

Density-dependent indirect effects: apparent mutualism and apparent competition coexist in a two-prey system

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ABSTRACT: A predator consuming multiple prey species usually causes indirect effects. Apparent mutualism results when multiple prey species reduce predation risk for each other by altering a predator's functional response. Short-term apparent competition occurs when multiple prey species increase predation risks for each other through the numerical response, i.e. increasing the predator's birth rate, or aggregative response, i.e. attracting a higher density of predators. Our objectives in this study were to determine the aggregative response and 2-prey functional response of a predator and to examine indirect effects over a range of prey densities. We used the clam *Macoma balthica* and juvenile blue crabs *Callinectes sapidus* as prey for adult blue crabs. In laboratory experiments, we determined the single-prey functional responses of the crabs to each prey species and the 2-prey functional response. We combined the 2-prey functional response with the known blue crab aggregative response to clams to estimate field predation rates. Our model predicts that at low prey densities, clams and juvenile blue crabs exhibit apparent mutualism, whereas at high clam densities, this relation switches to short-term apparent competition. These unexpected results highlight the need to incorporate multiple aspects of predation at multiple scales when considering indirect effects.

KEY WORDS: Predator–prey interactions · Functional response · Indirect effects · Blue crab · *Macoma balthica*

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INTRODUCTION

Predator–prey interactions and indirect effects

Indirect effects of species interactions are prevalent in food webs and can be more important to predator–prey dynamics than direct effects (Wootton 1994, Menge 1995, Kaplan & Denno 2007). Indirect effects can occur when a predator feeds on multiple prey species (Holt & Lawton 1994). Two of the most common indirect effects are apparent mutualism and apparent competition. Apparent mutualism gener-

ally occurs in a 2-prey system when a predator consumes fewer of each species than it would in a 1-prey system because the predator divides its foraging time between the 2 species, thus changing the predator's functional response (Colton 1987). If this response is one-way, it is known as apparent commensalism. Apparent commensalism can help stabilize predator–prey interactions (Oaten & Murdoch 1975) because it can change a Type II or destabilizing functional response to a Type III or stabilizing functional response (Holling 1959, Hassell et al. 1977). Apparent competition occurs when the presence of one prey species

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increases the predator density (i.e. changes either the predator's numerical or aggregative response), thus increasing predation on the other species (Holt & Lawton 1994). This occurs either through increasing the predator population growth rate (Settle et al. 1996, Carvalheiro et al. 2008) or through a local increase in predator density due to predator movement (Holt & Kotler 1987, Brown & Mitchell 1989, Murakami & Nakano 2002).

Study organisms

The blue crab *Callinectes sapidus* Rathbun, 1896, is an important benthic predator in Chesapeake Bay (Virnstein 1977). Large adult crabs are opportunistic omnivores, feeding primarily on bivalves (~50% of diet) and crustaceans (~30%) as well as fish and polychaetes (Hines et al. 1990). Blue crabs are cannibalistic, with adults feeding on juveniles (Hines & Ruiz 1995). Because cannibalism represents a major source of mortality for juvenile blue crabs, juveniles congregate in shallow waters (<1 m), where adults are less abundant (Hines & Ruiz 1995, Hines et al. 1995), and in structured habitats that provide a predation refuge (Everett & Ruiz 1993).

Macoma balthica Linnaeus, 1758, is a small (shell length < 40 mm) tellinid clam that is the dominant biomass in unvegetated mud habitats within the mesohaline regions of Chesapeake Bay (Holland et al. 1977) and is a major source of food for blue crabs (Baird & Ulanowicz 1989). *M. balthica* avoids predation by burying deeply, up to 35 cm, in the sediment (Hines & Comtois 1985). The blue crab exhibits a Type III functional response to *M. balthica* in both the laboratory (Eggleston et al. 1992) and field (Seitz et al. 2001). The blue crab also exhibits a strong aggregative response to clams in general and *M. balthica* in particular (Clark et al. 1999a,b, Seitz et al. 2008). Indeed, clam density explains 93% of the variance of large crab density (Seitz et al. 2003). Hereafter, references to clams will imply *M. balthica*.

Study aims

In the present study, our objectives were to define the 2-prey functional response of adult blue crabs to clams and juvenile blue crabs and to determine the indirect effects in this system. To determine indirect effects, it is necessary to examine both the functional response, which is the likely mechanism responsible for indirect mutualism (Colton 1987), and the numeri-

cal or aggregative responses, which may lead to indirect competition (Holt & Lawton 1994). It seems likely that the relative strength of these responses will determine whether the net indirect effect will be positive or negative (Abrams & Matsuda 1996). While many studies have examined either the predator functional, numerical, or aggregative response in a system (e.g. Colton 1987, Settle et al. 1996, Rott et al. 1998, Murakami & Nakano 2002), few studies have integrated these responses because of the differences in temporal and spatial scales (Tschanz et al. 2007). The functional response operates on a small spatial and temporal scale as it addresses predator feeding in a local prey patch over a short time period. The numerical and aggregative responses operate over a longer time scale and a larger area as they deal with increases in predator populations over generations or the movement of predators among foraging areas. We used a series of predation experiments to determine both the single-species and the 2-species functional responses of adult blue crabs to clams and juvenile blue crabs. We then modeled field predation rates by combining the 2-prey functional response with the known predator aggregative response to estimate the indirect effect of clams on the predation risk for juvenile blue crabs in the field. By combining processes that occur at multiple scales, we were able to identify indirect effects in this system over a wide range of prey densities and gain a more holistic understanding of the interactions between these species.

MATERIALS AND METHODS

Laboratory setup

All of the functional response experiments were performed at the Smithsonian Environmental Research Center (SERC) wet laboratory. Experimental trials were conducted in 1 × 2 m tanks with flow-through water from the Rhode River (Chesapeake Bay, Maryland, USA). Each tank was divided into 2 sections (1 m²) with plastic Vexar¹ barrier (DuPont) mesh. Replicates within each experiment were randomly assigned to tanks and were run in both sections simultaneously. The tanks were filled with 12.5 cm of sand collected from Canning House Bay within the Rhode River. The water temperatures were 22.2 ± 3.3°C (standard deviation, SD), and the salinities were 12.2 ± 1.7 (YSI Model 85).

¹Use of trade names does not imply endorsement by the National Marine Fisheries Service, NOAA

Large *Callinectes sapidus*, with a mean carapace width (CW) of 145 ± 13 mm, were collected from the Rhode River using an otter trawl (3 m mouth, 50 mm mesh, and 7 mm bag liner) for use as predators. The predator's CW did not vary among treatments (ANOVA, $F_{22,76} = 1.10$, $p = 0.371$). Prior to use in experimental trials, the predators were held in tanks with flowing water and fed ad libitum with a commercial shrimp diet (Ziegler). Crabs were starved for 24 h prior to use to standardize hunger levels; blue crabs evacuate their guts within 18 h (McGaw & Reiber 2000). Each crab was only used once. Clams, with an average shell length (SL) of 25.6 ± 5.0 mm (SD), were collected from the Rhode River with a suction sampler and were kept in flowing water until used. The average SL in each trial did not differ among treatments (Kruskal-Wallis test statistic = 20.9, $p = 0.231$). Juvenile *C. sapidus* prey (CW 26.1 ± 5.4 mm) were provided by the Center for Marine Biotechnology's hatchery program (Zmora et al. 2005), held in tanks with flowing water, and fed ad libitum with a pelleted shrimp diet (Zmora et al. 2005). The average CW in each trial did not differ among treatments (Kruskal-Wallis test statistic = 22.1, $p = 0.139$). In the field, predation rates on hatchery crabs are the same as those on wild crabs, so the use of hatchery crabs is not expected to bias our results (Johnson et al. 2011).

For each experimental trial, the prey were established in the tank at the treatment-specific density and given time to bury and acclimate (clams: 24 h; juvenile *Callinectes sapidus*: 1 h). Following this time, a single adult blue crab predator was introduced into the tank. The crab was allowed to feed for 24 h and was then removed. At the conclusion of the trial, the sediment was sieved to collect and enumerate all remaining prey.

Single-species functional responses

We determined the functional response of crabs feeding on clams and juvenile blue crabs by performing feeding experiments at a range of prey densities (the number of replicates at each density are given in parentheses)—clams: 2 (2), 5 (6), 10 (5), 15 (5), 20 (8), and 40 (2) individuals m^{-2} ; juvenile *Callinectes sapidus*: 3 (4), 5 (9), 8 (4), 10 (6), 15 (3) individuals m^{-2} . We used maximum-likelihood estimation to fit the data to a Type I ($P_p = m$), II ($P_p = a/[1 + aT_hN]$), or III ($P_p = uN/[1 + vN + uT_hN^2]$) functional response model, where P_p is the proportional predation per predator (i.e. the number of prey eaten per predator divided by the initial number available), m is the con-

stant proportion of prey eaten at any prey density under a Type I functional response, N is the number of prey available, a is the instantaneous attack rate, and T_h is the handling time. In a Type III functional response, the equation is identical to a Type II model except that a is modeled as a function of prey density such that $a_1 = (u_1N_1)/(1 + v_1N_1)$, where u and v are parameters defining the instantaneous attack rate (Eggleston et al. 1992). We fit the number of prey eaten to the models using a binomial distribution, where P_p is the probability of being eaten, and N is the number of prey available in each trial. We selected the best model using the Akaike's information criterion (AIC) corrected for a small sample size (AIC_c) for each model (Burnham & Anderson 2002). In this and all similar analyses, we considered models with AIC_c values differing by <2 to explain the data equally well (Burnham & Anderson 2002). We also calculated the AIC_c weight, which is the normalized likelihood, for each model.

Prey choice experiment

We determined the predation rate of adult crabs feeding on clams and juvenile blue crabs simultaneously by performing feeding experiments at a range of prey densities with both prey present. The ratios of the abundance of clams:crabs per m^2 (replication at each combination is included in parentheses) used were 5:5 (7), 10:5 (5), 15:5 (3), 20:5 (1), 5:10 (5), 10:10 (5), 15:10 (4), 20:10 (2), 5:15 (3), 10:15 (3), 15:15 (1), and 20:20 (1). The total prey density ranged from 10 to 40 individuals m^{-2} . We plotted the proportion of clams available (A_M) against the proportion of clams in the diet (D_M) and used maximum likelihood to fit a series of models: (1) no preference (i.e. $D_M = A_M$), (2) preference for one prey item, and (3) prey switching. Preference was modeled as in Murdoch (1969):

$$D_M = \frac{cA_M}{1 - A_M + cA_M} \quad (1)$$

where c is a proportionality constant indicating predator preference. If $c > 1$, then the predator prefers the focal prey (in this case, *Macoma balthica*), and if $c < 1$, the predator prefers the alternative prey. Prey switching was modeled by making c a linear function of A_M . We also fit a second set of prey preference models as in Greenwood & Elton (1979):

$$D_M = \frac{1}{1 + \left(\frac{1}{cA_M}\right)^b} \quad (2)$$

where b indicates the degree of prey switching. When $b = 1$, no switching occurs, and when $b > 1$, switching occurs (Elliott 2004). We fit a model (4) where we set $b = 1$ for a simple preference model and another model (5) where b was allowed to vary to model prey switching. Two trials in which no prey, neither clams nor juvenile crabs, were eaten were not included because A_M could not be calculated. We assumed a normal distribution of errors. Because the variance is not expected to be constant over the range of data, we modeled the standard deviation (σ) as a function of D_M such that $\sigma = \sigma_{\max} D_M (1 - D_M)$, where σ_{\max} is proportional to the maximum value of σ . This gives a hump-shaped structure to σ , so that σ at $D_M = 1$ and $D_M = 0$ is 0 (as expected), and at $D_M = 0.5$, σ is at its maximum value of $\sigma_{\max}/4$. This method allowed us to account for predictable differences in variance over the range of data and is analogous to weighted least-squares regression (Quinn & Keough 2002). We selected the best model using the AIC_c of each model (Burnham & Anderson 2002).

Two-prey functional response

We used a modified Type III functional response to model the effect of multiple prey species on the functional response. We assumed a Type III response because the crabs had a Type III response to both species in isolation (see 'Results' below), and although a Type II response can be changed to a Type III by the addition of a second prey item (Holling 1959, Akre & Johnson 1979), there is no mechanism proposed that could change a Type III to a Type II response under such circumstances. We considered that the availability of alternative prey affects the attack rate (similar to Colton 1987):

$$a_1 = \frac{u_1 N_1}{1 + v_1 N_1 + w_{2,1} \frac{N_2}{N_1 + N_2}} \quad (3)$$

where a_1 is the attack rate on Species 1 (the focal prey), N_1 and N_2 are the abundances of Species 1 and 2, u_1 and v_1 are parameters that modify the attack rate based on the abundance of the focal species, and $w_{2,1}$ is a parameter that modifies the attack rate on Species 1 based on the proportional abundance of Species 2 (the alternative prey). When w is positive, the presence of alternative prey reduces the rate of predation, especially at lower densities of the focal prey, leading to a more pronounced Type III functional response and an extension of the low density threshold. We modeled the change of the functional

response as a function of the proportional availability of the alternative prey rather than the absolute number. Using the absolute density of prey would result in a vanishingly small attack rate at high alternative prey densities regardless of the density of the focal species, which is unrealistic. Additionally, because the blue crab is a chemosensory/tactile forager, its encounter rate with a prey species will be proportional to its relative, not absolute, density. Thus, the attack rate on one species is likely to vary with the relative density of the alternative species. We used maximum likelihood to fit 4 models to the combined data from both the single and 2-prey predation experiment ($n = 94$): (1) No interaction, where neither prey influences the attack rate on the other (i.e. $w_{2,1} = w_{1,2} = 0$); (2) 2-way interaction, in which both prey influence the attack rate on the other such that $w_{2,1} > 0$ and $w_{1,2} > 0$; (3) and (4) 1-way interactions in which one species influences the attack rate on the other (i.e. $w_{i,j} > 0$ and $w_{j,i} = 0$). We fit the number of prey eaten to the models using a binomial distribution where P_p was the probability of being eaten and N was the number of prey available in each trial. We selected the best model using the AIC_c of each model (Burnham & Anderson 2002).

Modeling field predation rates on juvenile blue crabs

Clam density was an excellent predictor of blue crab density, explaining 93 % of the variation in adult blue crab density (Seitz et al. 2003). We used the known aggregative response of blue crabs to clams (Seitz et al. 2003) to estimate the density of large blue crabs over a range of clam densities; note that this equation does not include small crabs, such as those used as prey in this experiment:

$$\text{Crabs m}^{-2} = \frac{5.99 + 1.98e^{0.006 \text{ Clams m}^{-2}}}{66} \quad (4)$$

We then incorporated this relationship into our 2-prey functional response model by multiplying the density of predators by the functional response, which gives the per-predator predation rate, to predict the predation risk of juvenile blue crabs in the field over a range of prey densities. We modeled the predation risk over 1 to 20 crabs m^{-2} and 0 to 300 clams m^{-2} . The range of clam and juvenile crab densities is well within those in Chesapeake Bay (Orth & van Monfrans 1987, Seitz et al. 2001, 2008), and the range of predator crab densities is 0.12 to 0.27 individuals m^{-2} , which is lower than that used in the laboratory predation experiment.

RESULTS

Single-species functional response

Adult blue crabs exhibited a Type III functional response to both clams and juvenile blue crabs (Table 1, Fig. 1). The evidence for a Type III functional response to juvenile blue crabs was strong, with the Type III having an AIC_c weight of 1.00 (Table 1). The evidence for a Type III functional response to clams was also very strong, with a weight of 0.99. In both cases, the ΔAIC_c for the next best model was >10 , indicating no support for the other models. We observed predator satiation in both cases, with the number of prey eaten leveling at high prey densities and the proportion eaten declining (Fig. 1).

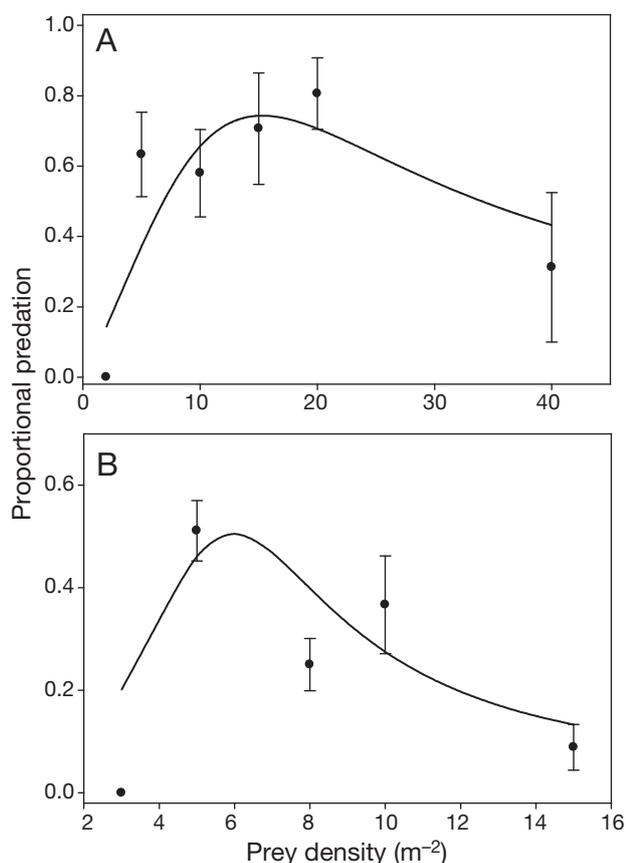


Fig. 1. *Callinectes sapidus* response to *Macoma balthica* and juvenile *Callinectes sapidus*. Single-species functional response of blue crabs to (A) clams ($n = 28$) and (B) juvenile blue crabs ($n = 26$). Points are the average predation at each density ± 1 SE. Lines represent the maximum likelihood estimates for a Type III functional response. Maximum likelihood parameter estimates (± 1 SE; see 'Materials and methods: Single-species functional responses' for definitions): (A) clam: $u = 0.067 \pm 0.025$, $v = -0.040 \pm 0.027$, $T_h = 0.063 \pm 0.016$, $R^2 = 0.21$; (B) juvenile blue crabs: $u = 0.028 \pm 0.006$, $v = -0.28 \pm 0.026$, $T_h = 1.02 \pm 0.22$, $R^2 = 0.40$

Table 1. Ranking of single-species functional response models with clams *Macoma balthica* and juvenile blue crabs *Callinectes sapidus* as prey using AIC_c . See 'Materials and methods: Single-species functional responses' for model descriptions

Model	Parameters	AIC_c	ΔAIC_c	Likelihood	AIC_c weights
Clams					
Type III	3	236.84	0.00	1.00	1.00
Type I	2	259.41	22.57	0.00	0.00
Type II	1	266.94	30.10	0.00	0.00
Juvenile blue crabs					
Type III	3	89.47	0.00	1.00	0.994
Type I	2	100.10	10.63	0.00	0.005
Type II	1	103.05	13.58	0.00	0.001

Predator choice experiment

Adult blue crabs did not exhibit prey switching in the choice experiments. The crabs may have had a slight preference for clams (Fig. 2), although this model had only slightly more weight than the no-preference model (Table 2), indicating that the data cannot be used to distinguish between the 2 models. Models from Murdoch (1969) did marginally better than those from Greenwood & Elton (1979), though the ΔAIC_c were <2 , indicating equal support. We present the best fit Murdoch preference model and the no-preference model in Fig. 2 and conclude that the adult crabs may exhibit a slight preference for clams, although the support for this is ambiguous.

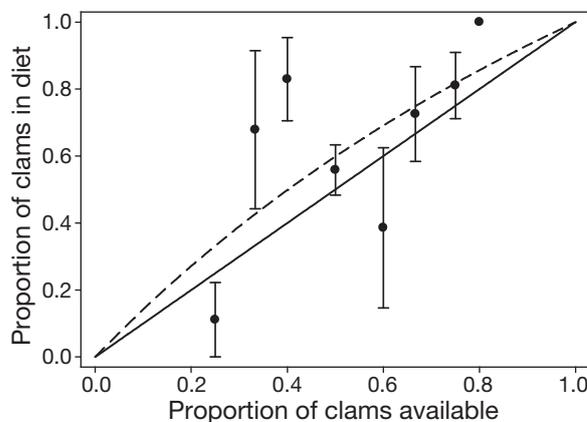


Fig. 2. *Macoma balthica*. Proportion of clams in the diet of crabs in predator choice experiments ($n = 38$). Points are the average predation at each density (± 1 SE). Lines represent the model of no predator preference (solid line) and the maximum likelihood estimates for the predator preference model (dashed line). The maximum likelihood estimate for c , the predator preference parameter, is 1.47 ± 0.37

Table 2. Ranking of prey choice models and 2-prey functional response models with clams (*M*) and juvenile blue crabs (*C*) as prey using AIC_c . In prey choice models, M: models after Murdoch (1969); G: models after Greenwood & Elton (1979). See 'Materials and methods: Two-prey functional response' for detailed model descriptions

Model	Parameters	AIC_c	ΔAIC_c	Likelihood	AIC_c weights
Prey choice models					
Preference (M)	2	27.39	0.00	1.00	0.33
No preference	1	27.63	0.24	0.89	0.29
Preference (G)	2	28.85	1.46	0.48	0.16
Switching (M)	3	29.62	2.23	0.33	0.11
Switching (G)	3	29.63	2.24	0.33	0.11
2-prey functional response models					
2-way interaction	8	918.43	0.00	1.00	0.58
<i>C</i> – <i>M</i> interaction	7	919.07	0.64	0.73	0.42
<i>M</i> – <i>C</i> interaction	7	931.42	12.99	0.00	0.00
No interaction	6	932.12	13.68	0.00	0.00

Two-prey functional response

The 2 models with the most support of the data were the crab–clam interaction and the 2-way interaction models (Table 2). The interaction refers to the effect of one species reducing the attack rate on the other. Because the 2-way interaction model, which implies indirect mutualism is occurring between the 2 prey species, is the better fitting of the 2 models and contains one extra parameter, we conclude that there is evidence for retaining this parameter, and we use this model to draw our inferences. However, we do so while noting that there is evidence for the crab–clam interaction model, which implies indirect commensalism.

Both the no-interaction and the clam–crab interaction models had AIC_c weights of <0.01 . The presence of clams reduced proportional predation on juvenile blue crabs by up to 0.14, or 50%, in the most likely model compared to the predicted predation with no clams present (Fig. 3A). Likewise, the presence of juvenile blue crabs reduced proportional predation on clams by up to 0.32, or 52%, compared to the predicted predation when no crabs were present (Fig. 3B). In neither species was there evidence of a qualitative change in the functional response; the response remained a Type III under all conditions, as evidenced by the shape of the functional response curve. The predation rate increased with prey density at low prey densities, indicating a Type III response, rather than decreasing,

which would indicate a Type II response (Taylor & Eggleston 2000). The estimated handling time for clams was about half of that for juvenile blue crabs, and the attack rate was higher under almost all conditions, resulting in a greater consumption rate of clams than juvenile blue crabs at the same prey density.

Modeling field predation rates on juvenile blue crabs

Our model predicts that the predation risk for juvenile blue crabs is lowest at an intermediate clam density (Fig. 4). When clams are absent, a high

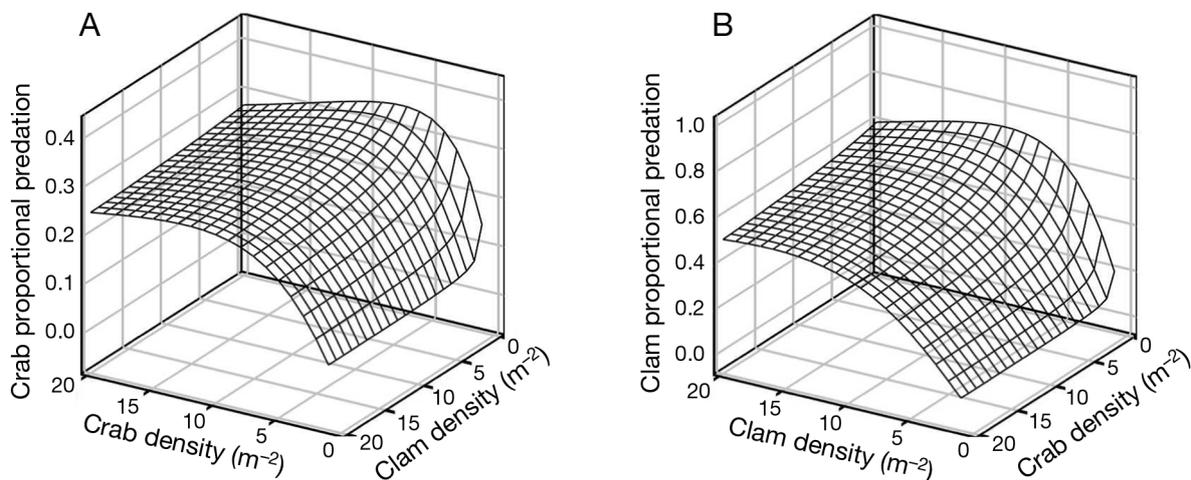


Fig. 3. Two-prey functional response surfaces for (A) juvenile blue crabs *Callinectes sapidus* and (B) clams *Macoma balthica* as predicted using the 2-way interaction model. Maximum-likelihood parameter estimates (± 1 SE) as follows: (A) juvenile blue crabs: $u = 0.18 \pm 0.023$, $v = 0.24 \pm 0.69$, $T_h = 0.10 \pm 0.13$, $w_{2,1} = 2.16 \pm 2.95$, $R^2 = 0.33$; (B) clams: $u = 0.21 \pm 0.09$, $v = 0.087 \pm 0.105$, $T_h = 0.051 \pm 0.013$, $w_{2,1} = 2.34 \pm 1.16$, $R^2 = 0.41$

proportional predation is predicted because, in the absence of alternative prey, predators focus their efforts on juvenile crabs. However, high clam densities attract more predators through an aggregative response (Clark et al. 1999a, Seitz et al. 2003), resulting in increased proportional predation on juvenile crabs (Fig. 4A). This increase can be as much as 95% compared to the predation rate when there are no clams present, translating into 62 more crabs eaten per day per 100 m² compared to predation rates expected at the same density in the absence of clams (Fig. 4B). At low to intermediate clam densities, the

clams reduce predation rates on juvenile crabs, without attracting enough predators to substantially raise the predation rate. This reduction in proportional predation is up to 48%, or 5 fewer crabs eaten per day per 100 m², compared to predation rates expected at the same density in the absence of clams. The large difference in the absolute number of crabs eaten is due to the fact that the largest percentage of increase occurs at high juvenile crab densities (20 individuals m⁻²) whereas the largest percentage of decrease occurs at low juvenile crab densities (3 individuals m⁻²).

DISCUSSION

Adult blue crabs exhibited a Type III functional response to both clams and juvenile blue crabs. The presence of clams changed the predator functional response to juvenile blue crabs primarily by lowering the peak predation rate. Similarly, juvenile blue crabs altered the functional response of blue crabs to clams. Although the presence of clams lowered predation rates on juvenile blue crabs in the laboratory, the inclusion of field-based data on the predator aggregative response suggests that the lowest predation rates on juvenile blue crabs should occur at low to intermediate densities of clams in the field.

We neither saw nor expected a shift in the functional response from a Type III response in our 2-prey functional response models. Although a Type II functional response may change to a Type III with the addition of a second prey species through switching behavior (Holling 1959, Akre & Johnson 1979), no mechanism has been proposed for a Type III changing to a Type II response. A similar reduction in predation rate with an increase of alternative prey densities without a corresponding qualitative change in the functional response can occur with predators displaying a Type II functional response (Colton 1987).

The functional response of adult blue crabs to juvenile blue crabs seemed to be dependent on the size of the juveniles. With smaller (20 to 40 mm CW) juvenile crabs, adults exhibit a Type III functional response (present study), but with larger (30 to 70 mm CW) juveniles, the functional response changes into a Type II functional response (Dittel et al. 1995). This is likely due to the relative importance of encounter (or attack) rate and handling time. With small juveniles, the predation rate is limited primarily by encounter rates, and the handling time is minimal; small crabs are more difficult to find but easier to subdue and consume. This leads to a Type III functional response (Seitz et al. 2001). With larger juve-

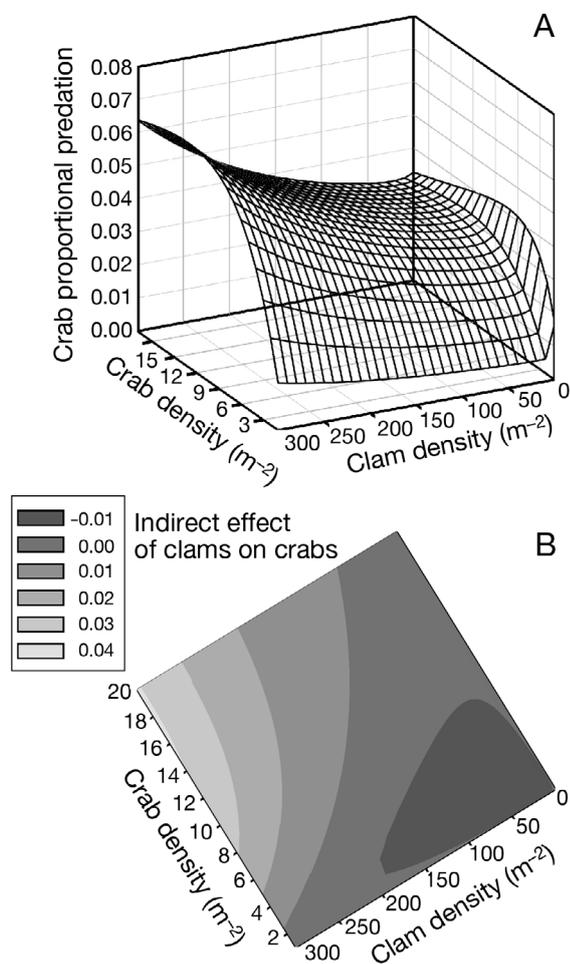


Fig. 4. *Callinectes sapidus* predation. (A) Daily proportional predation rate on juvenile blue crabs in the field, predicted by incorporating the predator aggregative response with the 2-prey predator functional response. (B) Contour map of the indirect effects of clam *Macoma balthica* populations on juvenile blue crabs. Indirect effects are calculated by subtracting the daily proportional predation rate at each point from the daily proportional predation rate at the same crab density with no clams present. Negative numbers indicate densities that result in apparent mutualism, and positive numbers indicate densities that result in short-term apparent competition

niles, the predation rate is limited more by handling time, with encounter rate becoming less important; large crabs are easier to find but more difficult to subdue and consume. This leads to a Type II functional response (Seitz et al. 2001). Given the slight preference that adult blue crabs may have for clams, it is likely that the presence of clams would change the Type II functional response exhibited to larger juveniles to a Type III response (Chesson 1989), but this remains to be tested.

Clams exerted an indirect effect on juvenile blue crabs and vice versa by reducing the predation rate when available as an alternative prey (Wootton 1994). When this indirect effect is bidirectional, as is most likely in this case, it is known as apparent mutualism (e.g. Abrams 1987a,b). When it is unidirectional, as there is some support for in the present study, it is known as apparent commensalism. Such a reduction in predation with an increase in alternative prey is common (Lester & Harmsen 2002, Heimpel et al. 2003, Rickers & Scheu 2005), especially when the alternative prey species is preferred (Eubanks & Denno 2000, Svenning et al. 2005, Tschanz et al. 2007). The mechanism behind this reduction is generally either predator satiation, predator switching, or preference (Murdoch 1969, Holt & Lawton 1994, Tschanz et al. 2007), and both the first and last processes seem to be in effect in this system. However, even at high clam densities, adult crabs still preyed on juvenile crabs, indicating that if there is a preference for clams, it is weak. This result is not unexpected because crab are opportunistic omnivores and are thus likely to eat whatever they are able to find (Hines et al. 1990).

Our model predicts that clams should exert a second indirect effect on juvenile blue crabs through the predator aggregative response. In the field, adult blue crab densities are determined primarily by bivalve densities (Clark et al. 1999a, Seitz et al. 2003), indicating strong top-down control of the clam populations. Thus, high densities of clams lead to short-term apparent competition with juvenile blue crabs by increasing predator density and thus the predation rate on juvenile blue crabs (Holt 1977, Rott et al. 1998). Such indirect effects can occur over several generations, by high alternative prey densities stimulating growth of the predator population (Settle et al. 1996, Carvalheiro et al. 2008) or, as in the present study, by patch-scale movement of predators (Holt & Kotler 1987, Brown & Mitchell 1989, Murakami & Nakano 2002). Because it operates by the latter mechanism, the predator response in the present study is a short-term effect. Because

the relationship here involves cannibalism, it is unclear what the effects would be in the long term because cannibalism will likely reduce future recruitment to the adult stage, which is the predator in the present case.

By combining the predator functional response and aggregative response, we predict that this 2-prey system will exhibit apparent mutualism or short-term apparent competition depending on the prey densities. At low clam densities, the clam presence reduces the predation rate on juvenile blue crabs through a modification of the predator functional response, as observed in our experiments. At high clam densities, although the effect of clams on the functional response continues, the aggregative response of predators results in an increase in the predation rate on juvenile crabs. The non-linear responses that change at different scales interact to produce this result (Abrams & Matsuda 1996).

It is possible that agonistic interactions among adult crabs might decrease predation rates at high predator densities (e.g. Mansour & Lipcius 1991, Clark et al. 1999a,b). However, the range of predator density predicted at 0 and 300 clams m^{-2} by the aggregative response model we used is only 0.12 and 0.27 crabs m^{-2} , whereas experiments examining agonism typically occur at a much higher density range (e.g. 0.5 to 4 crabs m^{-2}) (Mansour & Lipcius 1991, Kuhlmann & Hines 2005) or in a field enclosure with crabs competing for small patches of low-density prey (Clark et al. 1999b). Because agonism decreases with increasing prey density and with decreasing predator density (Mansour & Lipcius 1991, Clark et al. 1999b), we expect that its net effect will be minimal at the highest prey and predator densities used in our field modeling. Indeed, in laboratory experiments, the effect of agonism at 1 crab m^{-2} on the per-predator predation rates is negligible (Kuhlmann & Hines 2005). Finally, a field experiment with free-ranging predators estimated that agonism resulted in a ~15 to 20% reduction in predation rate between treatments (Hines et al. 2009), whereas our model predicts variations in predation on juvenile crabs of more than 95% with changing densities of clams. Thus, although agonism would likely have an effect in the field, given the small range in predator density predicted, the overall low predator density, and the small effect size relative to the effect size we predict, it is unlikely to change our conclusions.

How frequently indirect effects are density dependent is difficult to estimate. Most studies reporting apparent mutualism or commensalism rely on experiments in which predator densities are controlled and

which are designed to examine either the predator functional response or predator switching behavior (e.g. Eubanks & Denno 2000, Webster & Almany 2002, Rickers & Scheu 2005). Studies reporting short-term apparent competition typically rely on experiments in which predators are free to move and alternative prey treatments are often either presence or absence and which are designed to examine the predator aggregative response (e.g. Settle et al. 1996, Rott et al. 1998, Murakami & Nakano 2002). These studies all leave the possibility of density-dependent indirect effects open. In the only other study to our knowledge that included estimates of both the functional response and the aggregative response of predators, the prey species had a consistent indirect effect on each other (Tschanz et al. 2007). We suggest that several characteristics of a system may make it more likely to show such changes in the indirect effect. First, having a predator species that is highly mobile is probably important because a strong aggregative response is necessary for a switch from apparent mutualism to competition. Second, having one or more of the prey species sessile would also contribute because mobile prey could change their density in response to the predator density and change the overall patterns (Schreiber et al. 2006).

Indirect effects are responsible for up to 60 % of the changes to community structure resulting from experimental manipulations (Menge 1995) but are often under-explored (Kaplan & Denno 2007). The present study highlights the importance of examining both the predator functional response and the predator aggregative response when considering indirect effects in ecological systems and represents, to our knowledge, the first time that such density-dependent indirect effects have been suggested by experimental data. Indirect effects are, by their nature, non-linear, and the interaction of 2 or more effects is likely to lead to unexpected results (e.g. Abrams & Matsuda 1996).

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