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Habitat context influences predator interference interactions and the strength of resource partitioning

A. Randall Hughes · Jonathan H. Grabowski

Abstract Despite increasing evidence that habitat structure can shape predator–prey interactions, few studies have examined the impact of habitat context on interactions among multiple predators and the consequences for combined foraging rates. We investigated the individual and combined effects of stone crabs (*Menippe mercenaria*) and knobbed whelks (*Busycon carica*) when foraging on two common bivalves, the hard clam (*Mercenaria mercenaria*) and the ribbed mussel (*Geukensia demissa*) in oyster reef and sand flat habitats. Because these species co-occur across these and other estuarine habitats of varying physical complexity, this system is ideal for examining how habitat context influences foraging rates and the generality of predator interactions. Consistent with results from previous studies, consumption rates of each predator in isolation from the other were higher in the sand flat than in the more structurally complex oyster reef habitat. However, consumption by the two predators when combined surprisingly did not differ between the two habitats. This counterintuitive result probably stems from the influence of habitat structure on predator–predator interactions. In the sand-flat habitat, whelks significantly reduced their consumption of their less preferred prey when crabs were present. However, the structurally more complex oyster reef habitat appeared to reduce interference interactions among predators, such that consumption rates when the predators co-occurred did not differ from predation rates when alone. In addition, both habitat context and predator–predator interactions increased resource partitioning by strengthening predator dietary selectivity. Thus, an understanding of how habitat characteristics such as physical complexity influence interactions among predators may be critical to predicting the effects of modifying predator populations on their shared prey.

Keywords Context dependency · Habitat structure · Oyster reef · Predator dietary selectivity · Predator interference

A. R. Hughes (✉)
Bodega Marine Laboratory and Section of Evolution
and Ecology, University of California-Davis,
P.O. Box 247, Bodega Bay, CA 94923, USA
e-mail: arhughes@ucdavis.edu

J. H. Grabowski
Gulf of Maine Research Institute,
350 Commercial St., Portland, ME 04101, USA

Introduction

Ecologists are increasingly realizing the importance of multi-species interactions and their consequences for community structure and ecosystem function (Chapin et al. 2000; Shurin et al. 2002; Duffy et al. 2005; Ives et al. 2005). Recently, several lines of research have converged on examining the role of species interactions in a food web context (Shurin et al. 2002; Duffy et al. 2005; Ives et al. 2005). Of primary interest is whether interactions in a multi-species assemblage can be predicted by combining the pair-wise interactions of the component species, or whether emergent effects arise (Strong 1992). For example, there is a rapidly growing literature on emergent multiple predator effects on prey such as risk enhancement (i.e., more prey are consumed than expected based on the single predator effects) as

well as risk reduction (i.e., fewer prey are consumed than expected based on the single predator effects; Soluk and Collins 1988; Sih et al. 1998).

In addition to a growing understanding of how interactions among multiple predator species impact prey consumption, there is a long history of research on the effects of habitat context on predator–prey interactions. Predator foraging efficiency generally varies inversely with habitat heterogeneity (Diehl 1992; Beck and Watts 1997; Beukers and Jones 1997; Cowlishaw 1997), and predator–prey interactions can change dramatically in response to habitat complexity (Crowder and Cooper 1982; Werner et al. 1983; Schriver et al. 1995; Grabowski and Powers 2004). In general, individual predators consume fewer prey in more structurally complex habitats (Peterson 1982; Blundon and Kennedy 1982; Irlandi and Peterson 1991; Finke and Denno 2002; Grabowski 2004; Warfe and Barmuta 2004). The fact that structurally complex habitats (e.g., submerged macrophytes, oyster reefs, coral reefs) often support greater abundances and diversity than unstructured habitats is often attributed to reduced predation in these habitats (Heck and Wetstone 1977; Summerson and Peterson 1984; Beck 2000; Lenihan et al. 2001; Grabowski et al. 2005), although these patterns could also be due to greater propagule retention or enhanced food concentration in complex habitats (Tegner and Dayton 1981; Summerson and Peterson 1984).

The negative effects of structural complexity on predation success probably depend on a combination of several factors. Refuge availability for prey is often positively associated with habitat structure (Huffaker 1958) and can stabilize predator–prey interactions by providing habitat patches where predators are no longer capable of accessing prey resources. For example, whelk predation on clams is lower in seagrass habitats than in unvegetated areas; this reduction in predation is greater for clams living in and among the dense seagrass roots than those living above the seagrass root mat, suggesting that the belowground structure physically prevents whelks from readily locating and extracting subsurface clams (Peterson 1982). Even when habitat complexity does not completely remove the risk of predation, the very elements of habitats that create structure can decrease the foraging efficiency of predators by interfering with a predator's ability to locate and handle prey (Crowder and Cooper 1982; Summerson and Peterson 1984). For instance, crabs spend more time handling non-prey shell fragments in structurally complex shell/sand mixtures, reducing their overall foraging efficiency on clams (Sponaugle and Lawton 1990).

Despite a growing emphasis on multiple predator effects and the well-documented impact of habitat complexity on predator foraging efficiency in individual predator–prey interactions, understanding of the effects of habitat context on predator–predator interactions is limited (but see Siddon and Witman 2004). Habitat structure can reduce intraspecific interference competition among predators, and thereby counteract negative effects of habitat complexity on individual foraging effectiveness (Grabowski and Powers 2004). Thus, in some cases when multiple predators are present, increased structural complexity may result in greater overall prey consumption than in less complex habitats (Finke and Denno 2002; Siddon and Witman 2004; Griffen and Byers 2006). Determining how habitat context generally affects interactions among predators will require sorting out the relative strength of these counteracting mechanisms. Given that variation in habitat complexity is a feature of most if not all ecological systems, understanding how such variability influences interactions among predators and the resulting consequences for prey survivorship is critical to our ability to model trophic interactions and food web dynamics.

In estuarine systems, species often co-occur across habitats of varying complexity, making them ideal systems in which to examine the impact of habitat variation on species interactions. In estuaries of the southeastern US, stone crabs (*Menippe mercenaria*) and knobbed whelks (*Busycon carica*) utilize seagrass meadows, sand flats, and oyster reefs to forage for common bivalve prey such as hard clams (*Mercenaria mercenaria*) and ribbed mussels (*Geukensia demissa*) (Irlandi and Peterson 1991; Nakaoka 2000). Previous field and laboratory studies indicate that crabs (Summerson and Peterson 1984; Sponaugle and Lawton 1990) and whelks (Irlandi and Peterson 1991) have higher consumption rates in unvegetated sand flats than structurally complex habitats such as seagrass meadows or oyster reefs. Yet despite a long history of research examining the impact of predation on bivalve survivorship and growth rates (e.g., Peterson 1982; Sponaugle and Lawton 1990; Irlandi and Peterson 1991; Micheli and Peterson 1999; Nakaoka 2000), little is known of how habitat characteristics influence the potential interactions between the multiple species of predators that consume bivalve prey in this system.

We investigated the interactions between stone crabs and knobbed whelks when foraging on two common bivalves, hard clams and ribbed mussels. Although whelks are incapable of consuming stone crabs, these crabs do occasionally consume whelks (Williams 1984), suggesting the potential for predator interference when crab and whelk encounters are common. At the sizes

used in our experiment (see below) actual intraguild predation is unlikely, although behavioral interference between predators possibly still occurs. We assessed the impact of habitat context on predator interactions by conducting the experiment in habitats of differing structural complexity and refuge availability: sand flat (simple) versus oyster reef (more complex) habitat. Characteristics other than habitat complexity also differ between these habitats, such as the presence of shell as a potential physical barrier to predators in the oyster reef.

We included multiple bivalve prey species to mimic the presence of alternative prey items in nature and allow for potential resource partitioning (Ives et al. 2005). In addition, prey switching by crabs (Siddon and Witman 2004; Griffen and Byers 2006) and whelks (Walker 1988; Nakaoka 2000) has been documented in previous studies, highlighting the potential importance of including alternative prey. Although both predators consume epifaunal and infaunal prey species, the common intertidal bivalve species used in this experiment probably differ in their susceptibility to predominantly surface-feeding crabs and burrowing whelks. In sand flat habitats, hard clams live in the sediment, whereas mussels reside on the sediment surface; in oyster reefs, mussels attach themselves on the surface of the shell layer, while clams are found just beneath the oyster shell layer. Thus, variation in the susceptibility of the prey to particular predators is potentially magnified in the oyster reef, where the shell functions as an additional barrier between surface and burrowing organisms. Determining how predator interactions and habitat context influence predator selection of prey and subsequent prey survivorship will increase our understanding of how these factors contribute to the distribution, abundance, and diversity of prey species in coastal estuaries.

One of the strengths of this system for examining multi-species trophic interactions is that each predator leaves behind characteristic predation marks: crabs chip or crush bivalve shells, while whelks file the edge of the shell (Peterson 1982; Irlandi and Peterson 1991; Nakaoka 2000). Thus, assuming that predators do not crush or file prey that were previously consumed by another predator species or died from natural causes, the shell fragments remaining after a bivalve is consumed can be used to distinguish among predators and to evaluate species-specific relative rates of predation. Although the shell markings used to infer predator consumption patterns could overestimate crab consumption if some of the crushed bivalve shells were first filed open and consumed by whelks, we did not find any evidence of crushed shells with file markings. We hypothesized that:

1. Predation rates by each predator are reduced in the habitat providing a structural refuge for prey (i.e., oyster reef).
2. Overall predation rates are lower than expected when both predators are present due to a negative interaction between the predators.
3. Habitat complexity reduces this negative interaction between predators, which could counteract reductions in per capita foraging rates.
4. Habitat complexity and multiple predators each influence predator selectivity of prey.

Materials and methods

Study design

This study was conducted in a randomized complete block design with two replicates per treatment per block and four blocks through time, beginning in August 2000. Treatments were randomly assigned to each of 16 mesocosms (see below) in a balanced $2\times2\times2$ factorial design, with habitat (sand flat or oyster reef), stone crab (presence or absence), and knobbed whelk (presence or absence) as fixed factors. Predator and prey densities were based on our observations and a previous field survey (Nakaoka 2000). We used an additive design: stone crab treatments received one *Menippe* [mean carapace width (SE)=104.7 (2.6) mm]; whelk treatments received two *Busycon* [mean length (SE)=142.4 (2.5) mm; 193.1 (2.4) mm]; and multiple predator treatments received one *Menippe* and two *Busycon*. Because crabs generally consume prey at higher rates than whelks (J. Grabowski, personal observation), we included multiple whelks per treatment to achieve similar rates of predation across treatments.

The experiment took place in 16 large, flow-through mesocosms encasing experimental habitat plots in a concrete tank (6 m×9 m×1.2 m) at the University of North Carolina–Institute of Marine Sciences (UNC–IMS). Each mesocosm consisted of a plastic cylindrical pool (1.7 m diameter=~2 m^2) enclosed on the sides with 6-mm plastic fence that extended 1.2 m from the bottom of the pool. The mesocosms were covered with 10-mm-mesh bird netting on top to prevent escape of enclosed organisms and deter bird predation.

Before each run of the experiment (treated as blocks in time), we collected predators and mussels from the field. Predators were starved for at least 3 days before the start of the experiment. Stone crabs were collected using baited crab pots, while whelks and mussels were collected by hand. Hard clams were obtained from

Mark Hooper, Hooper Family Seafood, Smyrna, North Carolina. The experimental pools were assembled by first stocking each mesocosm with 95 l of sieved (10-mm mesh) sand. Twenty-five adult clams of known size [mean shell length (SE)=50.1 (0.1) mm] were then added to each mesocosm to allow them enough time (approximately 2 h) to burrow naturally in the sand. Following the addition of clams, the oyster reef treatments received 19 l of dead oyster shell scattered carefully on top of the mud to avoid clam mortality. In addition, 57 l of vertically oriented shells of dead oysters was added to these treatments to mimic the vertical structure of natural oyster reefs. Once the reefs were constructed, 25 mussels [mean length (SE)=76.8 (0.3) mm] were spread across the surface of each habitat. These prey densities are within the range of what we have observed in Back Sound, North Carolina (J. Grabowski, unpublished data). The holding pond was then filled with flowing (0.27–0.29 l/s; Grabowski 2004), unfiltered seawater from Bogue Sound, North Carolina, via the UNC–IMS seawater system so that each mesocosm was submerged under 1 m of seawater. At this time, predators were added to the relevant treatments. The experiment was run for 14 days; at the end of this period the stone crabs and whelks were removed from the mesocosms, the water was drained from the pond, and the number of prey eaten by each predator was quantified. In addition, the sand was sieved to recover all remaining live prey items, which were then measured. Treatments were randomly reassigned to pools, new predators and prey were collected, and each of the habitats reconstructed for each subsequent run.

Data analyses

For each experimental replicate, we recovered all prey items and used the characteristic predation marks left by crabs (i.e., crushed or chipped shells) and whelks (i.e., filed shells) to score them as consumed by a crab, consumed by a whelk, dead but undamaged by predators, or alive. We then calculated predation (proportion of prey consumed out of total prey available at the beginning of the experiment) and overall mortality (i.e., proportion of natural mortality plus predation out of the total prey available) for each predator treatment. We conducted four-way factorial ANOVAs on each response variable with block, habitat (oyster or sand), whelk (presence or absence), and crab (presence or absence) as fixed factors. All ANOVAs met the assumptions of the Shapiro–Wilk test for normality and the Levene test for homogeneity of variance.

Following the above ANOVAs, we analyzed the effect of habitat context on each predator by comparing

the total predation rate of each predator in the sand flat and oyster reef using planned independent contrasts. To examine the mechanisms underlying changes in overall predation, we used two-tailed Student's t-tests to compare for each predator and habitat the number of prey consumed by a particular predator in the multiple predator treatment to the number consumed by that same predator in the single species treatment.

In addition to changes in overall predation, we evaluated the potential for predator dietary selectivity by comparing the selection index (range=0.0–1.0, with 1.0 indicating high preference; Chesson 1983) of each predator to the null hypothesis of no preference (0.5) using a Student's t-test. We also used Student's t-tests to examine whether or not prey selectivity changed in response to habitat context or the presence of another predator.

To examine the effects of mussel prey depletion on our results, we first excluded the one temporal block with >10% natural prey mortality and ran a four-way factorial ANOVA as described above. Next, we excluded the 15 replicates (1 whelk/sand; 4 stone crab/sand; 4 both/sand; 2 stone crab/oyster; 4 both/oyster) in which no live mussels remained at the end of the experiment and performed a factorial ANOVA on total predation rate with habitat, whelk, and crab as the factors. Because mussels may achieve a refuge at low densities (Guillemain et al. 1997), we further excluded the six replicates (1 stone crab/sand; 2 both/sand; 1 stone crab/oyster; 2 both/oyster) with three or fewer live mussels and ran the same analysis. All analyses were conducted using JMP 4.0 (SAS Institute 2001).

Results

The four-way factorial ANOVA revealed that individual and combined effects of stone crabs and whelks on total predation differed by habitat (habitat×whelk×stone crab $F_{1,32}$=5.7, P=0.02, see Table 1 for full statistics). When alone, planned independent contrasts revealed that both whelks ($F_{1,32}$=10.4, P=0.003) and stone crabs ($F_{1,32}$=5.3, P=0.03) consumed more prey in the sand flat than the oyster reef (Fig. 1). Despite this lower predation in the oyster reef than the sand flat in the individual predator treatments, total prey consumed in the multiple predator treatment did not differ detectably between the two habitats ($F_{1,32}$=0.3, P=0.55; Fig. 1). The analysis of overall mortality (without correcting for prey depletion) yielded similar results (habitat×whelk×crab $F_{1,32}$=4.7, P=0.04) with the exception that mortality also varied by block ($F_{3,32}$=3.3, P=0.03). An analysis of natural mortality

alone (excluding predation) confirmed that natural mortality varied by block ($F_{3,32}=12.73$, $P<0.001$), but not by habitat or predator treatment. This temporal block effect was driven by higher natural prey mortality in the second trial of the experiment (mean=23.2%) compared to the other three trials (mean=5.9%), potentially resulting from higher average water temperatures during this time period (National Oceanographic Data Center, http://www.nodc.noaa.gov).

The similarity between habitats in overall consumption in the multiple predator treatment was due to reductions in prey consumption by both predators in the sand flat (rather than as a consequence of greater consumption in the oyster reef; Fig. 2, see Table 2 for estimates of predation on each prey species by habitat
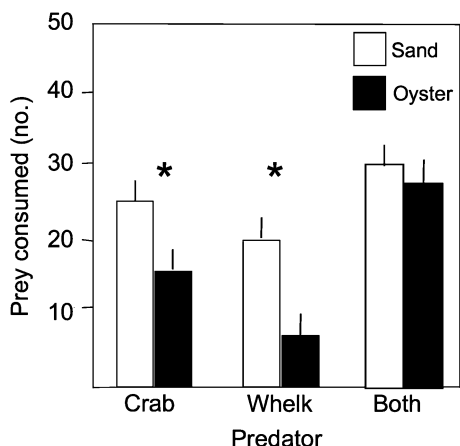

Fig. 1 Total number of prey (hard clams and mussels) consumed in the stone crab (*Menippe mercenaria*) only (*Crab*), whelk (*Busycon carica*) only (*Whelk*), and combined stone crab and whelk (*Both*) treatments. Means are least squares means+1 SE. *$P\leq0.05$

Table 1 Results from ANOVA on total predation rate. *SS* Sums of squares, *MS* mean square

Factor	df	SS	F	P
Block	3	0.10	1.1	0.36
Habitat	1	0.27	9.2	0.005
Whelk	1	0.84	28.6	0.0001
Crab	1	2.22	76.1	0.0001
Block×habitat	3	0.03	0.3	0.81
Block×whelk	3	0.04	0.5	0.67
Block×crab	3	0.27	3.1	0.04
Habitat×whelk	1	0.02	0.6	0.43
Habitat×crab	1	0.001	0.02	0.88
Whelk×crab	1	0.05	1.7	0.2
Block×whelk×crab	3	0.09	1.0	0.38
Block×habitat×whelk	3	0.08	1.0	0.42
Block×habitat×crab	3	0.15	1.7	0.18
Habitat×whelk×crab	1	0.17	5.7	0.02
Block×habitat×whelk×crab	3	0.10	1.2	0.33
Error	32	0.93	MS=0.03	

and predator treatment). On sand flats, there was no detectable reduction in predation by stone crabs when each prey species was considered separately (*t*-tests, *t*<1.4, *P*>0.10; Fig. 2a, b), but stone crabs decreased their overall prey consumption when whelks were present (*t*-test, *t*=2.2, *P*=0.05). In contrast, predation by whelks was dramatically lower on mussels (*t*-test, *t*=3.6, *P*=0.009; Fig. 2d) but not on hard clams (*t*-test, *t*=1.9, *P*=0.54; Fig. 2c) when both predators were present. Neither predator significantly altered its consumption of either prey species in the oyster reef (Fig. 2).

As illustrated in Fig. 2, both predators displayed clear dietary selectivity: crabs preferred to consume mussels (mean selectivity index=0.96, *t*-test, *t*=24.49, *P*<0.0001) and whelks preferred to consume clams (mean selectivity index=0.77, *t*-test, *t*=5.13, *P*<0.0001). Crab dietary selectivity for mussels increased in the oyster reef compared to the sand flat (*t*-test, *t*=1.95, *P*=0.03). In contrast, whelk selectivity of clams did not differ by habitat (*t*-test, *t*=1.23, *P*=0.12), but significantly increased in response to the presence of crabs (*t*-test, *t*=2.71, *P*=0.005), particularly in the sand flat. Interestingly, crabs showed a trend towards increased selectivity of mussels in response to whelks in sand (*t*-test, *t*=1.42, *P*=0.09) and decreased selectivity of mussels in response to whelks in oyster (*t*-test, *t*=1.25, *P*=0.12).

Additional analyses suggested that prey depletion did not confound our results. For example, the results of a four-way ANOVA that excluded the temporal block with high prey mortality resulted in similar estimates of significance for the interaction between habitat and predator identity (habitat×whelk×crab $F_{1,24}=3.16$, $P=0.08$). Similarly, omitting all replicates with fewer than three live mussels remaining did not change our finding that predator interactions varied by habitat (habitat×whelk×crab $F_{1,35}=6.27$, $P=0.02$).

Discussion

Our results agree with previous findings indicating that habitat complexity can influence predator–prey

Table 2 Least square means (SE) of predation rate on each prey by habitat and predator treatment

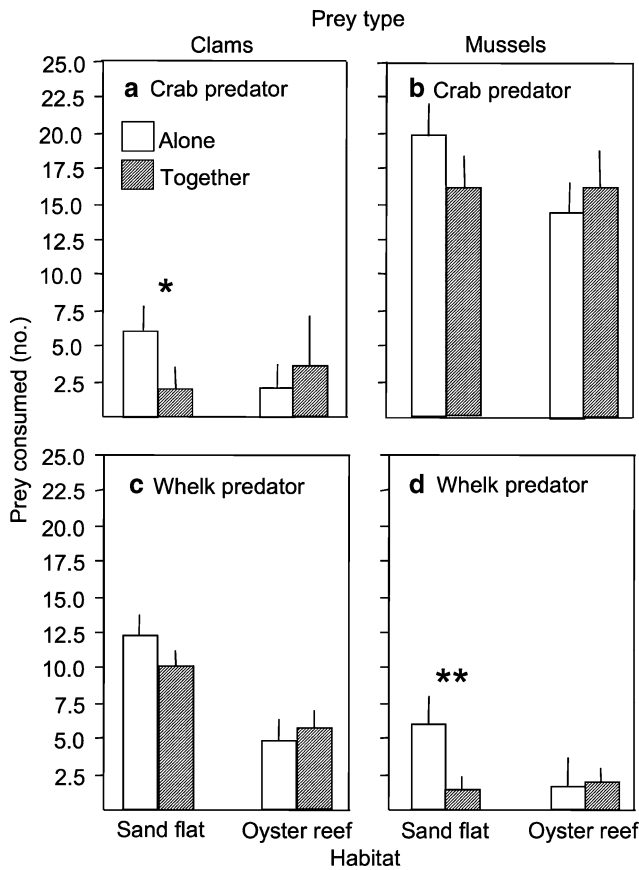| Habitat	Prey	Predator		
		Whelk	Stone crab	Whelk+ stone crab
Sand flat	Mussel	0.28 (0.09)	0.81 (0.09)	0.72 (0.09)
	Clam	0.57 (0.07)	0.25 (0.07)	0.55 (0.07)
Oyster reef	Mussel	0.08 (0.09)	0.59 (0.09)	0.75 (0.10)
	Clam	0.22 (0.07)	0.08 (0.07)	0.41 (0.08)

Fig. 2 Number of prey (clams or mussels) consumed by **a**, **b** stone crabs or **c**, **d** whelks when predators are alone (*open bars*) or together in combined predator treatment (*solid bars*) in sand flat or oyster reef habitats, means+1 SE. Stone crabs also consume fewer total prey in sand flats when they are with whelks (data not shown; *P*<0.05). *P=0.10, **P<0.01

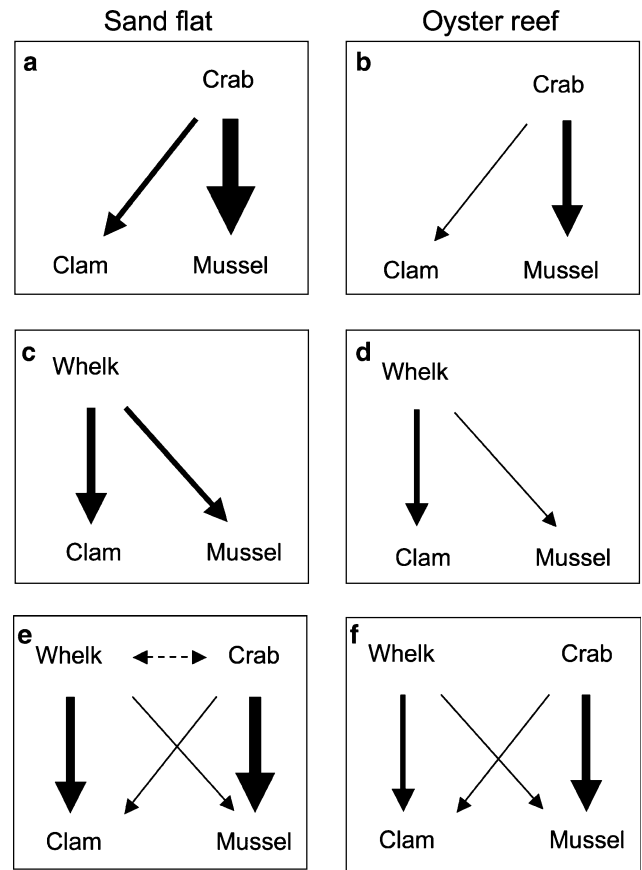Fig. 3a–f Changes in predator–prey interaction strength across sand flat (*left column*) and oyster reef (*right column*) habitats. *Width of arrow* indicates strength of effect, and all effects shown were negative. Individual effects of **a**, **b** stone crabs and **c**, **d** whelks on their prey in sand flat or oyster reef. Crabs consumed more mussels than clams while whelks consumed more clams than mussels. **e**, **f** Combined effects of whelks and stone crabs in sand flat and oyster reef, indicating reduced consumption of both prey by stone crabs and reduced consumption of mussels by whelks. The prey preferences are consistent between habitats. The *dashed arrow* between the two predators in **e** depicts hypothesized predator–predator behavioral interference

interactions. Furthermore, they demonstrate that the effect of structural complexity on predator–predator interactions can nullify the positive effects of habitat complexity for prey. Although individual predator foraging rates were lower in the oyster reef than the sand flat, combined predation was equivalent in the two habitats as a consequence of lower than expected combined predation in the sand flat (Fig. 3). In addition, our results show that habitat complexity and predator interactions can independently increase predator dietary selectivity (i.e., lower consumption of less preferred prey items).

The characteristic predation marks left by each predator in this system provide some insight into the behavioral changes responsible for the observed reductions in prey consumption in the sand flat. For instance, the comparison of prey consumed by whelks when alone versus with stone crabs reveals that whelks sharply reduced their consumption of mussels in the

sand flat when crabs were present (Fig. 2). As mentioned previously, mussels reside on the sediment surface, and thus this decrease may be due to a behaviorally mediated reduction in surface foraging activity (e.g., Sih et al. 1998; Dill et al. 2003; Grabowski and Kimbro 2005) in response to the threat of predation by stone crabs. This mechanism is further supported by the fact that whelks did not reduce consumption of their preferred prey item, hard clams (Fig. 2), which burrow within the sediment. Even in the absence of aboveground structural complexity, whelks can forage for clams beneath the sediment surface and simultaneously avoid stone crabs. Interestingly, whelks did not increase their consumption of clams to

compensate for their reduced predation on mussels in the sand flat when stone crabs were present; thus, the results were a consequence of an overall reduction in predation rather than a shift from surface foraging on mussels to sub-surface foraging on clams.

Surprisingly, decreased predation in the sand flat was not only driven by a decrease in whelk foraging on mussels, but also by reduced overall prey consumption by stone crabs (Fig. 2). This result was unanticipated because whelks do not represent a threat to crabs. Two factors related to the chemical sensory abilities of predators and prey in this system may explain how the presence of whelks reduces stone crab foraging efficiency. First, hard clams reduce feeding in response to a water-borne chemical signal from whelks (Irlandi and Peterson 1991; Nakaoka 2000); this reduction in feeding presumably also reduces chemical cues emitted by clams, potentially rendering the clams more difficult for stone crabs to locate in the multiple predator treatment. The trend towards increased crab selectivity of mussels in the sand flat supports this hypothesis. Second, the presence of chemical cues from a potential alternative prey (i.e., whelks) may have caused stone crabs to spend less time foraging for bivalves and more time pursuing whelks, effectively a form of behavioral prey switching. Each of these mechanisms is likely to be stronger in the sand flat than the oyster reef if the structural complexity of the reef generates sufficient turbulence to dissipate chemical signals (Weissburg and Zimmer-Faust 1993), thereby potentially reducing the strength of both of the hypothesized chemically mediated interactions.

Our demonstration of reduced consumption in the presence of another predator in the sand flat may help to reconcile discrepancies among previous field and laboratory experiments in this system. Numerous studies (e.g., Littler et al. 1989; Diehl 1992; Beukers and Jones 1997; Grabowski 2004; but see Grabowski and Powers 2004) have shown that predation is generally lower in structurally complex habitats such as oyster reefs. Our single-predator trials confirmed these results, with significantly higher predation by stone crabs and whelks in the sand flat than the oyster reef (Fig. 1). These data, combined with slightly higher densities of these predators in the sand flat in the field (Nakaoka 2000), all lead to the expectation that prey mortality in nature is higher in the sand flat than in the oyster reef. However, clam mortality in the field is actually lower in the sand flat than in the oyster reef during the portion of the year that these predators are most active (Nakaoka 2000). Although we found equivalent predation in the two habitats rather than higher predation in the oyster reef, our multiple

predator trials suggest that such a counter-intuitive result may be a consequence of interactions between predators that reduce their prey consumption in the unstructured sand flat. These results indicate the need for further investigation of how habitat context affects predator–predator interactions to determine whether reduced foraging efficiency in complex habitats is generally counterbalanced by the suppressed interference interactions among predators where structure is greater.

It is becoming clear that behavioral modifications are integral to species interactions (Micheli 1997; Dill et al. 2003; Trussell et al. 2003; Werner and Peacor 2003; Schmitz et al. 2004; Byrnes et al. 2006). Despite the potential for stone crabs to consume whelks, we did not observe any intraguild predation in our experiment, eliminating lowered predator densities as an explanation for the reduction in prey consumption in the sand flat and indicating that behavioral interactions among predators are likely driving changes in consumption patterns (Fig. 3). Furthermore, our study suggests that habitat complexity may combine with animal behavior to structure ecological communities not only by increasing refuge use by prey in the presence of predators (e.g., Micheli 1997; Trussell et al. 2003), but also by reducing interference interactions among predators. If intermediate-level consumers such as whelks and crabs aggregate in more complex habitats to avoid their predators, this behavioral release could be an important component of how these systems are structured.

In addition to causing changes in the overall number of prey consumed, habitat context and predator–predator interactions both increased resource partitioning in the form of predator dietary selectivity in our study. Resource partitioning is thought to be ubiquitous in nature as a means of species coexistence (Chesson 1991), but there are surprisingly few empirical demonstrations of resource partitioning in multiple predator trials (Ives et al. 2005). We show that whelks increased their selectivity of clams in response to competition and/or the threat of intraguild predation when crabs were present. This finding emphasizes the importance of including multiple prey in studies of predator–predator interactions, as resource partitioning is not possible unless diverse resources are available (e.g., Pfennig et al. 2006). In addition, crabs increase their selectivity of mussels in the oyster reef as compared to the sand flat, lending further support to the importance of habitat context to species interactions.

We manipulated key components of the benthic food web in a controlled setting to contribute to our understanding of the mechanisms that potentially

mediate patterns of prey survivorship and their distribution in nature. While mesocosm studies are effective at isolating specific mechanisms that may be important, the findings should be incorporated into field studies to confirm the role of these mechanisms in structuring more natural communities. If top predators such as sea birds were to increase stone crab use of structured habitats, which has been demonstrated for blue crabs (Micheli 1997; Micheli and Peterson 1999), we would expect increased predator densities to result in even greater predation on bivalves in oyster reefs than sand flats.

Not only do our results potentially help to explain why predictions based on single-interaction (e.g., one predator and one prey) experiments may not scale up to patterns in natural communities, but they also suggest that we need to be careful when equating different habitats or sites based on similarities in a composite measure such as prey density or diversity. Overall prey mortality in our multiple predator treatments did not differ between the oyster reef and the sand flat (Fig. 1). However, this similarity was due to different mechanisms operating in each habitat, and therefore, changes in predator abundances would probably have very different effects in the two habitats. For instance, the loss of stone crabs due to over-fishing may not cause a dramatic change in overall prey mortality in the sand flat because whelks would compensate for their absence. In contrast, removal of stone crabs from oyster reef habitats could result in a considerable decline in bivalve prey mortality. An understanding of such complex predator interactions will be important for predicting how continued losses in biodiversity and components of ecological habitats interact to affect community structure (Chapin et al. 2000; Schmitz and Sokol-Hessner 2002), particularly since this loss is often focused on predators.

There is growing concern over widespread habitat destruction in ecologically valuable habitats such as coral reefs, seagrass meadows, oyster reefs, and forests (Botsford et al. 1997; Vitousek et al. 1997; Jackson et al. 2001; Peterson et al. 2003). For example, only a fraction of historical oyster reefs in the southeastern US remain because of removal of habitat during harvesting and subsequent disease, reduced water quality, and siltation (Rothschild et al. 1994). Our results suggest that changes in these structurally complex habitats may have even greater implications than previously realized in light of the effects of habitat context on species interactions. A greater understanding of how multi-species interactions vary across habitats of differing structural complexity is needed to guide conservation decisions and future restoration efforts.

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