

## UNINTENDED FACILITATION BETWEEN MARINE CONSUMERS GENERATES ENHANCED MORTALITY FOR THEIR SHARED PREY

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**Abstract.** We manipulated predator densities and prey vulnerability to explore how interactions between two predators affect overall mortality of their shared prey. Our three-member study system included eastern oysters (*Crassostrea virginica*) and two of its major consumers: southern oyster drills (*Stramonita haemastoma*) and stone crabs (*Menippe adina*). Field experiments demonstrated that drills and crabs foraging together generated higher than expected oyster mortality based on each species operating independently, even though crabs also killed some drills. In subsequent laboratory trials, we experimentally mimicked the handling of oysters by foraging crabs and confirmed that crabs facilitated drills by breaching oyster valves, thereby granting easy access for drills to their prey. Facilitation between co-occurring predators is uncommon and typically occurs because the behavior or habitat selection of a prey species is altered by the presence of one predator, consequently making the prey more susceptible to another predator. Whereas oysters are sedentary regardless of the predator field, we observed an entirely different mechanism that resulted in predator facilitation. This involved direct attacks on the physical defenses of oysters by one predator that ultimately increased the overall consumption rate of foraging species. These dynamics significantly enhanced mortality risk for a foundation species within an estuarine ecosystem.

**Key words:** *Crassostrea virginica*; eastern oyster; emergent multiple-predator effect; facilitation; intraguild predation; *Menippe adina*; oyster reef; risk enhancement; *Stramonita haemastoma*; trophic cascade.

### INTRODUCTION

In ecosystems with co-occurring predator species that differ in foraging behavior or predator–prey interactions, there is growing interest in quantifying the combined effects that multiple predators have on shared prey (Sih et al. 1998). Recent progress has made it abundantly clear that understanding these multiple-predator effects (MPEs) are necessary for accurately predicting food–web dynamics. Experimentalists have found that combined predators can operate independently (substitutable; Hixon and Carr 1997), or generate higher (facilitation; Losey and Denno 1998), or lower (interference; Crowder et al. 1997) prey mortality than expected based on each predator foraging alone. Sih et al. (1998) termed deviations from predator independence as emergent MPEs, and after weighing the available studies, concluded that risk enhancement for shared prey is not common. Rather, competitive interference interactions between predatory species typically reduce the effectiveness of at least one predator in locating and consuming the shared prey. The low representation of predator facilitation in multiple-predator scenarios contrasts with the emerging paradigm that facilitation

plays a major role in defining ecological exchanges and regulating community structure. These positive interactions have been shown to significantly affect niche concepts, population dynamics at high densities, and succession patterns (Bruno et al. 2003). In this report, we documented predator facilitation between two marine invertebrates that significantly affected mortality risk for a foundation species within an estuarine ecosystem.

Multiple-predator scenarios can also affect food-web dynamics that have implications beyond the abundance of the shared prey. For instance, the discovery and examination of trophic cascades in marine and freshwater communities have significantly advanced our understanding of food-web ecology (Pace et al. 1999, Polis et al. 2000). Predation (top-down regulation) is a fundamental principle behind trophic cascades, as direct reduction (Myers et al. 2007) or behavioral suppression (Grabowski 2004) of intermediate predators can indirectly result in a significant increase in the abundance of more basal resources. However, these cascades are more likely in systems characterized by simple, highly stratified food webs. Increasing predator diversity (i.e., having multiple predators) or including omnivorous species typically dampens the propagation of trophic cascades through food webs (Polis et al. 2000, Finke and Denno 2004). We used our findings of predator facilitation to further explore how multiple-predator effects should

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influence the strength of trophic cascades in an estuarine system.

Estuarine food webs are highly reticulated rather than linear chains (e.g., Jackson et al. 2001), and should be significantly influenced by complex interactions such as the combined effects of multiple predators. Foundation species such as oysters, in concert with the “strong interactors” that prey upon them, provide a model system for exploring these dynamics, as well as trophic cascades. This is because oysters maintain dual ecosystem roles: serving as a major conduit of energy through coastal food webs, and providing biogenic structure that mediates interactions among diverse assemblages of fishes and invertebrates (Hughes and Grabowski 2006).

We focused our experiments on a community that included eastern oysters (*Crassostrea virginica*) as the shared prey of southern oyster drills (*Stramonita haemastoma*) and stone crabs (*Menippe adina*). Previous research has identified oyster drills as an important predator of eastern oysters within the northern Gulf of Mexico, where drills can reach densities  $> 40$  drills/m<sup>2</sup> and limit the abundance of oysters (Brown and Alexander 1994). In some instances, drills have caused  $>90\%$  oyster mortality within individual reefs (Butler 1985). One trophic level up, Lindberg and Marshall (1984) included drills as a significant component in the diet of stone crabs. Because stone crabs prey on drills, a reasonable prediction would be that stone crabs could aid in the biological control of drills through either numerical or behaviorally mediated effects. If true, this could release ecologically and economically important oysters from top-down regulation in much the same way that sharks historically limited stingray populations, which subsequently reduced the natural mortality of another estuarine bivalve: the bay scallop (Myers et al. 2007). However, stone crabs not only prey upon drills, but also consume oysters. In fact, Brown and Haight (1992) noted that stone crabs showed a slight preference for oysters over drills as prey items. Therefore, predicting the patterns of oyster mortality and trophic cascades affecting oyster reefs when both oyster drills and stone crabs are present has remained elusive.

With these food-web interactions in mind, we manipulated predator densities and prey vulnerability to consider the following: (1) are there numerical or behaviorally mediated interactions between drills and crabs via predation, competition or facilitation that affect oyster mortality rates (experiments 1 and 3); and (2) are the effects of multiple predators upon oyster mortality characterized as risk enhancing, risk reducing, or independent (experiment 2)?

#### METHODS

Examining species interactions within the oyster–drill–crab web involved three separate experiments from June 2006 to January 2007. For all experiments, drills were collected from bagged oysters kept underneath the Dauphin Island Sea Lab (DISL) vessel dock, on Dauphin

Island, Alabama, USA. Hatchery-reared oysters were collected from the same bags, or from nearby marsh creeks when small reef clumps were required. Stone crabs were collected from crab pots deployed near DISL. Drills and crabs were held for 4 days prior to experimentation, while oysters were collected 1–2 days before experimental runs and scraped to remove epifauna. In every experiment, sizes and weights of all specimens were monitored to ensure consistency among treatments, and only small ( $<5\%$ ) differences were observed.

The first experiment examined if direct or indirect interactions between oyster consumers could alter the foraging behavior of drills, which are themselves subject to mortality by stone crabs. This experiment was conducted in two  $2.5 \times 0.5 \times 0.5$ -m (length  $\times$  width  $\times$  height) recirculating seawater (23‰ salinity, 25.5°C) tanks at DISL. A 5-cm layer of washed sand was used in each tank to represent the natural matrix surrounding small oyster clumps. At opposite, randomly assigned ends of the tanks, high- (60 oysters) and low-density (12 oysters) oyster patches were created in 0.25-m diameter circles. The experimental design included a single factor: absence or presence of a stone crab tethered within the high-density patch ( $83.6 \pm 1.5$  mm [mean  $\pm$  SE] carapace width, CW). At the beginning of every trial, six drills ( $32.6 \pm 0.7$  mm, shell length, SL) were placed in the center of each tank on the sand matrix. The drill and crab densities selected for these experiments closely approximated predator densities observed over nearby oyster reefs, and are well below the maximum density reported by Brown and Alexander (1994). Drills were allowed to select among habitats over a 48-hour period, after which the trials were halted and we recorded recovery rate and position (high-density patch, low-density patch, sand matrix, or tank wall) of live drills. We also documented mortality rates of oysters ( $35.3 \pm 0.3$  mm SL) within the high-density patch. With only two tanks, trials were run on six occasions during June of 2006 ( $n = 6$  trials for each treatment). Treatment (no crab, crab) designations were completely randomized so time was not used as a blocking factor in our statistical analyses. We tested for crab effects on (1) proportion of drills that selected the high-density oyster patch and (2) proportional oyster mortality within the high-density patch, using  $t$  tests on arcsine-transformed data. Transformations were required to stabilize variances between groups.

Building from the results of drill–crab interactions in the first experiment, we compared single and multiple predator effects on oysters during July and November of 2006 in a second set of experiments to determine if predators acted independently or demonstrated emergent MPEs. These trials were conducted in 1.2-m<sup>2</sup> circular cages placed over subtidal flats adjacent to DISL property. Cages were constructed of 4-mm Vexar (Dupont, Wilmington, Delaware, USA) stretched around PVC skeletons. Cage bottoms were skirted by a 20-cm metal flange that was driven completely into the sediment, and each cage top received sewn-on Vexar lids to exclude other potential consumers.

We used a  $2 \times 2$  orthogonal design to include all possible predator combinations: 0 drills and 0 crab; 6 drills and 0 crab; 0 drills and 1 crab; and 6 drills and 1 crab. An additive design was employed since interaction strengths (predation rates) between drills and oysters vs. crabs and oysters were not expected to be substitutable (but see Griffen [2006] for limitations). As before, drill and crab densities in this experiment closely approximated predator densities on local reefs. During July, we deployed eight cages, and ran trials on three separate occasions ( $n = 6$  for each predator treatment). Each cage was stocked with 50 loose oysters ( $50.2 \pm 3.4$  mm SL), and the various predator treatments were randomly assigned among cages across the three runs (treatments were not blocked by time). Cages were checked daily to ensure they remained sealed. Otherwise, drills ( $42.5 \pm 0.6$  mm SL) and crabs ( $80.1 \pm 1.9$  mm CW) were allowed to forage undisturbed for 96 hours, then all predators and prey were removed and we tallied live and dead specimens.

We repeated this field experiment in November with the following amendments: (1) rather than using loose oysters, we stocked cages with 50 live oysters ( $51.1 \pm 3.7$  mm SL) that were naturally cemented together in small clumps (3–20 live oysters per reef clump). This second presentation of oysters was needed for our conclusions to be applicable across the range of natural reef forms; (2) 12 cages were deployed, so only two runs were needed to achieve six replicates (treatments were randomized among cages and between runs); and (3) during July, temperatures ranged from  $28^\circ\text{C}$  to  $33^\circ\text{C}$ , and salinity was measured at 24–30‰, while in November, temperature was recorded at  $17$ – $20^\circ\text{C}$ , and salinity was measured at 16–28‰.

The effects of multiple predators on oyster mortality during the field experiments were tested using separate two-way ANOVAs for the July and November trials. In each case, drills and crabs were considered as factors on arcsine-transformed oyster mortality. Transformations were required to stabilize variances between groups. We also examined how predator-driven oyster mortality data compare to additive and multiplicative risk models by performing the two-way ANOVAs using untransformed and log-transformed data, respectively (Sih et al. 1998). A significant interaction term between predator treatments would indicate that combined predation rates were not independent (i.e., predators had emergent effects).

July and November field experiments suggested that oyster predators might have facilitated one another, and therefore we conducted a final lab experiment to identify the mechanism responsible for this. Facilitation between drills and crabs was unexpected based upon the results of experiment 1, and therefore we revisited the potential interactions between drills and crabs in this final experiment to better understand what regulates predation on oysters. These experiments were conducted in four  $0.33 \times 0.2 \times 0.25$ -m (length  $\times$  width  $\times$  height)

aquaria tanks at DISL during January of 2007. Seawater at 23‰ salinity and  $25.5^\circ\text{C}$  was again circulated through the tanks, but a sand substrate was not included.

We suspected some form of oyster handling by crabs resulted in facilitation (almost all dead oysters in the field experiment appeared to have been killed by crabs based on shell fragments), and therefore we wanted to quantify which species received the soft-tissue food resource available from oysters once the shells of individual prey were breached. Our design included the same four predator treatments as in the field experiments, plus oyster shell condition as an additional factor. This produced a three-way orthogonal ( $2 \times 2 \times 2$ ) design. Five loose oysters ( $48.1 \pm 8.7$  mm SL), drills ( $n = 0$  or 6), and crabs ( $n = 0$  or 1) were added to the tanks as in the field experiments. Half the trials proceeded with undamaged oysters and the other half were performed with oysters that had their edge breached using bolt cutters to simulate crab attacks on the shell margin. In contrast, drill attacks result in  $<1$ -mm holes in oyster shell and were not expected to facilitate crabs (Brown and Haight 1992, Brown and Alexander 1994). Damaged and undamaged oysters were weighed (whole wet mass) before placing them in aquaria with the various predator treatments. Drills ( $53.1 \pm 4.9$  mm SL) and crabs ( $98.6 \pm 13.9$  mm CW) foraged for 24 hours, after which predators were removed and the contents of the tanks filtered through a  $150\text{-}\mu\text{m}$  sieve to capture all oyster fragments. Oysters were again weighed and the difference in before/after mass was used to determine the amount of oyster tissue consumed by predators. Since boring through oyster shell is a rate-limiting step in drill feeding, we were particularly interested to see if oyster drills benefited disproportionately once any oyster was breached using our crab-handling mimic. Using four tanks, trials were run on six occasions to generate three replicates for each unique treatment, which were completely randomized among tanks and runs. We examined how predator combinations and shell condition affected the nutritional benefit obtained by crabs and drills using a three-way ANOVA with drills, crabs, and shell condition as factors on  $\log(x + 1)$ -transformed oyster mass loss (soft tissue consumed). Transformations were required to stabilize variances between groups.

## RESULTS

Oysters suffered mortality from both predators, but interspecific interactions within the oyster–drill–crab system were complex and partially counterintuitive. In our preliminary laboratory experiment, habitat selection of drills was extremely dependent on crab presence ( $P = 0.006$ ; Table 1). In crab-free treatments, nearly 80% of drills were found foraging within the high-density oyster patch. Alternatively, less than 5% of the drills selected the high-density patch when a tethered crab was present. It was notable, however, that most drills did not select the low-density oyster patch when crabs were present,

TABLE 1. Effects of interspecific interactions between southern oyster drills and stone crabs on eastern oyster mortality.

Factor	df	MD	<i>t</i>	<i>P</i>	
Drill selection of high-density oyster patch					
Crab presence	10	-0.87	-4.89	0.006	
Oyster mortality in high-density oyster patch					
Crab presence	10	0.173	1.994	0.074	
Factor	SS	df	MS	<i>F</i>	<i>P</i>
Oyster mortality: multiple-predator effects using loose oysters					
Crab presence	2.746	1	2.746	99.917	<0.0001
Drill presence	2.000	1	2.000	72.786	<0.0001
Crab × drill	0.368	1	0.368	13.374	0.001
Error	0.632	23	0.027		
Oyster mortality: multiple-predator effects oysters reef clumps					
Crab presence	0.401	1	0.401	63.29	<0.0001
Drill presence	0.081	1	0.081	12.83	0.0019
Crab × drill	0.026	1	0.026	4.159	0.0549
Error	0.013	20	0.001		
Oyster consumption: risk enhancement for the shared resource					
Oyster condition	3.207	1	3.207	13.474	0.0021
Crab presence	0.994	1	0.994	4.177	0.0578
Drill presence	0.918	1	0.918	3.857	0.0672
Oyster condition × crab	0.035	1	0.035	0.146	0.7077
Oyster condition × drill	1.178	1	1.178	4.949	0.0408
Crab × drill	0.106	1	0.106	0.444	0.5148
Oyster condition × crab × drill	0.081	1	0.081	0.341	0.5673
Error	3.808	16	0.238		

Note: MD is the mean difference between groups.

but rather the sand matrix or tank walls adjacent to the high-density patch (80%). When only drills were present in the tanks, 16% of oysters in the high-density patch were killed and eaten, while double that proportion (32%) were consumed in treatments that included a crab, although the difference was nonsignificant ( $P = 0.074$ ; Table 1). Crabs killed no drills during these trials.

In field experiments, both drills and crabs caused significant oyster mortality based upon comparisons with no-predator controls regardless of oyster presentation (loose or reef clumps) (Table 1; Fig. 1). Moreover, the combined effects of predators suggested that there were emergent multiple-predator effects, indicated by significant or near-significant interaction terms between predator treatments for untransformed (compared with additive risk: loose oysters,  $P = 0.01$ ; clumped oysters,  $P = 0.05$ ), log-transformed (compared with multiplicative risk: loose oysters,  $P < 0.0001$ ; clumped oysters,  $P = 0.08$ ), and arcsine-transformed data (Table 1).

Despite the June laboratory data that suggested crabs might limit the foraging activity of drills, our field experiments showed that these two predators operated synergistically, resulting in risk enhancement for oysters in treatments with both drills and crabs (Fig. 1). If each predator had performed independently, we would have expected roughly 77% or 62% oyster mortality for the trials in which we used loose oysters, based on additive or multiplicative risk models, respectively (Fig. 1).

However, we observed mortality well above either of these predictions (89%). Although prey mortality was lower in all treatments during November when we stocked cages with clumped rather than loose oysters, similar trends were observed. Risk models predicted oyster mortalities at 25% (additive) or 24% (multiplicative), but the percentage of oysters consumed by predators was actually 1.5 times higher (37%; Fig. 1). Surprisingly, this was true even though crabs killed and likely consumed 25% of all drills included in the field experiments, as evidenced by drill fragments recovered at the conclusion of our runs.

The only significant ( $P < 0.05$ ) effects in our third experiment to identify the mechanism for predator facilitation, using oyster tissue consumption as the response variable, were oyster condition ( $P = 0.002$ ) and the interaction between oyster condition and drill presence ( $P = 0.04$ ; Table 1). Conversely, the interaction between oyster condition and crab presence was highly nonsignificant ( $P = 0.7$ ; Table 1), although both drill and crab consumption increased when oyster shells were damaged (Fig. 2). In treatments with intact shells, drills essentially consumed no oyster tissue over 24 hours whether crabs were present or not (Fig. 2). However, six drills together were able to consume approximately 30 g of oyster tissue over 24 hours if oysters were damaged to mimic prior handling, regardless of crab presence (Fig. 2). These data indicate drills can rapidly consume the

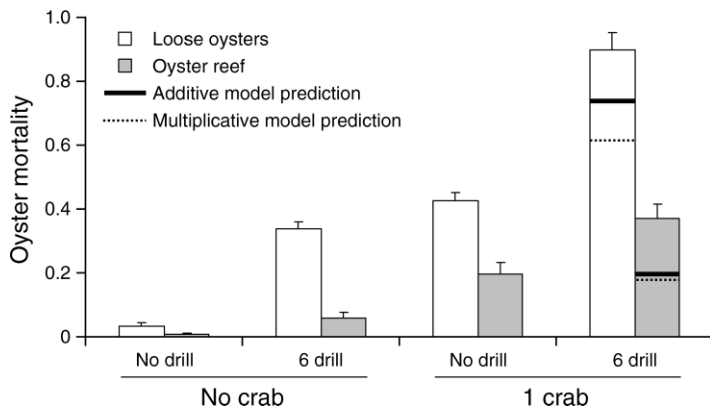


FIG. 1. Oyster mortality (fractional rates) inside field cages ( $1 \text{ m}^2$ ) in a  $2 \times 2$  orthogonal experiment with southern oyster drills ( $n = 0$  or 6 drills per cage) and stone crabs ( $n = 0$  or 1 crab per cage) as predators. The experiments were conducted using two prey presentations: single, loose oysters in July (white bars) and oyster reef clumps in November (gray bars). Data were recorded following a foraging interval of 96 hours, and all bars represent the mean of six replicates ( $\pm$ SE). Expected mortality rates of oysters when both predators were present are provided for additive (solid line) and multiplicative (dotted line) risk models.

food resource available from oysters only if they can gain access to soft-body tissue without having to slowly bore through shell themselves. Therefore, drills disproportionately benefited from having another agent that more readily breached oyster shell (crabs in the field trials and bolt cutters that mimicked crabs in the final laboratory experiment).

#### DISCUSSION

We designed a set of experiments to determine how complex interactions involving two predators, oyster drills and stone crabs, would affect mortality of eastern oysters. Based on our first experiment, we predicted that relative to each predator operating alone, crabs should suppress the foraging behavior of drills, resulting in reduced risk for oysters in multiple-predator treatments. Because crabs can consume oysters as well as inhibit the foraging of drills, however, we did not expect crabs to indirectly release oysters from top-down control. Surprisingly, our subsequent experiments provided evidence that oysters were subject to enhanced risk in treatments with both predators.

There was an unexpected positive interaction between predators that generated enhanced oyster mortality in this estuarine community. Specifically, crabs facilitated drill foraging by breaching oyster valves, thereby granting easy access for drills to oyster tissue. Otherwise, drills must excavate small holes in oyster shell, which is difficult enough that drills will forage in groups to overcome the defenses of large oysters (Brown and Alexander 1994). Essentially, drills switched feeding modes from predation to scavenging and appeared to consume oyster tissue that crabs had already accessed. This was observed during experiments in which oyster valves were experimentally breached to mimic prior crab handling (Table 1, Fig. 2), as well as during field experiments when we recovered two drills feeding from inside oyster valves that were obviously opened by crabs based on shell fragments (Brown and Haight 1992). Subsequent to drills "stealing" soft tissue that became available following attacks by crabs on oysters, we speculate that crabs targeted new oysters with increased

frequency to acquire additional prey resources for themselves. Since crabs are capable of breaching shell relatively quickly, the end result was enhanced mortality for oysters. Although we lack concrete evidence for the exact response of stone crabs to the behavior of drills, our conclusion is supported by the observation that nearly all of the oysters killed in field experiments were attacked by crabs based on recovered shell fragments.

Previously, Sih et al. (1998) concluded that elevated risk for prey in multiple-predator scenarios would be uncommon. This is because prey are sometimes capable of switching between predator-specific defense mechanisms, and because predator-predator interactions such as interference competition or intraguild predation reduce the effectiveness of one or both predators (Sih 1980, Polis and Holt 1992). Nearly all reports of predator facilitation that result in risk enhancement for a shared prey are based on two elements: one predator chases or alters the habitat selection of the prey, and this makes they prey more susceptible to

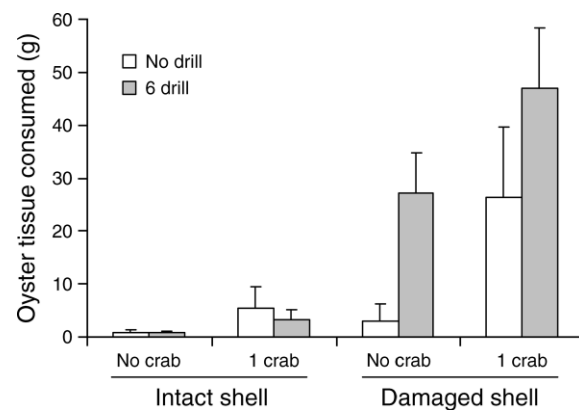


FIG. 2. Oyster tissue consumed in a three-factor orthogonal experiment with southern oyster drills ( $n = 0$  or 6 drills per cage) and stone crabs ( $n = 0$  or 1 crab per cage) as consumers and oyster shells either left intact or breached to mimic predator handling. Data were recorded following a foraging interval of 48 hours, and all bars represent the mean ( $\pm$ SE) of three replicates.

attacks from another predator. For instance, Losey and Denno (1998) found that foliar-foraging predators promoted “dropping” behavior by an aphid that made it subject to high mortality via ground-foraging predators. Settled oysters are immobile, and thus habitat selection and fleeing behaviors of prey did not account for the synergism between drills and crabs. Instead, we observed enhanced risk for oysters because stone crabs aided oyster drills in overcoming the physical defenses of their shared prey. This is a previously unreported mechanism for predator facilitation within MPE studies. As in other cases demonstrating predator synergism, the aid provided by crabs to drills was unintended, and may even have negative impacts on crabs if they have to dedicate significantly more time toward handling oysters in order to acquire food.

We speculate drills were attempting to balance the conflicting demands of resource acquisition and predator avoidance (Sih 1980). While drills overwhelmingly avoided oyster patches with tethered crabs during laboratory trials, during subsequent experiments crabs facilitated drills via provision of breeched oysters. We did note that even in the laboratory trials where drills emigrated from oyster patches if a tethered crab was present, they did not move into the other, less rewarding oyster patch. Rather, drills lined the perimeter of the oyster patch that included a stone crab, either in the sand matrix or on the tank walls. We hypothesize that drills may have made brief forays during field experiments into the immediate vicinity of the crabs to feed on the relatively large oysters we employed in our trials (also, 5% of drills in the laboratory were collected in the same patch as the tethered crab). Some percentage of drills (~25%) may have been intercepted and killed by crabs during these encounters.

A remaining question is why drills would select foraging habitats in the wild that bring them into contact with a potential predator. Although stone crabs may aid drills in obtaining nutrition, organisms generally select habitats based on the predation refuge they provide rather than associated foraging benefits (*sensu* Heck et al. 2003). While our experiment was not designed to test how habitat complexity mitigated encounters between foraging species, other researchers have noted that the physical structure provided by oyster reefs can dampen intraspecific (Grabowski and Powers 2004) and interspecific (Hughes and Grabowski 2006) interactions. Our results indicated that regardless of reef complexity (loose shell or small reef clumps) drills and crabs foraged synergistically, suggesting that more complex reefs did not isolate the foraging behaviors of these two species. It is possible that drills have the ability to recognize situations in which the risk presented by stone crabs is low (*sensu* Sih 1980), particularly in natural reef environments when crabs are able to locate and feed on oysters, which is their preferred prey (Brown and Haight 1992). This may explain the co-occurrence of crabs and drills over large (among reefs in high salinity

environments) and small (<1 m) scales within oyster reef habitats (Lindberg and Marshall 1984, Butler 1985).

Using a trophic cascade framework, we hypothesized that stone crabs might have direct numerical or behaviorally mediated effects on drill foraging. We expected this could relieve some of the mortality risk for oysters that is attributed to drills, which can consume >90% of oysters on some reefs (Butler 1985). Typically however, trophic cascades have been most readily observed in systems where each trophic level only preyed upon the next lower level. More recent treatments have shown how omnivory can dampen or even shift the phase of trophic cascades. Spiller and Schoener (1990) found that removing lizards (tertiary consumers) from Bahamian islands resulted in increased leaf damage, rather than the decrease in herbivory (via primary consumers) predicted by linear models. This occurred because lizards were also important predators of the primary consumers on the islands. Likewise, our data support a growing literature that has found omnivory (demonstrated here by stone crabs that killed both drills and oysters) alters the strength of trophic cascades within food webs (Polis and Holt 1992). Our data also support previous results indicating that multiple predators interacting with a prey species tend to dampen the potential for trophic cascades to propagate down food chains (Finke and Denno 2004). We found no evidence of a trophic cascade whereby oysters benefit from crab presence, although crabs did kill some drills as well as alter their microhabitat selection. Quite oppositely, drills and crabs operated synergistically to generate elevated oyster mortality.

Since most species at mid or high trophic levels are generalists and feed at multiple trophic levels (Pimm and Lawton 1978), potential competitors can also engage in predator-prey interactions, thereby creating triangular compartments within food webs. Polis and Holt (1992) defined this subset of omnivory as intraguild predation (IGP). Because IGP merges predatory and competitive exchanges between foraging species, complex dynamics result that could not be predicted from studies with predation and competition considered separately (Polis and Holt 1992). In multiple-predator scenarios, risk enhancement for the shared prey should be uncommon because competition, and particularly IGP, between predatory species typically reduces the effectiveness of at least one predator in locating or consuming the shared prey (Sih et al. 1998). However, our data provide a clear example of risk enhancement for a shared prey despite additional predator-prey interactions between the two consumers (i.e., crabs preyed upon drills). Facilitation was the mechanism that generated enhanced oyster mortality in this triangular food web. Although we lack sufficient data to conclude that our study system operated under the IGP framework (specifically, the degree to which crabs and drills compete over oysters), we can suggest that ecological exchanges in triangular food webs are not limited to predation and competition,

but can simultaneously include some positive relationships between species that also prey on one another (Polis and Holt 1992) or compete over limiting resources (Holbrook and Schmitt 2004).

Managing living resources will require increased attention for complex trophic interactions such as multiple-predator effects, as it has become increasingly apparent that community structure and dynamics cannot be predicted by simply summing all pairwise connections within an ecosystem. Applied to conservation biology, stone crabs are not an effective means of biological control for drills that will release oysters from top-down regulation. Within the oyster-drill-crab assemblage, work is needed to determine how exactly oyster drills manage the conflicting demands of prey acquisition and predator avoidance in the presence of stone crabs (a potential predator, but also a facilitator), and over what temporal and spatial scales these interactions occur. Our manipulative experiments clearly indicated that unintended facilitation between two foraging species could alter the flow of energy through an estuarine food web. A critical next step should be to correlate the distribution of stone crabs and oyster drills in the field with local mortality rates of oysters to see how common facilitation appears to be for these animals foraging in the wild. More broadly, theoretical and empirical treatments of positive interactions in food webs will continue to provide a more robust understanding, in combination with other emergent MPEs such as interference competition, of the processes that drive prey survival, niche shifts, species coexistence, and trophic cascades (Bruno et al. 2003).

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