

Using the functional response of a consumer to predict biotic resistance to invasive prey

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Abstract. Predators sometimes provide biotic resistance against invasions by nonnative prey. Understanding and predicting the strength of biotic resistance remains a key challenge in invasion biology. A predator's functional response to nonnative prey may predict whether a predator can provide biotic resistance against nonnative prey at different prey densities. Surprisingly, functional responses have not been used to make quantitative predictions about biotic resistance. We parameterized the functional response of signal crayfish (*Pacifastacus leniusculus*) to invasive New Zealand mud snails (*Potamopyrgus antipodarum*; NZMS) and used this functional response and a simple model of NZMS population growth to predict the probability of biotic resistance at different predator and prey densities. Signal crayfish were effective predators of NZMS, consuming more than 900 NZMS per predator in a 12-h period, and Bayesian model fitting indicated their consumption rate followed a type 3 functional response to NZMS density. Based on this functional response and associated parameter uncertainty, we predict that NZMS will be able to invade new systems at low crayfish densities (<0.2 crayfish/m²) regardless of NZMS density. At intermediate to high crayfish densities (>0.2 crayfish/m²), we predict that low densities of NZMS will be able to establish in new communities; however, once NZMS reach a threshold density of ~ 2000 NZMS/m², predation by crayfish will drive negative NZMS population growth. Further, at very high densities, NZMS overwhelm predation by crayfish and invade. Thus, interacting thresholds of propagule pressure and predator densities define the probability of biotic resistance. Quantifying the shape and uncertainty of predator functional responses to nonnative prey may help predict the outcomes of invasions.

Key words: biotic resistance; crayfish; New Zealand mud snail; *Pacifastacus leniusculus*; *Potamopyrgus antipodarum*; predation; propagule pressure; San Lorenzo River, California, USA; stream; type 3 functional response.

INTRODUCTION

The process of biological invasion is strongly influenced by the prevalence of consumers in the nonnative species' introduced range (Elton 1958). In the introduced range, the lack of predators may enable the release and spread of nonnative prey (i.e., enemy release; Darwin 1859, Elton 1958, Colautti et al. 2004). Alternatively, nonnative species may face novel enemies in the invaded community to which they are completely naive and have not adapted defenses (Colautti et al. 2004, Parker and Hay 2005, Parker et al. 2006). These predators can provide biotic resistance to nonnative prey (Elton 1958, Mack et al. 2000). However, many nonnative species still flourish and spread in the presence of consumers. These conflicting observations raise the

question: What influences the ability of a predator to provide biotic resistance to invasion by nonnative prey?

Biotic resistance due to predation depends on at least four factors: prey propagule pressure (i.e., the number of individuals that is initially introduced to an area), prey reproductive rate, predator abundance, and the functional response of the predator to the prey. In this paragraph we outline a framework for the relationship between these four factors and biotic resistance. We illustrate this graphically with a simple model (Fig. 1) that shows the relationships between nonnative prey population growth and predation based on functional feeding responses described by Holling (1959). Initially, the nonnative prey population is controlled by propagule pressure. Once established, this population can subsequently increase via reproduction, governed by its fecundity. At least during the early stages of introduction, a nonnative prey population that is well-suited to the new environment and does not experience strong competition from native species is likely not resource-limited, and thus will exhibit a relatively constant per capita birth rate. Initially, this constant per capita birth

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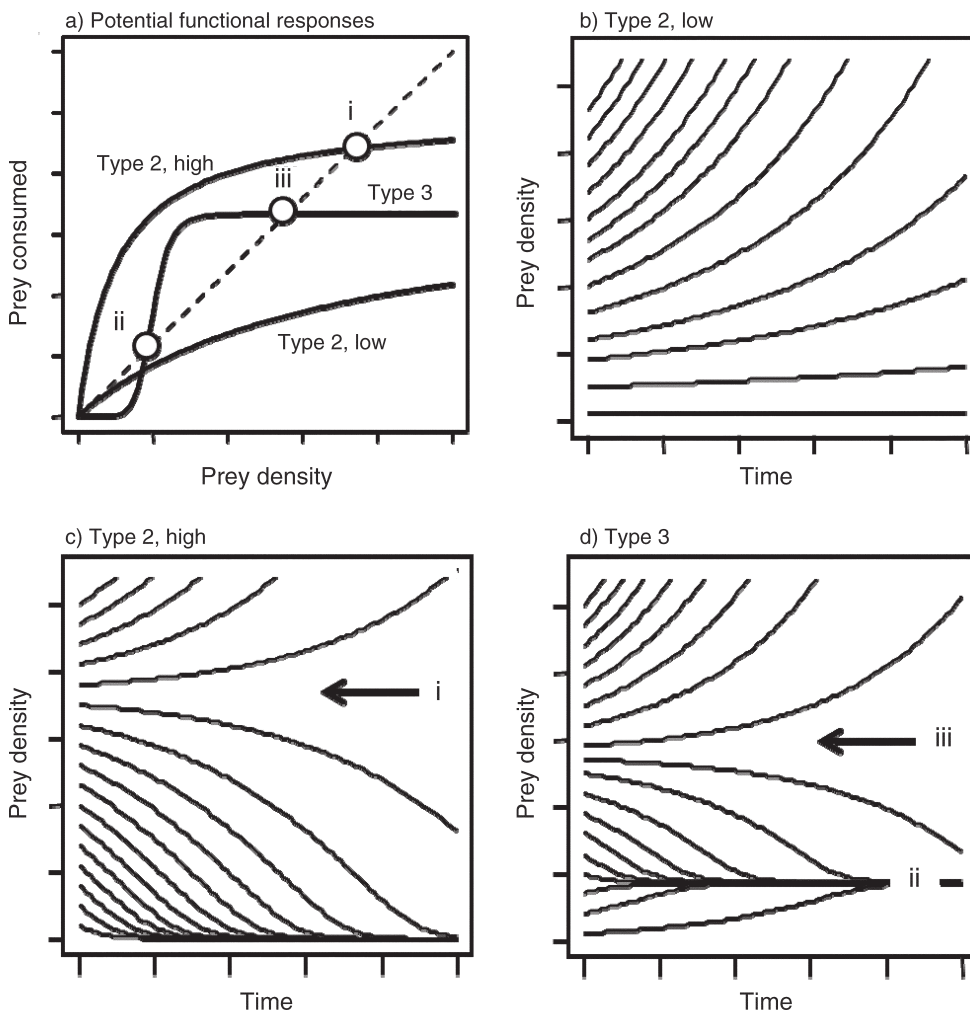


FIG. 1. Conceptual diagram illustrating how population trajectories of nonnative prey are influenced by the interaction between predator functional response and prey density. (a) Three potential functional responses for the number of prey consumed as a function of prey density: a type-2 functional response with a low attack rate, a type-2 functional response with a high attack rate, and a type-3 functional response. The dashed black line shows the number of prey born as a function of prey density, corresponding to a constant per capita birth rate. These functional responses interact with prey birth rate and prey abundance to control the predicted prey population trajectory through time. (b–d) Prey population trajectories across different starting prey populations, for functional responses that are (b) type 2 (low), (c) type 2 (high), and (d) type 3. Key thresholds that represent key stable or unstable (arrows) equilibrium in prey density are denoted with lowercase roman numerals, corresponding to both the functional response [panel (a)] and the population trajectories [panels (b)–(d)].

rate will drive exponential population growth; however, predation can regulate such growth. Assuming that predator abundance is independent of nonnative prey abundance during the stage of prey establishment, the predator’s functional response (Solomon 1949, Holling 1959) to nonnative prey can determine whether prey are excluded from establishing, become established but do not proliferate and spread, or become overabundant and spread to new locations (i.e., invade; see also Murdoch and Oaten 1975, Gascoigne and Lipcius 2004). For example, if a predator exhibits a type 2 functional response, but the attack rate of the predator is insufficient to keep up with the prey’s birth rate (curve type 2 [low] in Fig. 1a), the nonnative prey population

will grow exponentially (Fig. 1b); in other words, the predator will not provide biotic resistance and the prey will invade. Alternatively, if the attack rate of the type 2 functional response is sufficiently high (curve type 2 [high] in Fig. 1a), predators may provide biotic resistance by driving low prey populations toward extinction (Fig. 1c). However, as propagule pressure, and thus initial prey abundance increase, predator foraging can become saturated, allowing prey populations to increase via reproduction (Fig. 1c). In this case there is a threshold propagule pressure beyond which the novel prey can invade (point i in Fig. 1). In contrast, if the predator exhibits a sigmoid type 3 functional response (curve type 3 in Fig. 1a), even low propagule

pressure can allow the prey population to establish (Fig. 1d). At intermediate prey densities, predators will decrease prey abundances to a low level (point ii in Fig. 1). Under this scenario, predators provide partial biotic resistance to prey by controlling population growth, though they cannot exclude prey from establishing. Beyond some threshold propagule pressure (point iii in Fig. 1), prey will saturate a predator that exhibits a type 3 functional response and proliferate (Fig. 1d). With a type 3 functional response, prey can establish either at low abundance due to low predation or at high abundance because prey overwhelm biotic resistance. Thus, determining the shape and parameters of the functional response of a consumer to a novel prey can illuminate the potential for biotic resistance at different densities of the invader and predator, although, surprisingly, such an approach has not been performed (Maron and Vila 2001).

Here we investigated the functional response of a stream consumer, signal crayfish (*Pacifastacus leniusculus*), to a novel prey, New Zealand mud snails (*Potamopyrgus antipodarum*), and use this relationship to quantify the potential for biotic resistance to the invading prey. New Zealand mud snails (NZMS) were first detected in the western United States in the 1980s (Bowler 1991). In the last three decades, these highly fecund and parthenogenetic snails have spread to at least one water body in every western state except New Mexico (Benson and Kipp 2011). Mud snails can dramatically alter invaded streams, reaching densities of $>500\,000$ individuals/m², comprising $>95\%$ of invertebrate biomass, and dominating stream carbon and nitrogen cycling (Hall et al. 2003, 2006). While various predators and pathogens have been documented as important sources of mortality for NZMS in their native range (e.g., Levri 1998, Lively 1999, Holomuzki and Biggs 2006, Holomuzki et al. 2009), there is little understanding of how predation could impact NZMS populations in their introduced range (Vinson and Baker 2008). NZMS, due to their shell and operculum, are somewhat resistant to predation by North American fishes (Brenneis et al. 2011); in one study, $>53\%$ of NZMS fed to rainbow trout (*Oncorhynchus mykiss*) survived passage through the digestive tract (Vinson and Baker 2008). However, feeding studies have documented that crayfish consume introduced NZMS and that their predation is lethal (Pintor et al. 2008, Brenneis et al. 2011). Furthermore, New Zealand crayfish (*Paraneoharporus planifrons*) consume NZMS in their native range (Parkyn et al. 1997). It is therefore possible that crayfish are important predators of NZMS in their introduced range. Here we examine the role of signal crayfish, an omnivore that is native throughout Washington and Oregon and introduced in California (United States Geological Survey 2011), as a potential source of biotic resistance to invading NZMS. Signal crayfish have been established for approximately 100 years in California (Riegel 1959), and studies of predation by nonnative

species suggest that introduced predators can have similar predatory responses to prey as native predators (e.g., Kelly et al. 2002, Hooff and Bollens 2004). We ask, what is the functional response of signal crayfish to NZMS? We predict that crayfish will exhibit type 3 functional response dynamics to NZMS and will be able to provide biotic resistance to NZMS invasion at low to intermediate prey densities and high consumer densities.

METHODS

To determine whether crayfish could prevent the invasion of NZMS, we determined whether crayfish feed on NZMS in the field and identified possible human-mediated NZMS propagule pressures. We then used laboratory feeding trials to infer how crayfish feeding rates respond to variation in NZMS densities (i.e., the shape and strength of their density-dependent functional response) and used these to estimate NZMS per capita mortality rates due to crayfish predation. We combined these estimates with field-based estimates of NZMS fecundity rates derived from the literature to forecast the probability of observing NZMS invasion vs. crayfish-mediated biotic resistance over a range of hypothetical crayfish and NZMS densities representative of their densities observed in the field. We used a probabilistic framework throughout our analyses to propagate the uncertainty of our predictions.

Crayfish as predators of NZMS

Our focal study system, the San Lorenzo River, is a coastal river that runs through Santa Cruz, California, USA and drains into the Monterey Bay in the Pacific Ocean. Signal crayfish were introduced to the San Lorenzo River in 1912 (Riegel 1959) and are abundant throughout the river. NZMS were discovered in the lower reaches of the San Lorenzo River in 2005.

We determined NZMS densities in August 2010 at three sites in the San Lorenzo: a low-, an intermediate-, and a high-density NZMS site. At each of these three sites we took six samples using a surber stream bottom sampler (500- μ m mesh size; Wildco Wildlife Supply, Yulee, Florida, USA) along a transect that spanned the stream channel. We also counted NZMS on rocks and/or wood across three transects at each site ($n = 21$ rocks per transect). To estimate the size distribution of NZMS we measured individuals in a subsample of each surber sample (± 0.1 mm).

To determine whether crayfish consume NZMS in the wild, we collected ≥ 20 crayfish from each of the three sites by snorkeling. All crayfish were frozen and their cardiac stomachs dissected under a dissecting microscope to look for presence of NZMS under natural conditions. The NZMS found in crayfish stomachs were usually fragmented with only the tip of the shell spire intact; therefore, we used number of spires as a conservative index for crayfish consumption of NZMS.

To examine potential human-mediated NZMS propagule pressures in this system, we estimated the number

of NZMS that can be transported from one water body to another on felt-bottom wading boots commonly worn by recreational anglers. We wore boots while working in the high-density NZMS site for 5 min or 4 h, placed the boots in tubs of water at the laboratory, and counted the number of NZMS that came off each pair of boots.

We quantified densities of signal crayfish in the San Lorenzo watershed and Scott Creek (a nearby watershed that has not yet been invaded by NZMS) by electrofishing 20 and 16 reaches in each, respectively, that were distributed from headwater tributaries to the lower mainstem. Reaches were ~40 m in length and were surveyed in the two watersheds during June 2009 and June 2008, respectively. We isolated reaches with blocknets and performed three passes using a backpack electrofisher. We estimated abundances based on the depletion method of Zippin (1958) and converted abundance to density by dividing estimated abundance by the total wetted area of the study reach.

Quantifying the functional response

To determine the shape and strength of the functional response of signal crayfish to NZMS, we performed laboratory feeding trials in which we fed different densities of NZMS to signal crayfish to estimate crayfish feeding rates. Between May and August 2010 we collected experimental crayfish from the San Lorenzo River in Henry Cowell Redwoods State Park. Based on monitoring the spread of NZMS (J. W. Moore, unpublished data), the collection site for crayfish represents the edge of the NZMS invasion front and has had small abundances of NZMS for at least one year. Snails were collected in the lower watershed where they were more abundant. We caught crayfish by snorkeling and NZMS by brushing snails off rocks.

Crayfish were housed in indoor aquaria under ambient light with recirculating water from the San Lorenzo River. Water temperature was maintained between 16.5° and 18.5°C. Tanks contained gravel and rocks to provide shelter for crayfish. Snails were kept in plastic containers filled with San Lorenzo River water. We fed *Spirulina* powder to snails before feeding trials. Crayfish were fed frozen chironomid larvae and dried alder (*Alnus rubra*) leaves until 40 h and 16 h prior to commencement of feeding trials. We measured the carapace length of each crayfish from the anterior end of the rostrum to the posterior edge of the carapace (± 0.1 mm). All crayfish used in feeding trials were mature animals between 44 and 58 mm in carapace length, were between molts, and had all appendages intact. This size class represents the sizes of ~85% of all individuals caught during crayfish density surveys in 2008 and 2009. We used snails with shell length ~2 mm and longer.

Feeding trials were run from June to September 2010. Crayfish were placed individually in 16-quart plastic containers (16 quarts is 15.1 L; 35.5 × 24 cm base). Containers were sanded on the bottom to provide

traction for crayfish movement but were left bare of gravel. Each container was filled with 6 L of San Lorenzo River water and aerated with an aquarium pump. Feeding trials were held in the laboratory between the hours of 13:00 and 19:00 with low levels of ambient light. Water temperature was maintained between 16.5° and 18.5°C, which was within the observed range of temperatures in San Lorenzo River from June to September (between 14.8° and 18.5°C). Crayfish were placed in the containers one day before the feeding trial commenced so that they could acclimate to the container overnight. We then added $n = 1, 5, 10, 25, 50, 75, 100, 150, 200, 300,$ or 500 NZMS to each container. Each crayfish was given 30 min to commence eating NZMS. If after 30 min the crayfish consumed no snails, we recorded that it ate zero NZMS. We started timing the feeding trials after the crayfish ate its first snail. Each consumed snail was counted and immediately replaced. Thirty minutes after feeding initiation, the crayfish was removed from the container and snails were counted to ensure that we recorded the accurate number of snails consumed. We used each crayfish only once and performed three replicates of each NZMS density.

To examine whether crayfish have similar feeding rates over shorter and longer time spans to those rates observed during 30-min feeding trials, we repeated these procedures for 15-min feeding trials, using $n = 10, 25, 35, 50,$ and 75 NZMS (one each). Additionally, we ran two 12-h feeding trials in which crayfish were fed 1000 NZMS without replacement.

In order to quantify the shape and strength of the functional response, we fit a flexible type 3 functional response model to observed rates of crayfish feeding as a function of snail density. Specifically,

$$c(N) = \frac{aN^m}{1 + ahN^m} + \varepsilon \quad (1)$$

(e.g., Vucic-Pestic et al. 2010) where $c(N)$, the number of snails eaten by an individual crayfish per minute, is a function of the snail density N (snails/m²), as well as the crayfish's attack rate (a), handling time (h), the shape parameter m (also known as the hill exponent), and process noise (ε), which we assumed was normally distributed $\mathcal{N}(0, \sigma)$. This formulation of the type 3 functional response converges to a type 2 form when $m = 1$ and a type 1 functional response when $h = 0$ as well.

We obtained posterior probability distributions for each parameter using a Bayesian framework, specifically, a Hilborn sampling-importance-resampling (SIR) algorithm (described further in Moore and Semmens 2008). This method iteratively draws a vector of proposed parameter values from specified prior distributions and accepts the proposed vector of parameters proportional to its likelihood given the data. The iterative nature of the algorithm results in vectors of accepted parameter values whose final distributions converge on posterior probability distributions with

sufficient iterations. We implemented this SIR algorithm in R (R Development Core Team 2010), assumed vague uniform priors for parameters h , m , and σ (constraining $m \geq 1$) and a vague log-uniform prior for parameter a , and iterated the procedure until 2000 posterior parameter vectors had been accepted. Our use of a Bayesian approach to obtaining a distribution of functional response parameters differs from other studies that focus on obtaining single best-performing (e.g., maximum likelihood) parameter estimates (but see Smout et al. 2010). Therefore, it permitted us to propagate uncertainty involved in parameter estimation to our subsequent calculations of biotic resistance.

Predicting biotic resistance

Crayfish would be expected to provide biotic resistance to NZMS invasion if crayfish predation caused a NZMS per capita mortality rate (M) that is greater than the NZMS per capita fecundity rate (F) (Fig. 1). A distribution of NZMS per capita mortality rates (M) was estimated as

$$M = \frac{aN^m}{1 + ahN^m} \frac{1}{N} CT \quad (2)$$

where vectors of associated a , h , and m parameters were obtained from our functional response algorithm (see Eq. 1), N and C are hypothetical densities of NZMS and crayfish (see *Methods*, last paragraph), and T is the daily time (in minutes) that crayfish spend actively foraging. Given that crayfish are predominantly nocturnal foragers (Guan and Wiles 1998), we assumed that daily foraging time was normally distributed around a mean of 12 h with 1 h standard deviation [$T \sim \mathcal{N}(720, 60)$].

Estimates of NZMS per capita fecundity rates (F) were obtained on the basis of the observed size-frequency distribution of NZMS at our study sites and the allometric relationship between an individual female's body size (shell length) and its size class's fecundity (offspring \times individual $^{-1} \times$ day $^{-1}$) as determined by Hall et al. (2006; Appendix A). In order to incorporate both the true variation of the allometric relationship and the uncertainty of its estimation, we first determined the mean (μ_f) and standard deviation (σ_f) of a distribution of likely per capita fecundity rates, $F \sim \mathcal{N}(\mu_f, \sigma_f)$. We did so by calculating

$$\mu_f = \frac{1}{n} \sum_1^n \sum_{i=1}^6 p_i f_{i,n} \quad (3)$$

and

$$\sigma_f = \sqrt{\frac{1}{n} \sum_1^n \left[\left(\sum_{i=1}^6 p_i f_{i,n} \right) - \mu_f \right]^2} \quad (4)$$

where p_i is the proportion of individuals observed in the i th of six size classes (Appendix B), and $f_{i,n}$ is the size class's per capita fecundity that is realized in each of $n =$

1000 random draws from its distribution of per capita fecundities ($f_{i,n} \sim N(\bar{f}_i, \sigma_i)$; see Appendix A). Stochastic variation in size-specific fecundities were specified as being fully correlated across size classes, such that large and small size classes were assumed to experience high or low fecundities simultaneously.

To predict whether NZMS invasion would be prevented by crayfish predation, we then determined the NZMS net per capita growth rate ($F - M$) across a range of hypothetical crayfish and NZMS densities representative of those observed in our field sampling (1–10 000 NZMS/m 2 and 0–1.0 crayfish/m 2). We determined both the expected net per capita growth rate and its associated probability by independently bootstrapping each F and M distribution 1000 times for each combination of hypothetical crayfish and NZMS densities and calculating the proportion of draws in which the per capita fecundity exceeded the per capita mortality rate. This model assumes a single starting density for NZMS, and thus describes a local response to NZMS introduction. The fecundity rate, F , does not incorporate additional propagules that may enter a system through dispersal over time.

RESULTS

Crayfish as predators of NZMS

New Zealand mud snails exhibited densities of 4511 ± 1504 snails/m 2 (mean \pm SE) at the high-density NZMS site, 259 ± 116 snails/m 2 at the intermediate-density site, and 15 ± 9 snails/m 2 at the low-density site. Most individuals were either <3.0 mm or 4.0–4.5 mm in size (Appendix B). Gut dissections revealed that at least 65% (13/20) of crayfish caught at the high-density NZMS site had recently consumed NZMS, 19% (4/21) of crayfish caught at the intermediate-density site had consumed NZMS, and at the low-density site, 0% (0/22) had consumed NZMS. We found 7.9 ± 2.8 spires in the cardiac stomachs of crayfish caught at the high-density NZMS site (mean \pm SE) and 1 ± 0.7 spires in cardiac stomachs of crayfish from the intermediate-density site. We were unable to determine the true number of snails per stomach or consumption rate because it is likely that many NZMS spires were crushed beyond recognition and the crayfish gastric evacuation rate was not quantified; therefore, these values are conservative and likely dramatically underestimate the true number of NZMS that crayfish consumed in the field. However, this provides evidence that crayfish are lethal predators of NZMS.

After working in the high-density NZMS site, a pair of wading boots that was worn for 5 min had an average of 7 NZMS (range 3–9 NZMS) and a pair worn for 4 h had an average of 30 NZMS (range 22–38 NZMS). These results suggest that NZMS propagules may spread easily among streams on gear commonly worn by recreational anglers. Crayfish densities were highly variable across the 36 sites in the San Lorenzo and nearby Scott Creek watershed, averaging 0.25 ± 0.25

crayfish/m² (mean \pm SD), but some reaches had densities of up to 0.90 crayfish/m².

Quantifying the functional response

Feeding trials and fitting the functional response revealed a saturating relationship between NZMS abundance and crayfish's foraging rates (Fig. 2). The best estimate of the shape parameter, m , was 3.93, indicating a sigmoidal, or type 3, functional response. However, the posterior distribution of m was wide (95% confidence interval, CI₉₅: 1.06–7.72) indicating uncertainty in the specific shape parameter (Fig. 2a). The best estimate of handling time was 0.89 min/NZMS (mean, 0.86; CI₉₅, 0.57–1.24), indicating that crayfish can eat a maximum of \sim 1.1 NZMS/min. This maximum feeding rate was observed at densities of NZMS that are \sim 1000 NZMS/m² or greater (Fig. 2a). Based on these feeding trials that lasted 30 min, we estimate that a single crayfish can eat $>$ 900 NZMS in a 12-h period. This estimate of a crayfish's 12-h consumption rate corresponds with observations from our two feeding trials in which crayfish were allowed to feed continuously for 12 h on an initial abundance of 1000 NZMS; in those trials we observed crayfish eat 994 and 946 snails in 12 h.

Predicting biotic resistance

We predict that crayfish can affect partial biotic resistance under certain combinations of NZMS and crayfish abundances (Fig. 3), given our quantified functional response and previously quantified NZMS fecundity. First, at crayfish densities that are below \sim 0.2 crayfish/m², NZMS population growth rate exceeds their mortality from predation by crayfish ($F > M$), regardless of NZMS population size (Fig. 3a). Second, at low NZMS densities, across all crayfish densities, we predict that NZMS populations will initially increase. This increase is expected because crayfish exhibit relatively low consumption rates at low NZMS densities due to their type 3 functional response (see Fig. 1d). Certain combinations of crayfish and NZMS densities may limit NZMS population sizes. For example, at densities of \sim 0.4 crayfish/m² and 2000 NZMS/m² the NZMS net per capita growth rate is zero. Crayfish predation is expected to drive negative population growth rates of NZMS at crayfish densities that are $>$ 0.6 crayfish/m² and at NZMS densities that are between \sim 200 and 2000 NZMS/m². Due to nonsymmetric parameter distributions, invasion probabilities did not necessarily correspond to the expectations of net growth. That is, even when the expected per capita growth rate was predicted to be zero, the probability of having positive growth could still exceed 0.5 (e.g., while births equal deaths at 1.2 crayfish/m² and 2000 NZMS/m², the probability that births exceed deaths is \sim 0.63 at these densities). There are thus many combinations of NZMS and crayfish densities that have uncertain potential for biotic resistance, with increasing or decreasing NZMS populations (Fig. 3).

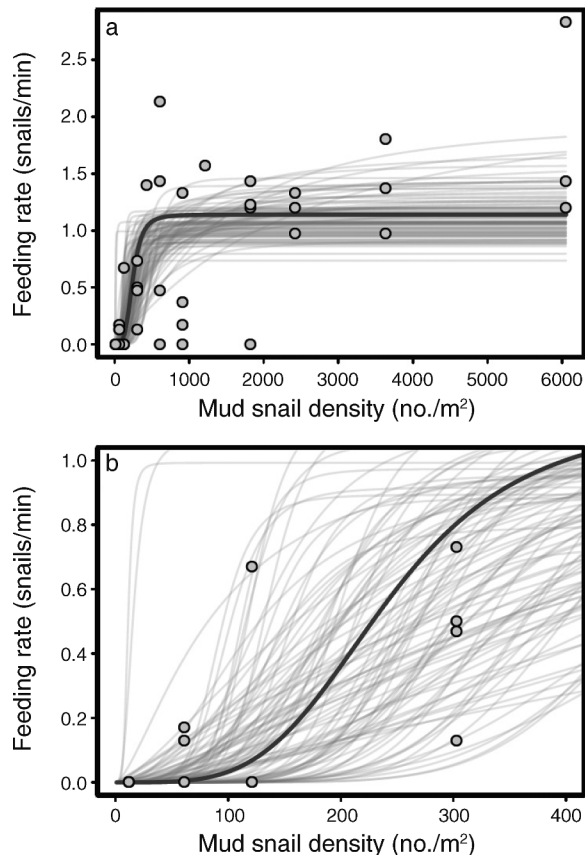


FIG. 2. The functional response of crayfish (*Pacifastacus leniusculus*) to invasive New Zealand mud snails (NZMS; *Potamopyrgus antipodarum*). Shown is the number of snails eaten per minute by a single crayfish as a function of NZMS density. Each feeding trial is represented by a gray-filled circle. The best model fit is shown with the heavy line. Model uncertainty is also indicated by a random subset of the accepted model draws shown with thin gray lines, a small subset of the accepted model vectors that define the posterior probability. The functional response is shown for (a) the entire range of the feeding trial as well as (b) focused in on the origin to highlight model uncertainty. Two outliers are not shown in this graph (NZMS/m², NZMS/min: 1211, 4.53 and 908, 5.93); these data were included in the model fitting.

DISCUSSION

In an era of increasing invasions, identifying what factors influence predators' potential to resist invasions is an important step toward predicting whether newly introduced prey will become invasive. We quantified the ability of signal crayfish to control NZMS population growth based on their functional response and thresholds of crayfish and NZMS densities. Because crayfish exhibit sigmoid type 3 functional response dynamics to NZMS, consuming NZMS at slower rates when NZMS density is low (Fig. 2), we predict that crayfish will not measurably depress population growth at low NZMS densities (Fig. 3). However, at certain combinations of crayfish and NZMS densities, NZMS could experience zero population growth, implying that NZMS can

establish but will be unable to spread. Further, given high enough crayfish and NZMS densities, we predict that crayfish will reduce the NZMS growth rate below zero (Fig. 3). Due to this type 3 functional response relationship, the system may be exhibiting “partial” biotic resistance (Carlsson et al. 2010); predators may be able to limit the growth and spread of the invader, though predators are not able to absolutely exclude the invader from establishing in the community (Levine et al. 2004).

Other studies have emphasized abiotic conditions that may limit NZMS expansion (Loo et al. 2007), including conductivity (Herbst et al. 2008) and flow regimes (Cross et al. 2011); our results suggest that predation may also be important for predicting the spread of NZMS. This study also represents the first documentation of high predation rates on NZMS in their invaded range. While juvenile salmon and rainbow trout feed on NZMS (e.g., Bersine et al. 2008), NZMS often survive this consumption. Previous studies of consumption by naive crayfish on NZMS documented low consumption rates (<10 NZMS consumed per crayfish in an 18-h period; Pintor et al. 2008). Here we observed that signal crayfish commonly feed on NZMS in the field, that their consumption is lethal, and that a single crayfish can consume >900 NZMS in a 12-h period. This level of consumption can produce partial biotic resistance at high crayfish densities (Fig. 3). Given that biotic resistance is dependent on crayfish densities (Fig. 3), factors that influence crayfish density such as water temperature, pH, and predation (Lodge and Hill 1994, Englund 1999, France and Collins 2002) would in turn control biotic resistance of NZMS. While it might be tempting to use these results to consider the potential of introducing crayfish as a biocontrol agent of NZMS, we strongly urge against this, as crayfish are notorious invasive species in their own right (Lodge et al. 2000).

Our results indicate that high NZMS propagule pressures can overwhelm the partial biotic resistance offered by high crayfish densities. NZMS are primarily transported via movement of infested equipment including clothing and fishing gear (Hosea and Finlayson 2005, Davidson et al. 2008). We observed that a single pair of wading boots can bring in 30 NZMS/pair. The San Lorenzo and Scott Creek watersheds both contain steelhead (*Oncorhynchus mykiss*) populations that are heavily targeted by anglers; therefore, anglers moving NZMS frequently between fishing spots could easily drive high propagule pressures of NZMS. Fewer than 100 anglers moving from a high-density NZMS site to a new site could drive NZMS past the threshold propagule pressure at which crayfish are unable to provide biotic resistance (Fig. 3). Efforts to guide and educate angler behavior may be critical to minimizing the anthropogenic spread of NZMS.

Here we quantified the potential for biotic resistance in a controlled laboratory experiment. Whether or not

this potential is realized in the field may be mediated by factors such as NZMS finding spatial refugia from predation, seasonal variation in crayfish foraging, and availability of alternative prey. Our study determined the functional response of crayfish to NZMS in simple tanks. NZMS would be expected to find some refuge from predators in the field. However, crayfish are mobile consumers that are adept at rapidly exploiting resource patches (e.g., Pintor and Sih 2009), and previous studies have found that crayfish predation is particularly decimating for other species of snails (Nyström et al. 1999, McCarthy et al. 2006). Our study design may have underestimated search and handling times by not accounting for spatial refugia. Previous studies have documented that crayfish activity levels peak during warmer months (e.g., Correia 1998, Gherardi et al. 2000), so we may anticipate that crayfish forage less actively during the winter. And although Stenroth et al. (2006) suggest that crayfish diets are consistent across seasons, alternative prey could potentially change the functional response of crayfish to NZMS by inducing a prey switch at low NZMS densities. Spatial refugia and alternative prey could contribute to a type 3 functional response with reduced rates of predation at low prey densities. In the context of our findings, low prey detection, seasonal changes in predator activity, and alternative prey could shift the curves in Figs. 2 and 3 to the right, thus widening the window for invasion. Furthermore, our feeding trials were conducted during the day, and crayfish are primarily nocturnal foragers (Guan and Wiles 1998). However, NZMS are also nocturnal (Benson and Kipp 2011), and will therefore remain vulnerable to crayfish predation, as evidenced by our findings that crayfish predate on NZMS in the field. Finally, our model does not include a background mortality parameter for NZMS. Adding such a parameter could slightly decrease the population growth rate of NZMS and thus expand the parameter region of resistance, but given the high fecundity of NZMS, this change would most likely be minimal.

We also note that our approach focuses on the response of consumption rates of crayfish to different NZMS densities, but does not include a numerical response of crayfish. After initial establishment of NZMS, crayfish could show a numerical response to NZMS that could increase the strength of biotic resistance. However, given the difference in generation time between NZMS (a few months to maturity; Lassen 1979) and signal crayfish (three years to maturity; Guan and Wiles 1999), the crayfish population would likely not show a numerical response until after NZMS had already invaded. It may take time for crayfish to develop a search image for NZMS (Carlsson et al. 2009), which may explain the different rates of predation observed in our study and that of Pintor et al. (2008). Crayfish population growth may also be limited by non-trophic processes (e.g., competition for shelter; Lodge and Hill 1994). A numerical response of crayfish to NZMS invasion has

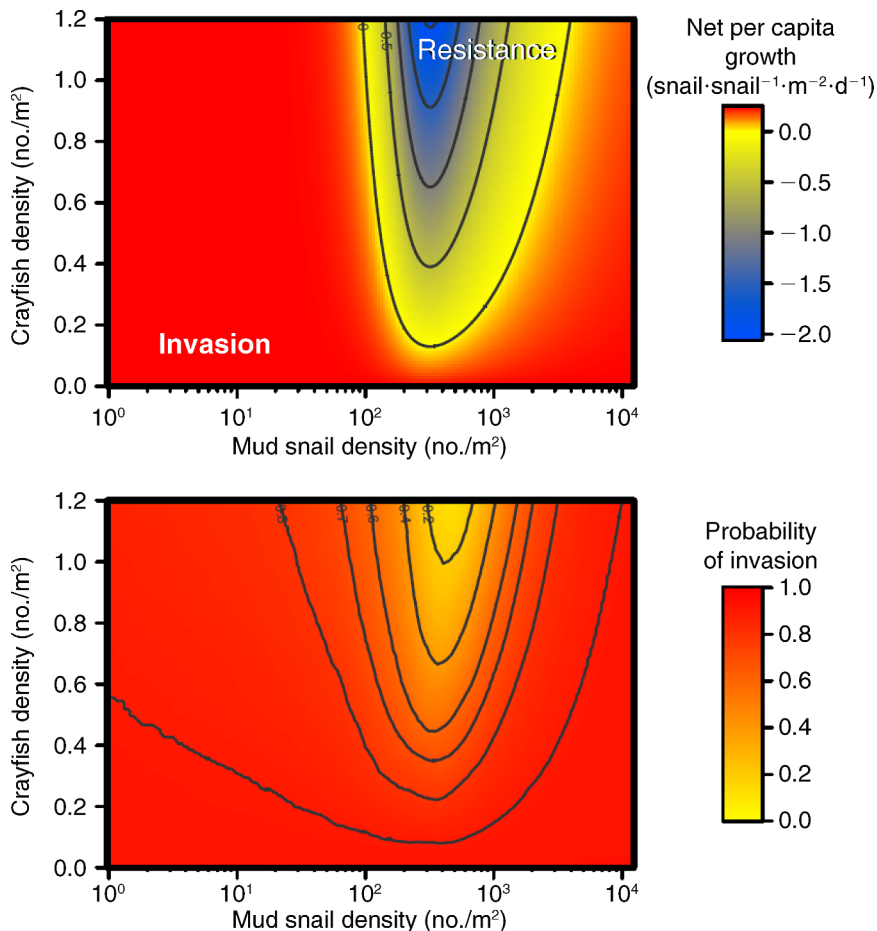


FIG. 3. Predicted biotic resistance to NZMS invasion by crayfish. Predictions are based on the observed range of crayfish densities and their quantified functional response and include uncertainty in parameters (see *Methods* for more details). (a) The average net per capita growth of NZMS is shown as a function of NZMS and crayfish density. Warmer colors indicate higher population growth rate, leading to invasion, while cooler colors indicate negative population growth, leading to biotic resistance. Isoclines are shown with solid black lines. (b) The probability of invasion is shown as a function of NZMS and crayfish density. Probability of invasion is the proportion of iterations that resulted in positive population growth rate of NZMS (see *Methods* for more details). Warmer colors indicate a higher probability of invasion. Note that NZMS density is shown on a log scale.

potential consequences for the community that we did not explore; specifically, a subsidizing effect of NZMS on the crayfish population could create apparent competition between NZMS and native benthic invertebrates, potentially harming the native community more than helping it (Noonburg and Byers 2005).

Our study and approach offer important implications for the field of invasion biology. Although Ricciardi (2001) concluded that aquatic invasive species usually facilitate the establishment of new invaders and increase the rate of new invasions (i.e., create an invasional meltdown; Simberloff and Von Holle 1999), our results suggest that some nonnative species may resist rather than facilitate new invasions. While invasional meltdown is an alarming scenario, the ability of one invasive species to provide invasion resistance against another might be an important phenomenon. In addition, type 3 functional responses

predict thresholds and alternative states in invasions (Figs. 1 and 3)—prey may be able to establish, but can invade only once threshold prey densities saturate predators. Our approach to predicting biotic resistance quantifies these thresholds as propagule pressures and predator densities, information that is potentially relevant to forecasting invasion risk and targeting management actions. This novel use for functional responses has important implications for invasion ecology; it illuminates the role of predators in resisting invasions, and by quantifying invasion thresholds it may help managers predict the outcomes of species introductions and biocontrol efforts.

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LITERATURE CITED

- Benson, A. J., and R. M. Kipp. 2011. *Potamopyrgus antipodarum*. USGS Nonindigenous Aquatic Species Database, Gainesville, Florida, USA.
- Bersine, K., V. E. F. Brenneis, R. C. Draheim, A. M. Wargo Rub, J. E. Zamon, R. K. Litton, S. A. Hinton, M. D. Sytsma, J. R. Cordell, and J. W. Chapman. 2008. Distribution of the invasive New Zealand mudsnail (*Potamopyrgus antipodarum*) in the Columbia River Estuary and its first recorded occurrence in the diet of juvenile Chinook salmon (*Oncorhynchus tshawytscha*). *Biological Invasions* 10:1381–1388.
- Bowler, P. 1991. The rapid spread of the freshwater hydrobiid snail *Potamopyrgus antipodarum* (Gray) in the middle Snake River, southern Idaho. *Proceedings of the Desert Fishes Council* 23:28–44.
- Brenneis, V. E. F., A. Sih, and C. E. de Rivera. 2011. Integration of an invasive consumer into an estuarine food web: direct and indirect effects of the New Zealand mud snail. *Oecologia* 167:169–179.
- Carlsson, N. O. L., J. M. Jeschke, N. Holmqvist, and J. Kindberg. 2010. Long-term data on invaders: When the fox is away, the mink will play. *Biological Invasions* 12:633–641.
- Carlsson, N. O. L., O. Sarnelle, and D. L. Strayer. 2009. Native predators and exotic prey—an acquired taste? *Frontiers in Ecology and the Environment* 7:525–532.
- Colautti, R. I., A. Ricciardi, I. A. Grigorovich, and H. J. MacIsaac. 2004. Is invasion success explained by the enemy release hypothesis? *Ecology Letters* 7:721–733.
- Correia, A. M. 1998. Seasonal and circadian foraging activity of *Procambarus clarkii* (Decapoda, Cambaridae) in Portugal. *Crustaceana* 71:158–166.
- Cross, W. F., C. V. Baxter, K. C. Donner, E. J. Rosi-Marshall, T. A. Kennedy, R. O. Hall, Jr., H. A. Wellard Kelly, and R. S. Rogers. 2011. Ecosystem ecology meets adaptive management: food web response to a controlled flood on the Colorado River, Glen Canyon. *Ecological Applications* 21:2016–2033.
- Darwin, C. R. 1859. *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. First edition. John Murray, London, UK.
- Davidson, T. M., V. E. F. Brenneis, C. de Rivera, R. Draheim, and G. E. Gillespie. 2008. Northern range expansion and coastal occurrences of the New Zealand mud snail *Potamopyrgus antipodarum* (Gray, 1843) in the northeast Pacific. *Aquatic Invasions* 3:349–353.
- Elton, C. S. 1958. *The ecology of invasions by animals and plants*. University of Chicago Press, Chicago, Illinois, USA.
- Englund, G. 1999. Effects of fish on the local abundance of crayfish in stream pools. *Oikos* 87:48–56.
- France, R. L., and N. C. Collins. 2002. Extirpation of crayfish in a lake affected by long-range anthropogenic acidification. *Conservation Biology* 7:184–188.
- Gascoigne, J. C., and R. N. Lipcius. 2004. Allee effects driven by predation. *Journal of Applied Ecology* 41:801–810.
- Gherardi, F., S. Barbaresi, and G. Salvi. 2000. Spatial and temporal patterns in the movement of *Procambarus clarkii*, an invasive crayfish. *Aquatic Sciences* 62:179–193.
- Guan, R., and P. R. Wiles. 1998. Feeding ecology of the signal crayfish *Pacifastacus leniusculus* in a British lowland river. *Aquaculture* 169:177–193.
- Guan, R., and P. R. Wiles. 1999. Growth and reproduction of the introduced crayfish *Pacifastacus leniusculus* in a British lowland river. *Fisheries Research* 42:245–259.
- Hall, R. O., M. F. Dybdahl, and M. C. VanderLoop. 2006. Extremely high secondary production of introduced snails in rivers. *Ecological Applications* 16:1121–1131.
- Hall, R. O., J. L. Tank, and M. F. Dybdahl. 2003. Exotic snails dominate nitrogen and carbon cycling in a highly productive stream. *Frontiers in Ecology and the Environment* 1:407–411.
- Herbst, D. B., M. T. Bogan, and R. A. Lusardi. 2008. Low specific conductivity limits growth and survival of the New Zealand mud snail from the Upper Owens River, California. *Western North American Naturalist* 68:324–333.
- Holling, C. S. 1959. Some characteristics of simple types of predation and parasitism. *Canadian Entomologist* 91:385–398.
- Holomuzki, J. R., and B. J. F. Biggs. 2006. Habitat-specific variation and performance trade-offs in shell armature of New Zealand mudsnails. *Ecology* 87:1038–1047.
- Holomuzki, J. R., R. L. Lowe, and B. J. F. Biggs. 2009. Spatiotemporal separation of New Zealand mudsnails from predatory fish. *Journal of the North American Benthological Society* 28:846–854.
- Hooff, R. C., and S. M. Bollens. 2004. Functional response and potential predatory impact of *Tortanus dextrilobatus*, a carnivorous copepod recently introduced to the San Francisco estuary. *Marine Ecology Progress Series* 277:167–179.
- Hosea, R. C., and B. Finlayson. 2005. Controlling the spread of New Zealand mud snails on wading gear. Administrative Report 2005-02. California Department of Fish and Game, Pesticide Investigations Unit, Rancho Cordova, California, USA.
- Kelly, D. W., J. T. A. Dick, and W. I. Montgomery. 2002. Predation on mayfly nymph, *Baetis rhodani*, by native and introduced *Gammarus*: direct effects and the facilitation of predation by salmonids. *Freshwater Biology* 47:1257–1268.
- Lassen, H. H. 1979. Reproductive effort in Danish mudsnails (Hydrobiidae). *Oecologia* 40:365–369.
- Levine, J. M., P. B. Adler, and S. G. Yelenik. 2004. A meta-analysis of biotic resistance to exotic plant invasions. *Ecology Letters* 7:975–989.
- Levri, E. P. 1998. Perceived predation risk, parasitism, and the foraging behavior of a freshwater snail (*Potamopyrgus antipodarum*). *Canadian Journal of Zoology* 76:1878–1884.
- Lively, C. M. 1999. Migration, virulence, and the geographic mosaic of adaptation by parasites. *American Naturalist* 153:S34–S47.
- Lodge, D. M., and A. M. Hill. 1994. Factors governing species composition, population size, and productivity of cool-water crayfishes. *Nordic Journal of Freshwater Research* 69:111–136.
- Lodge, D. M., C. A. Taylor, D. M. Holdich, and J. Skurdal. 2000. Nonindigenous crayfishes threaten North American freshwater biodiversity: lessons from Europe. *Fisheries* 25:7–20.
- Loo, S. E., R. Mac Nally, and P. S. Lake. 2007. Forecasting New Zealand mudsnail invasion range: model comparisons using native and invaded ranges. *Ecological Applications* 17:181–189.
- Mack, R. N., D. Simberloff, W. M. Lonsdale, H. Evans, M. Clout, and F. A. Bazzaz. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications* 10:689–710.
- Maron, J. L., and M. Vila. 2001. When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypotheses. *Oikos* 95:361–373.
- McCarthy, J. M., C. L. Hein, J. D. Olden, and M. J. Vander Zanden. 2006. Coupling long-term studies with meta-analysis to investigate impacts of non-native crayfish on zoobenthic communities. *Freshwater Biology* 51:224–235.
- Moore, J. W., and B. X. Semmens. 2008. Incorporating uncertainty and prior information into stable isotope mixing models. *Ecology Letters* 11:470–480.

- Murdoch, W. W., and A. Oaten. 1975. Predation and population stability. *Advances in Ecological Research* 9:1–131.
- Noonburg, E. G., and J. E. Byers. 2005. More harm than good: when invader vulnerability to predators enhances impact on native species. *Ecology* 86:2555–2560.
- Nyström, P., C. Bronmark, and W. Graneli. 1999. Influence of an exotic and a native crayfish on a littoral benthic community. *Oikos* 85:545–553.
- Parker, J. D., D. E. Burkepile, and M. E. Hay. 2006. Opposing effects of native and exotic herbivores on plant invasions. *Science* 311:1459–1461.
- Parker, J. D., and M. E. Hay. 2005. Biotic resistance to plant invasions? Native herbivores prefer non-native plants. *Ecology Letters* 8:959–967.
- Parkyn, S. M., C. F. Rabeni, and K. J. Collier. 1997. Effects of crayfish (*Paranephrops planifrons*: Parastacidae) on in-stream processes and benthic faunas: a density manipulation experiment. *New Zealand Journal of Marine and Freshwater Research* 31:685–692.
- Pintor, L. M., and A. Sih. 2009. Differences in growth and foraging behavior of native and introduced populations of an invasive crayfish. *Biological Invasions* 11:1895–1902.
- Pintor, L. M., A. Sih, and M. L. Bauer. 2008. Differences in aggression, activity and boldness between native and introduced populations of an invasive crayfish. *Oikos* 117:1629–1646.
- R Development Core Team. 2010. R: a language and environment for statistical computing, version 2.11.1. R Foundation for Statistical Computing, Vienna, Austria.
- Ricciardi, A. 2001. Facilitative interactions among aquatic invaders: Is an “invasional meltdown” occurring in the Great Lakes? *Canadian Journal of Fisheries and Aquatic Sciences* 58:2513–2525.
- Riegel, J. A. 1959. The systematics and distribution of crayfishes in California. *California Fish and Game* 45:29–50.
- Simberloff, D., and B. Von Holle. 1999. Positive interactions of nonindigenous species: invasional meltdown? *Biological Invasions* 1:21–32.
- Smout, S., C. Asseburg, J. Matthiopoulos, C. Fernández, S. Redpath, S. Thirgood, and J. Harwood. 2010. The functional response of a generalist predator. *PLoS ONE* 5:e10761.
- Solomon, M. E. 1949. The natural control of animal populations. *Journal of Animal Ecology* 18:1–35.
- Stenroth, P., N. Holmqvist, P. Nyström, O. Berglund, P. Larsson, and W. Graneli. 2006. Stable isotopes as an indicator of diet in omnivorous crayfish (*Pacifastacus leniusculus*): the influence of tissue, sample treatment, and season. *Canadian Journal of Fisheries and Aquatic Sciences* 63:821–831.
- United States Geological Survey. 2011. *Pacifastacus leniusculus*. USGS Nonindigenous Aquatic Species Database, Gainesville, Florida, USA.
- Vinson, M. R., and M. A. Baker. 2008. Poor growth of rainbow trout fed New Zealand mud snails *Potamopyrgus antipodorum*. *North American Journal of Fisheries Management* 28:701–709.
- Vucic-Pestic, O., B. C. Rall, G. Kalinkat, and U. Brose. 2010. Allometric functional response model: body masses constrain interaction strengths. *Journal of Animal Ecology* 79:249–256.
- Zippin, C. 1958. The removal method of population estimation. *Journal of Wildlife Management* 22:82–90.

SUPPLEMENTAL MATERIAL

Appendix A

Table of size-specific fecundities for NZMS (*Ecological Archives* A022-063-A1).

Appendix B

Table of observed size distribution of NZMS (*Ecological Archives* A022-063-A2).