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

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1 Running Head: Context dependency of predator interactions

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3 HABITAT CONTEXT INFLUENCES PREDATOR INTERFERENCE INTERACTIONS AND THE STRENGTH OF  
4 RESOURCE PARTITIONING

5  
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14 *Abstract.* Despite increasing evidence that habitat structure can shape predator-prey interactions,  
15 few studies have examined the impact of habitat context on interactions among multiple  
16 predators and the consequences for combined foraging rates. We investigated the individual and  
17 combined effects of stone crabs (*Menippe mercenaria*) and knobbed whelks (*Busycon carica*)  
18 when foraging on two common bivalves, the hard clam (*Mercenaria mercenaria*) and the ribbed  
19 mussel (*Geukensia demissa*) in oyster reef and sand flat habitats. Because these species co-occur  
20 across these and other estuarine habitats of varying physical complexity, this system is ideal for  
21 examining how habitat context influences foraging rates and the generality of predator  
22 interactions. Consistent with results from previous studies, consumption rates of each predator  
23 in isolation from the other were higher in the sand flat than in the more structurally complex  
24 oyster reef habitat. However, consumption by the two predators when combined surprisingly did  
25 not differ between the two habitats. This counterintuitive result probably stems from the  
26 influence of habitat structure on predator-predator interactions. In the sand-flat habitat, whelks  
27 significantly reduced their consumption of their less preferred prey when crabs were present.  
28 However, the structurally more complex oyster-reef habitat appeared to reduce interference  
29 interactions among predators, such that consumption rates when the predators co-occurred did  
30 not differ from predation rates when alone. In addition, both habitat context and predator-  
31 predator interactions increased resource partitioning by strengthening predator dietary selectivity.  
32 Thus, an understanding of how habitat characteristics such as physical complexity influence  
33 interactions among predators may be critical to predicting the effects of modifying predator  
34 populations on their shared prey.

35 *Key words:* context dependency; habitat structure; oyster reef; predator dietary selectivity;  
36 predator interference; resource partitioning; sand flat

37

37 INTRODUCTION

38 Ecologists are increasingly realizing the importance of multi-species interactions and  
39 their consequences for community structure and ecosystem function (Chapin et al. 2000, Shurin  
40 et al. 2002, Duffy et al. 2005, Ives et al. 2005). Recently, several lines of research have  
41 converged on examining the role of species interactions in a food web context (Shurin et al.  
42 2002, Duffy et al. 2005, Ives et al. 2005). Of primary interest is whether interactions in a multi-  
43 species assemblage can be predicted by combining the pair-wise interactions of the component  
44 species, or whether emergent effects arise (Strong 1992). For example, there is a rapidly growing  
45 literature on emergent multiple predator effects on prey such as risk enhancement (i.e., more  
46 prey are consumed than expected based on the single predator effects) as well as risk reduction  
47 (i.e., fewer prey are consumed than expected based on the single predator effects; Soluk and  
48 Collins 1988, Sih et al. 1998).

49 In addition to a growing understanding of how interactions among multiple predator  
50 species impact prey consumption, there is a long history of research on the effects of habitat  
51 context on predator-prey interactions. Predator foraging efficiency generally varies inversely  
52 with habitat heterogeneity (Diehl 1992, Beck and Watts 1997, Beukers and Jones 1997,  
53 Cowlshaw 1997), and predator-prey interactions can change dramatically in response to habitat  
54 complexity (Crowder and Cooper 1982, Werner et al. 1983, Schriver et al. 1995, Grabowski and  
55 Powers 2004). In general, individual predators consume fewer prey in more structurally  
56 complex habitats (Peterson 1982, Blundon and Kennedy 1982, Irlandi and Peterson 1991, Finke  
57 and Denno 2002, Grabowski 2004, Warfe and Barmuta 2004). The fact that structurally  
58 complex habitats (e.g., submerged macrophytes, oyster reefs, coral reefs) often support greater  
59 abundances and diversity than unstructured habitats is often attributed to reduced predation in

60 these habitats (Heck and Wetstone 1977, Summerson and Peterson 1984, Beck 2000, Lenihan et  
61 al. 2001, Grabowski et al. 2005), although these patterns could also be due to greater propagule  
62 retention or enhanced food concentration in complex habitats (Tegner and Dayton 1981,  
63 Summerson and Peterson 1984).

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

78         Despite a growing emphasis on multiple predator effects and the well-documented impact  
79 of habitat complexity on predator foraging efficiency in individual predator-prey interactions,  
80 understanding of the effects of habitat context on predator-predator interactions is limited (but  
81 see Siddon and Witman 2004). Habitat structure can reduce intraspecific interference  
82 competition among predators, and thereby counteract negative effects of habitat complexity on

83 individual foraging effectiveness (Grabowski and Powers 2004). Thus, in some cases when  
84 multiple predators are present, increased structural complexity may result in greater overall prey  
85 consumption than in less complex habitats (Finke and Denno 2002, Siddon and Witman 2004,  
86 Griffen and Byers 2006). Determining how habitat context generally affects interactions among  
87 predators will require sorting out the relative strength of these counteracting mechanisms. Given  
88 that variation in habitat complexity is a feature of most if not all ecological systems,  
89 understanding how such variability influences interactions among predators and the resulting  
90 consequences for prey survivorship is critical to our ability to model trophic interactions and  
91 food web dynamics.

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

106           We investigated the interactions between stone crabs and knobbed whelks when foraging  
107 on two common bivalves, hard clams and ribbed mussels. Although whelks are incapable of  
108 consuming stone crabs, these crabs do occasionally consume whelks (Williams 1984),  
109 suggesting the potential for predator interference when crab and whelk encounters are common.  
110 At the sizes used in our experiment (see below) actual intraguild predation is unlikely, although  
111 behavioral interference between predators possibly still occurs. We assessed the impact of  
112 habitat context on predator interactions by conducting the experiment in habitats of differing  
113 structural complexity and refuge availability: sand flat (simple) vs. oyster reef (more complex)  
114 habitat. Characteristics other than habitat complexity also differ between these habitats, such as  
115 the presence of shell as a potential physical barrier to predators in the oyster reef.

116           We included multiple bivalve prey species to mimic the presence of alternative prey  
117 items in nature and allow for potential resource partitioning (Ives et al. 2005). In addition, prey  
118 switching by crabs (Siddon and Witman 2004, Griffen and Byers 2006) and whelks (Walker  
119 1988, Nakaoka 2000) has been documented in previous studies, highlighting the potential  
120 importance of including alternative prey. Although both predators consume epifaunal and  
121 infaunal prey species, the common intertidal bivalve species used in this experiment probably  
122 differ in their susceptibility to predominantly surface-feeding crabs and burrowing whelks. In  
123 sand flat habitats, hard clams live in the sediment, whereas mussels reside on the sediment  
124 surface; in oyster reefs, mussels attach themselves on the surface of the shell layer, while clams  
125 are found just beneath the oyster shell layer. Thus, variation in the susceptibility of the prey to  
126 particular predators is potentially magnified in the oyster reef, where the shell functions as an  
127 additional barrier between surface and burrowing organisms. Determining how predator  
128 interactions and habitat context influence predator selection of prey and subsequent prey

129 survivorship will increase our understanding of how these factors contribute to the distribution,  
130 abundance, and diversity of prey species in coastal estuaries.

131         One of the strengths of this system for examining multi-species trophic interactions is  
132 that each predator leaves behind characteristic predation marks: crabs chip or crush bivalve  
133 shells, while whelks file the edge of the shell (Peterson 1982, Irlandi and Peterson 1991,  
134 Nakaoka 2000). Thus, assuming that predators do not crush or file prey that were previously  
135 consumed by another predator species or dead from natural causes, the shell fragments remaining  
136 after a bivalve is consumed can be used to distinguish among predators and to evaluate species-  
137 specific relative rates of predation. Although the shell markings used to infer predator  
138 consumption patterns could overestimate crab consumption if some of the crushed bivalve shells  
139 were first filed open and consumed by whelks, we did not find any evidence of crushed shells  
140 with file markings. We hypothesized that (1) predation rates by each predator are reduced in the  
141 habitat providing a structural refuge for prey (i.e., oyster reef); (2) overall predation rates are  
142 lower than expected when both predators are present due to a negative interaction between the  
143 predators; (3) habitat complexity reduces this negative interaction between predators, which  
144 could counteract reductions in per capita foraging rates; and (4) habitat complexity and multiple  
145 predators each influence predator selectivity of prey.

146

## 147 MATERIALS AND METHODS

### 148 *Study design*

149         This study was conducted in a randomized complete block design with 2 replicates per  
150 treatment per block and 4 blocks through time, beginning in August 2000. Treatments were  
151 randomly assigned to each of 16 mesocosms (see below) in a balanced 2 x 2 x 2 factorial design,



152 with habitat (sand flat or oyster reef), stone crab (presence or absence), and knobbed whelk  
153 (presence or absence) as fixed factors. Predator and prey densities were based on our  
154 observations and a previous field survey (Nakaoka 2000). We used an additive design: stone  
155 crab treatments received one *Menippe* (mean carapace width (SE) = 104.7 (2.6) mm); whelk  
156 treatments received two *Busycon* (mean length (SE) = 142.4 (2.5) mm; 193.1 (2.4) mm); and  
157 multiple predator treatments received one *Menippe* and two *Busycon*. Because crabs generally  
158 consume prey at higher rates than whelks (J. Grabowski, personal observation), we included  
159 multiple whelks per treatment to achieve similar rates of predation across treatments.

160 The experiment took place in 16 large, flow-through mesocosms encasing experimental  
161 habitat plots in a concrete tank (6 m x 9 m x 1.2 m) at the University of North Carolina-Institute  
162 of Marine Sciences (UNC-IMS). Each mesocosm consisted of a plastic cylindrical pool (1.7 m  
163 diameter =  $\sim 2$  m<sup>2</sup>) enclosed on the sides with 6 mm plastic fence that extended 1.2 m from the  
164 bottom of the pool. The mesocosms were covered with 10-mm mesh bird netting on top to  
165 prevent escape of enclosed organisms and deter bird predation.

166 Before each run of the experiment (treated as blocks in time), we collected predators and  
167 mussels from the field. Predators were starved for at least 3 days before the start of the  
168 experiment. Stone crabs were collected using baited crab pots, while whelks and mussels were  
169 collected by hand. Hard clams were obtained from Mark Hooper, Hooper Family Seafood,  
170 Smyrna, North Carolina. The experimental pools were assembled by first stocking each  
171 mesocosm with 95 liters of sieved (10-mm mesh) sand. Twenty-five adult clams of known size  
172 (mean shell length (SE) = 50.1 (0.1) mm) were then added to each mesocosm to allow them  
173 enough time (approximately 2 hours) to burrow naturally in the sand. Following the addition of  
174 clams, the oyster reef treatments received 19 liters of dead oyster shell scattered carefully on top

175 of the mud to avoid clam mortality. In addition, 57 liters of vertically oriented shells of dead  
176 oysters were added to these treatments to mimic the vertical structure of natural oyster reefs.  
177 Once the reefs were constructed, 25 mussels (mean length (SE) = 76.8 (0.3) mm) were spread  
178 across the surface of each habitat. These prey densities are within the range of what we have  
179 observed in Back Sound, North Carolina (J. Grabowski, unpublished data). The holding pond  
180 was then filled with flowing (0.27-0.29 L/s; Grabowski 2004), unfiltered seawater from Bogue  
181 Sound, NC, via the UNC-IMS seawater system so that each mesocosm was submerged under 1  
182 m of seawater. At this time, predators were added to the relevant treatments. The experiment  
183 was run for 14 days; at the end of this period the stone crabs and whelks were removed from the  
184 mesocosms, the water was drained from the pond, and the number of prey eaten by each predator  
185 was quantified. In addition, the sand was sieved to recover all remaining live prey items, which  
186 were then measured. Treatments were randomly reassigned to pools, new predators and prey  
187 were collected, and each of the habitats reconstructed for each subsequent run.

#### 188 *Data analyses*

189 For each experimental replicate, we recovered all prey items and used the characteristic  
190 predation marks left by crabs (i.e., crushed or chipped shells) and whelks (i.e., filed shells) to  
191 score them as consumed by a crab, consumed by a whelk, dead but undamaged by predators, or  
192 alive. We then calculated predation (proportion of prey consumed out of total prey available at  
193 the beginning of the experiment) and overall mortality (i.e., proportion of natural mortality plus  
194 predation out of the total prey available) for each predator treatment. We conducted 4-way  
195 factorial ANOVAs on each response variable with block, habitat (oyster or sand), whelk  
196 (presence or absence) and crab (presence or absence) as fixed factors. All ANOVAs met the

197 assumptions of the Shapiro-Wilk test for normality and the Levene test for homogeneity of  
198 variance.

199         Following the ANOVA, we analyzed the effect of habitat context on each predator by  
200 comparing the total predation rate of each predator in the sand flat and oyster reef using planned  
201 independent contrasts. To examine the mechanisms underlying changes in overall predation, we  
202 used two-tailed Student's t-tests to compare for each predator and habitat the number of prey  
203 consumed by a particular predator in the multiple predator treatment to the number consumed by  
204 that same predator in the single species treatment.

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

210         To examine the effects of mussel prey depletion on our results, we first excluded the one  
211 temporal block with greater than 10% natural prey mortality and ran a 4-way factorial ANOVA  
212 as described above. Next, we excluded the 15 replicates (1 whelk/sand; 4 stone crab/sand; 4  
213 both/sand; 2 stone crab/oyster; 4 both/oyster) in which no live mussels remained at the end of the  
214 experiment and performed a factorial ANOVA on total predation rate with habitat, whelk, and  
215 crab as the factors. Because mussels may achieve a refuge at low densities (Guillemain et al.  
216 1997), we further excluded the six replicates (1 stone crab/sand; 2 both/sand; 1 stone crab/oyster;  
217 2 both/oyster) with 3 or fewer live mussels and ran the same analysis. All analyses were  
218 conducted using JMP 4.0 (SAS Institute 2001).

219

## 220 RESULTS

221 The 4-way factorial ANOVA revealed that individual and combined effects of stone  
222 crabs and whelks on total predation differed by habitat (habitat\*whelk\*stone crab  $F_{1,32} = 5.7$ ,  $P =$   
223  $0.02$ , see Table 1 for full statistics). When alone, planned independent contrasts revealed that  
224 both whelks ( $F_{1,32} = 10.4$ ,  $P = 0.003$ ) and stone crabs ( $F_{1,32} = 5.3$ ,  $P = 0.03$ ) consumed more prey  
225 in the sand flat than the oyster reef (Fig. 1). Despite this lower predation in the oyster reef than  
226 the sand flat in the individual predator treatments, total prey consumed in the multiple predator  
227 treatment did not differ detectably between the two habitats ( $F_{1,32} = 0.3$ ,  $P = 0.55$ ; Fig. 1). The  
228 analysis of overall mortality (without correcting for prey depletion) yielded similar results  
229 (habitat\*whelk\*crab  $F_{1,32} = 4.7$ ,  $P = 0.04$ ) with the exception that mortality also varied by block  
230 ( $F_{3,32} = 3.3$ ,  $P = 0.03$ ). An analysis of natural mortality alone (excluding predation) confirmed  
231 that natural mortality varied by block ( $F_{3,32} = 12.73$ ,  $P < 0.001$ ), but not by habitat or predator  
232 treatment. This temporal block effect was driven by higher natural prey mortality in the second  
233 trial of the experiment (mean = 23.2%) compared to the other three trials (mean = 5.9%),  
234 potentially resulting from higher average water temperatures during this time period (National  
235 Oceanographic Data Center, [www.nodc.noaa.gov](http://www.nodc.noaa.gov)).

236 The similarity between habitats in overall consumption in the multiple predator treatment  
237 was due to reductions in prey consumption by both predators in the sand flat (rather than as a  
238 consequence of greater consumption in the oyster reef; Fig. 2, see Table 2 for estimates of  
239 predation on each prey species by habitat and predator treatment). On sand flats, there was no  
240 detectable reduction in predation by stone crabs when each prey species was considered  
241 separately (t-tests,  $t \leq 1.4$ ,  $P \geq 0.10$ ), but stone crabs decreased their overall prey consumption  
242 when whelks were present (t-test,  $t = 2.2$ ,  $P = 0.05$ , Fig. 2a). In contrast, predation by whelks

243 was dramatically lower on mussels (t-test,  $t = 3.6$ ,  $P = 0.009$ , Fig. 2d) but not on hard clams (t-  
244 test,  $t = 1.9$ ,  $P = 0.54$ ; Fig. 2c) when both predators were present. Neither predator significantly  
245 altered its consumption of either prey species in the oyster reef (Fig. 2).

246 As illustrated in figure 2, both predators displayed clear dietary selectivity: crabs  
247 preferred to consume mussels (mean selectivity index = 0.96, t-test,  $t = 24.49$ ,  $P < 0.0001$ ) and  
248 whelks preferred to consume clams (mean selectivity index = 0.77, t-test,  $t = 5.13$ ,  $P < 0.0001$ ).  
249 Crab dietary selectivity for mussels increased in the oyster reef compared to the sand flat (t-test,  $t$   
250  $= 1.95$ ,  $P = 0.03$ ). In contrast, whelk selectivity of clams did not differ by habitat (t-test,  $t = 1.23$ ,  
251  $P = 0.12$ ), but significantly increased in response to the presence of crabs (t-test,  $t = 2.71$ ,  $P =$   
252  $0.005$ ), particularly in the sand flat. Interestingly, crabs showed a trend towards increased  
253 selectivity of mussels in response to whelks in sand (t-test,  $t = 1.42$ ,  $P = 0.09$ ) and decreased  
254 selectivity of mussels in response to whelks in oyster (t-test,  $t = 1.25$ ,  $P = 0.12$ ).

255 Additional analyses suggested that prey depletion did not confound our results. For  
256 example, the results of a 4-way ANOVA that excluded the temporal block with high prey  
257 mortality resulted in similar estimates of significance for the interaction between habitat and  
258 predator identity (habitat\*whelk\*crab  $F_{1,24} = 3.16$ ,  $P = 0.08$ ). Similarly, omitting all replicates  
259 with fewer than 3 live mussels remaining did not change our finding that predator interactions  
260 varied by habitat (habitat\*whelk\*crab  $F_{1,35} = 6.27$ ,  $P = 0.02$ ).

261

## 262 DISCUSSION

263 Our results agree with previous findings indicating that habitat complexity can influence  
264 predator-prey interactions. Furthermore, they demonstrate that the effect of structural  
265 complexity on predator-predator interactions can nullify the positive effects of habitat

266 complexity for prey. Although individual predator foraging rates were lower in the oyster reef  
267 than the sand flat, combined predation was equivalent in the two habitats as a consequence of  
268 lower than expected combined predation in the sand flat (Fig. 3). In addition, our results show  
269 that habitat complexity and predator interactions can independently increase predator dietary  
270 selectivity (i.e., lower consumption of less preferred prey items).

271         The characteristic predation marks left by each predator in this system provide some  
272 insight into the behavioral changes responsible for the observed reductions in prey consumption  
273 in the sand flat. For instance, the comparison of prey consumed by whelks when alone versus  
274 with stone crabs reveals that whelks sharply reduced their consumption of mussels in the sand  
275 flat when crabs were present (Fig. 2). As mentioned previously, mussels reside on the sediment  
276 surface, and thus this decrease may be due to a behaviorally mediated reduction in surface  
277 foraging activity (e.g., Sih et al. 1998, Dill et al. 2003, Grabowski and Kimbro 2005) in response  
278 to the threat of predation by stone crabs. This mechanism is further supported by the fact that  
279 whelks did not reduce consumption of their preferred prey item, hard clams (Fig. 2), which  
280 burrow within the sediment. Even in the absence of aboveground structural complexity, whelks  
281 can forage for clams beneath the sediment surface and simultaneously avoid stone crabs.  
282 Interestingly, whelks did not increase their consumption of clams to compensate for their  
283 reduced predation on mussels in the sand flat when stone crabs were present; thus, the results  
284 were a consequence of an overall reduction in predation rather than a shift from surface foraging  
285 on mussels to sub-surface foraging on clams.

286         Surprisingly, decreased predation in the sand flat was not only driven by a decrease in  
287 whelk foraging on mussels, but also by reduced overall prey consumption by stone crabs (Fig. 2).  
288 This result was unanticipated because whelks do not represent a threat to crabs. Two factors

289 related to the chemical sensory abilities of predators and prey in this system may explain how the  
290 presence of whelks reduces stone crab foraging efficiency. First, hard clams reduce feeding in  
291 response to a water-borne chemical signal from whelks (Irlandi and Peterson 1991, Nakaoka  
292 2000); this reduction in feeding presumably also reduces chemical cues emitted by clams,  
293 potentially rendering the clams more difficult for stone crabs to locate in the multiple predator  
294 treatment. The trend towards increased crab selectivity of mussels in the sand flat supports this  
295 hypothesis. Second, the presence of chemical cues from a potential alternative prey (i.e.,  
296 whelks) may have caused stone crabs to spend less time foraging for bivalves and more time  
297 pursuing whelks, effectively a form of behavioral prey switching. Each of these mechanisms is  
298 likely to be stronger in the sand flat than the oyster reef if the structural complexity of the reef  
299 generates sufficient turbulence to dissipate chemical signals (Weissburg and Zimmer-Faust  
300 1993), thereby potentially reducing the strength of both of the hypothesized chemically-mediated  
301 interactions.

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

312 predators are most active (Nakaoka 2000). Although we found equivalent predation in the two  
313 habitats rather than higher predation in the oyster reef, our multiple-predator trials suggest that  
314 such a counter-intuitive result may be a consequence of interactions between predators that  
315 reduce their prey consumption in the unstructured sand flat. These results indicate the need for  
316 further investigation of how habitat context affects predator-predator interactions to determine  
317 whether reduced foraging efficiency in complex habitats is generally counterbalanced by the  
318 suppressed interference interactions among predators where structure is greater.

319         It is becoming clear that behavioral modifications are integral to species interactions  
320 (Micheli 1997, Dill et al. 2003, Trussell et al. 2003, Werner and Peacor 2003, Schmitz et al.  
321 2004, Byrnes et al. 2006). Despite the potential for stone crabs to consume whelks, we did not  
322 observe any intraguild predation in our experiment, eliminating lowered predator densities as an  
323 explanation for the reduction in prey consumption in the sand flat and indicating that behavioral  
324 interactions among predators are likely driving changes in consumption patterns (Fig. 3).  
325 Furthermore, our study suggests that habitat complexity may combine with animal behavior to  
326 structure ecological communities not only by increasing refuge use by prey in the presence of  
327 predators (e.g., Micheli 1997, Trussell et al. 2003), but also by reducing interference interactions  
328 among predators. If intermediate-level consumers such as whelks and crabs aggregate in more  
329 complex habitats to avoid their predators, this behavioral release could be an important  
330 component of how these systems are structured.

331         In addition to causing changes in the overall number of prey consumed, habitat context  
332 and predator-predator interactions both increased resource partitioning in the form of predator  
333 dietary selectivity in our study. Resource partitioning is thought to be ubiquitous in nature as a  
334 means of species coexistence (Chesson 1991), but there are surprisingly few empirical



335 demonstrations of resource partitioning in multiple-predator trials (Ives et al. 2005). We show  
336 that whelks increased their selectivity of clams in response to competition and/or the threat of  
337 intraguild predation when crabs were present. This finding emphasizes the importance of  
338 including multiple prey in studies of predator-predator interactions, as resource partitioning is  
339 not possible unless diverse resources are available (e.g., Pfennig et al. in press). In addition,  
340 crabs increase their selectivity of mussels in the oyster reef as compared to the sand flat, lending  
341 further support to the importance of habitat context to species interactions.

342         We manipulated key components of the benthic food web in a controlled setting to  
343 contribute to our understanding of the mechanisms that potentially mediate patterns of prey  
344 survivorship and their distribution in nature. While mesocosm studies are effective at isolating  
345 specific mechanisms that may be important, the findings should be incorporated into field studies  
346 to confirm the role of these mechanisms in structuring more natural communities. If top  
347 predators such as sea birds were to increase stone crab use of structured habitats, which has been  
348 demonstrated for blue crabs (Micheli 1997, Micheli & Peterson 1999), we would expect  
349 increased predator densities to result in even greater predation on bivalves in oyster reefs than  
350 sand flats.

351         Not only do our results potentially help to explain why predictions based on single-  
352 interaction (e.g., 1 predator and 1 prey) experiments may not scale up to patterns in natural  
353 communities, but they also suggest that we need to be careful when equating different habitats or  
354 sites based on similarities in a composite measure such as prey density or diversity. Overall prey  
355 mortality in our multiple-predator treatments did not differ between the oyster reef and the sand  
356 flat (Fig. 1). However, this similarity was due to different mechanisms operating in each habitat,  
357 and therefore, changes in predator abundances would probably have very different effects in the

358 two habitats. For instance, the loss of stone crabs due to over-fishing may not cause a dramatic  
359 change in overall prey mortality in the sand flat because whelks would compensate for their  
360 absence. In contrast, removal of stone crabs from oyster reef habitats could result in a  
361 considerable decline in bivalve prey mortality. An understanding of such complex predator  
362 interactions will be important for predicting how continued losses in biodiversity and  
363 components of ecological habitats interact to affect community structure (Chapin et al. 2000,  
364 Schmitz and Sokol-Hessner 2002), particularly since this loss is often focused on predators.

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

375

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385

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506

## 507 FIGURE LEGENDS

508 Fig. 1. Prey consumption by predator and habitat. Total number of hard clams and mussels  
509 consumed in the stone crab only, whelk only, and combined stone crab and whelk treatments.

510 Means are least squares means. Error bars represent +1 s.e. \* indicates  $P \leq 0.05$ . Each predator  
511 consumed significantly more prey items in the sand flat (open bars) than the oyster reef (solid  
512 bars) when alone, but consumption by both predators did not differ significantly by habitat.

513 Fig. 2. Prey consumption by predator, prey, and habitat. Error bars represent +1 s.e. (a-b)

514 Number of clams (a) and mussels (b) eaten by stone crabs when alone (open bars) and when with  
515 whelks (hatched bars) in the sand flat and the oyster reef. Stone crabs show a trend towards  
516 lower clam consumption in the sand flat when they are with whelks (\* $P = 0.10$ ), and they  
517 consume fewer total prey (clams and mussels) in the sand flat when they are with *Busycon* (data  
518 not shown;  $P \leq 0.05$ ). (c-d) Number of clams (c) and mussels (d) eaten by whelks when alone



519 (open bars) and when with stone crabs (hatched bars) in the sand flat and the oyster reef. Whelks  
520 consume fewer mussels in the sand flat when they are in the presence of stone crabs (\*\*P ≤  
521 0.01).

522 Fig. 3. Changes in interaction strength across sand flat (a-c) and oyster reef (d-f) habitats. Width  
523 of arrow indicates strength of effect, and +/- indicates direction of effect. (a-b) Individual effects  
524 of whelks and stone crabs on their prey in the sand flat. Crabs consume more mussels than  
525 clams, while whelks consume more clams than mussels. (c) Combined effects of whelks and  
526 stone crabs, indicating reduced consumption of mussels by whelks and reduced consumption of  
527 both prey by stone crabs. The dashed arrow between the 2 predators depicts hypothesized  
528 predator-predator behavioral interference. (d-e) Individual impacts of each predator on their prey  
529 in the oyster reef. The prey preferences are consistent between habitats. (f) The effects of each  
530 predator do not change when in the presence of the other predator compared to when alone.

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Table 1. Results from ANOVA on total predation rate.

d.f. = degrees of freedom; 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	

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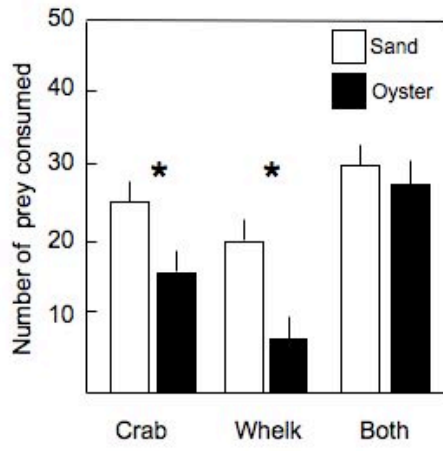
Table 2. Least square means (standard error) of predation rate on each prey by habitat and predator treatment.

		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)

535

536

Figure 1



536

537

Figure 2

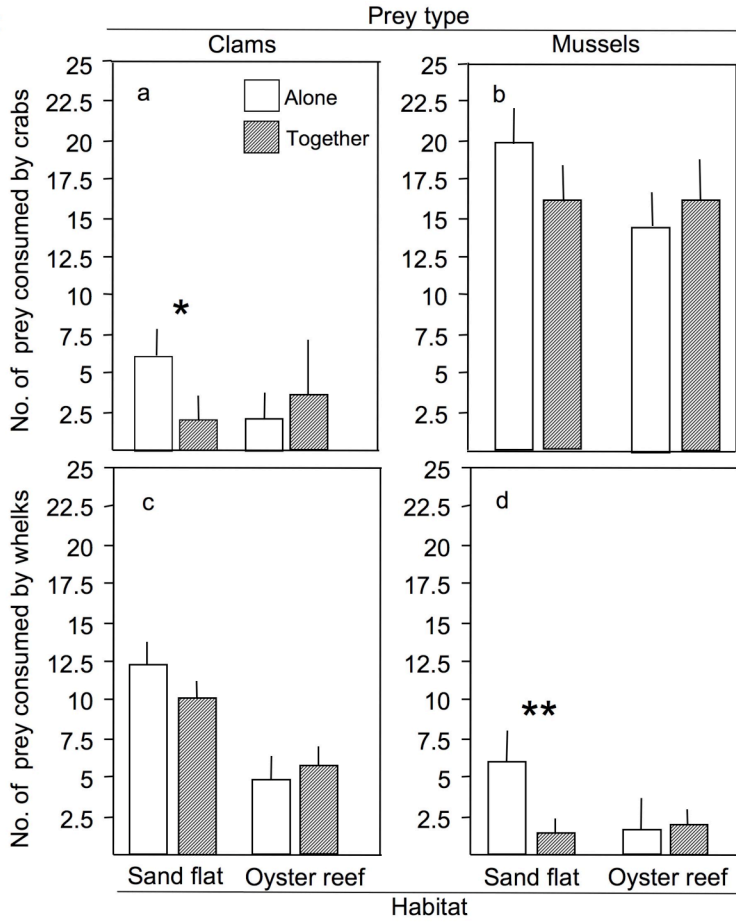


Figure 3

