Oregon	New Zealand	
Prey	Predator	Prey
Balanus glandula	Haustrum scobina	Chamaesipho columna
Cthamalus dalli	Haustrum scobina	Chamaesipho columna
Littorina sitkana	Haustrum scobina	Austrolittorina cincta
Lottia asmi	Haustrum scobina	Notoacmea spp.
Lottia digitalis	Haustrum scobina	Notoacmea spp.
Lottia pelta	Haustrum scobina	Notoacmea spp.
Mytilus californianus	Haustrum scobina	Xenostrobus pulex
Mytilus torssulus	Haustrum scobina	Xenostrobus pulex
Nucella ostrina	Haustrum haustorium	Haustrum scobina
Pollicipes polymerus	Haustrum scobina	Calantica spinosa
Semibalanus cariosus	Haustrum scobina	Chamaesipho columna

Table S30: Mean prey densities (m^{-2}) of the manipulated patches.

Species	AA4	AA6	AA7	BV1	IS1	MN1	MN2	SH1	SH2
Bg	2594.3	1710.5	2861.0	39588.6	765.7	110262.9	29531.4	114986.7	8144.8
Cd	2171.4	647.6	179.0	21516.2	441.9	994.3	2217.1	358.1	5131.4
La	1203.8	1112.4	822.9	464.8	937.1	293.3	5424.8	160.0	2792.4
Ld	457.1	121.9	80.0	190.5	198.1	45.7	163.8	34.3	1847.6
Lp	34.3	45.7	3.8	0.0	121.9	72.4	11.4	11.4	38.1
Mc	308.6	198.1	87.6	49.5	45.7	0.0	53.3	0.0	34.3
Mt	666.7	3.8	99.0	3.8	1321.9	7.6	141.0	22.9	975.2
No	266.7	110.5	80.0	1181.0	457.1	1939.0	274.3	761.9	232.4
Pp	3200.0	4773.3	14994.3	41.9	1904.8	0.0	3375.2	3.8	506.7
Sc	571.4	1352.4	495.2	99.0	251.4	11.4	1676.2	3.8	19.0

Table S31: Mean predator densities (m^{-2}) of the manipulated patches (first survey).

Species	AA4	AA6	AA7	BV1	IS1	MN1	MN2	SH1	SH2
No	266.7	110.5	80.0	1181.0	457.1	1939.0	274.3	761.9	232.4
Nc	11.4	7.6	22.9	22.9	3.8	22.9	171.4	11.4	0.0

Table S32: Mean predator densities (m^{-2}) of the manipulated patches (second survey).

Species	AA4	AA6	AA7	BV1	IS1	MN1	MN2	SH1	SH2
No	750.5	80.0	259.0	788.6	148.6	137.1	133.3	2518.1	99
Nc	7.6	7.6	72.4	15.2	0.0	0.0	95.2	26.7	0

Table S33: Feeding observations of the manipulated patches (first survey).

Species	AA4	AA6	AA7	BV1	IS1	MN1	MN2	SH1	SH2
NF	208	130	87	369	391	314	114	709	97
Bg	6	1	1	38	8	65	11	73	8
Cd	1	-	-	1	-	-	1	-	4
La	2	-	-	2	-	-	-	-	-
Ld	-	1	-	-	-	-	-	-	-
Lp	-	1	-	-	-	-	-	-	-
Mc	-	-	-	-	-	-	-	-	-
Mt	16	-	-	-	19	-	6	-	7
No	-	1	2	-	-	-	-	-	-
Pp	-	7	3	1	-	-	-	-	-
Sc	1	-	-	-	-	-	-	-	-

Table S34: Feeding observations of the manipulated patches (second survey).

Species	AA4	AA6	AA7	BV1	IS1	MN1	MN2	SH1	SH2
NF	751	148	237	155	94	140	175	610	74
Bg	7	1	2	22	2	24	6	171	5
Cd	1	-	-	-	-	1	1	-	-
La	-	-	3	-	-	-	-	-	-
Ld	-	-	-	-	-	1	-	-	-
Lp	-	-	1	-	-	-	-	-	-
Mc	1	-	-	-	-	-	-	-	-
Mt	8	5	5	-	8	-	2	-	-
No	-	-	1	1	-	-	-	-	-
Pp	-	5	1	-	-	-	-	-	-
Sc	2	-	-	-	-	-	-	-	-

Table S35: Mean expected handling times (in hours) of the manipulated patches (first survey).

Species	AA4	AA6	AA7	BV1	IS1	MN1	MN2	SH1	SH2
Bg	27.6	35.9	12	18.9	41.6	11.4	16.7	19.3	36.1
Cd	15.2	-	-	9.5	-	-	10.6	-	12.8
La	4.9	-	-	13.5	-	-	-	-	-
Ld	-	4.8	-	-	-	-	-	-	-
Lp	-	50.8	-	-	-	-	-	-	-
Mc	-	-	-	-	-	-	-	-	-
Mt	32.9	-	-	-	66.7	-	47.5	-	51.8
No	-	43.6	85.7	-	-	-	-	-	-
Pp	-	12.4	10.9	6.2	-	-	-	-	-
Sc	51.7	-	-	-	-	-	-	-	-

Table S36: Mean expected handling times (in hours) of the manipulated patches (second survey).

Species	AA4	AA6	AA7	BV1	IS1	MN1	MN2	SH1	SH2
Bg	30.3	44.3	17.4	12.4	9.8	12.2	10.9	22.7	28.1
Cd	16.8	-	-	-	-	12.9	12	-	-
La	-	-	3.5	-	-	-	-	-	-
Ld	-	-	-	-	-	21.6	-	-	-
Lp	-	-	142	-	-	-	-	-	-
Mc	307.4	-	-	-	-	-	-	-	-
Mt	51.7	12.1	24.9	-	35.8	-	30.7	-	-
No	-	-	136.3	103.5	-	-	-	-	-
Pp	-	18	1.9	-	-	-	-	-	-
Sc	80.6	-	-	-	-	-	-	-	-

Table S37: Feeding observations of the manipulated patches (first survey) for Nucella canaliculata.

Species	AA4	AA6	AA7	BV1	IS1	MN1	MN2	SH1
NF	5	23	19	4	3	4	35	8
Bg	-	1	-	1	-	1	7	1
Mc	-	1	-	-	-	-	-	-
Mt	-	-	2	-	-	-	-	-
Pp	-	1	-	-	-	-	-	-
Sc	-	-	-	-	-	-	-	-

Table S38: Feeding observations of the manipulated patches (second survey) for Nucella canaliculata.

Species	AA4	AA6	AA7	BV1	IS1	MN1	MN2	SH1
NF	13	26	63	5	1	5	83	8
Bg	1	-	-	1	-	1	1	7
Mc	-	-	-	-	-	-	-	-
Mt	-	-	1	-	-	-	-	-
Pp	-	-	2	-	-	-	-	-
Sc	1	-	-	-	-	-	-	-

Table S39: Mean expected handling times (in hours) of the manipulated patches (first survey) for Nucella canaliculata.

Species	AA6	AA7	BV1	MN1	MN2	SH1
Bg	30.7	-	10	9.1	12.1	21.6
Mc	10.1	-	-	-	-	-
Mt	-	64	-	-	-	-
Pp	8.6	-	-	-	-	-
Sc	-	-	-	-	-	-

Table S40: Mean expected handling times (in hours) of the manipulated patches (second survey) for Nucella canaliculata.

Species	AA4	AA7	BV1	MN1	MN2	SH1
Bg	8	-	10	10	8.6	26.7
Mc	-	-	-	-	-	-
Mt	-	13.4	-	-	-	-
Pp	-	14.7	-	-	-	-
Sc	117	-	-	-	-	-

Table S41: Mean predator and prey sizes (shell length, mm) in the manipulated patches.

Pred	Prey	PredSize	PreySize
Nucella canaliculata	Balanus glandula	14.5	1.6
Nucella canaliculata	Mytilus californianus	16.0	5.0
Nucella canaliculata	Mytilus trossulus	19.0	16.7
Nucella canaliculata	Not Feeding	13.5	
Nucella canaliculata	Pollicipes polymerus	15.0	5.3
Nucella canaliculata	Semibalanus cariosus	16.0	10.0
Nucella ostrina	Balanus glandula	12.7	1.7
Nucella ostrina	Chthamalus dalli	12.1	1.1
Nucella ostrina	Lottia asmi	13.6	4.4
Nucella ostrina	Lottia digitalis	13.5	5.5
Nucella ostrina	Lottia pelta	16.0	11.0
Nucella ostrina	Mytilus californianus	20.0	58.0
Nucella ostrina	Mytilus trossulus	13.7	11.0
Nucella ostrina	Not Feeding	13.2	
Nucella ostrina	Nucella ostrina	15.4	12.0
Nucella ostrina	Pollicipes polymerus	14.1	5.1
Nucella ostrina	Semibalanus cariosus	16.0	6.3