

Running head: predator and prey behaviors in seagrass

Variable prey density modifies the effects of seagrass habitat structure on  
predator-prey interactions

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1 **1. Abstract**

2 In seagrass habitats, high levels of structural complexity often enhance prey  
3 survival by reducing predator-prey encounter rates and predator foraging success.  
4 However, faunal density and biomass typically increase with seagrass structural  
5 complexity, such that variation in prey or predator density may contribute to or alter  
6 relationships between structural complexity and prey survival. We determined whether  
7 variability in prey density alters relationships between seagrass structural complexity and  
8 (i) prey survival, (ii) predator-prey encounter rates, and (iii) behavioral components of  
9 predator-prey interactions in eelgrass (*Zostera marina*) habitat. Our experiments  
10 involved observations of mesopredator (juvenile giant kelpfish *Heterostichus rostratus*)  
11 feeding success and behavior, and prey (grass shrimp *Hippolyte californiensis*) predator  
12 avoidance behavior within transplanted eelgrass habitat in laboratory mesocosms. We  
13 compared results between experiments in which we held prey density constant or  
14 increased prey density with eelgrass shoot density. We found that increasing prey density  
15 (but not eelgrass density) enhanced proportional prey survival and decreased the  
16 probability that mesopredators would attack prey, whereas increasing eelgrass density  
17 (but not prey density) decreased the likelihood that prey would attempt to escape from  
18 mesopredator attack. Predator-prey encounter rates were influenced both by prey density  
19 and eelgrass density, whereas mesopredator attack success was not influenced by either  
20 eelgrass density or prey density. Our results suggest that variable prey density modifies  
21 relationships between habitat structure and prey survival through a variety of behavioral  
22 mechanisms, and that factors that covary with habitat structure, such as prey density, may  
23 alter effects of habitat structure on predation.

24

25 Keywords: habitat structure, predation, seagrass, structural complexity, *Zostera marina*,

26 epifauna

27

## 28 **2. Introduction**

29 Habitat structure, the physical arrangement of objects in space, strongly  
30 influences organismal abundance and diversity in terrestrial, freshwater, and marine  
31 ecosystems (Willson 1974, Gorman & Karr 1978, Heck & Crowder 1991, McCoy & Bell  
32 1991, Petren & Case 1998, Beck 2000). A primary way in which habitat structure  
33 influences communities is through its influence on predator-prey relationships. A  
34 paradigm regarding the ecology of structured habitats is that predators are inhibited from  
35 finding and capturing prey by biotic or abiotic elements of habitat structure (e.g. Crowder  
36 & Cooper 1982, Stoner 1982, Orth et al. 1984, Gotceitas & Colgan 1990, Heck &  
37 Crowder 1991), which results in decreasing rates of predation (and increasing rates of  
38 prey survival) with increasing structural complexity or habitat heterogeneity (Van Dolah  
39 1978, Coen et al. 1981, Summerson & Peterson 1984, Savino & Stein 1989, Graham et  
40 al. 1998, Kunkel & Pletscher 2000, Anderson 2001, Orth & van Montfrans 2002, Tarr &  
41 Babbitt 2002, Davis et al. 2003). A variety of factors mediate this relationship, however,  
42 leading to variability in habitat-survival functions among studies, species, and habitats.  
43 At small scales (i.e. within patches), the size of predator and prey organisms relative to  
44 the size and spacing of structural elements may influence prey visibility and the ability of  
45 predators to maneuver through the habitat (Crowder & Cooper 1982, Bartholomew et al.  
46 2000, Manatunge et al. 2000). Behavioral responses of prey and predators to structure,

47 including predator foraging modes (Ryer 1988, Michel & Adams 2009) and prey  
48 microhabitat selection, activity levels, and decisions to hide or flee from predators (Stein  
49 and Magnuson 1976, Cook & Streams 1984, Main 1987) also may change with habitat  
50 structure and may influence predator-prey encounter rates. Encounter rates also may be  
51 influenced by habitat selection by predators, who may select highly complex patches in  
52 response to elevated prey density or in response to threats from higher-order predators  
53 (Gotceitas & Colgan 1990), or may select habitat patches of reduced complexity to trade  
54 off predation risk with foraging success (Crowder & Cooper 1982, Werner et al. 1983,  
55 Mullin et al. 1999). Finally, aspects of habitat structure at landscape scales, including  
56 proximity to the patch edge (Gates & Gysel 1978, Paton 1994, Bologna & Heck 1999,  
57 Selgrath et al. 2007), patch size (Andren 1994, Robinson et al. 1995, Irlandi 1997), and  
58 landscape context (Donovan et al. 1997) may exert strong influence on the ability of  
59 predators to find and capture their prey, and may alter relationships between structural  
60 complexity and prey survival (Hovel & Fonseca 2005).

61         Seagrasses form complex above and below ground structures in shallow marine  
62 systems around the world, and thereby serve as important foraging and refuge habitats for  
63 a great number of vertebrate and invertebrate organisms (Williams & Heck 2001). Due to  
64 their refuge value, to strong associations between prey and predator organisms with  
65 seagrass structure, and to widespread and accelerating loss and degradation of seagrass  
66 habitat (Orth et al. 2006), they also have served as important experimental model systems  
67 to determine how habitat structure at multiple spatial scales influences prey survival and  
68 predator foraging success (see reviews by Orth et al. 1984, Heck & Crowder 1991, Orth  
69 1992). In seagrasses, survival of epifaunal prey such as small crustaceans (e.g.,

70 amphipods, isopods, grass shrimp, and newly settled blue crabs) often is optimal at high  
71 levels of structural complexity (commonly is measured as shoot density, shoot height, or  
72 biomass per unit area) (Heck & Thoman 1981, Heck & Crowder 1991, Hovel & Lipcius  
73 2001; but see Schulman 1996). However, epifaunal density (Stoner 1980, Heck et al.  
74 1989, Orth 1992, Beck 2000) and diversity (Heck & Wetstone 1977, Attrill et al. 2000,  
75 Moore & Hovel 2010) also typically increase with seagrass structural complexity.  
76 Therefore variability in prey survival with seagrass structure may be due both to effects  
77 of structure on predator foraging success, and to variation in prey or predator density and  
78 community composition with structure. For instance, prey survival did not increase with  
79 seagrass structural complexity when prey and predator densities were experimentally  
80 increased with structural complexity (Mattila et al. 2008; see also Canion & Heck 2009),  
81 which contrasts the results of numerous studies using constant densities of prey and  
82 predators across gradients of habitat structure. Variability in organismal densities with  
83 habitat structure therefore should be considered when designing experiments to test for  
84 effects of habitat structure on survival (Mattila et al. 2008).

85         Our goal in this study was to determine whether variability in prey density alters  
86 relationships between seagrass structural complexity and (i) prey survival, (ii) predator-  
87 prey encounter rates, and (iii) behavioral components of predator-prey interactions in  
88 eelgrass (*Zostera marina*) habitat. To accomplish this we conducted mesocosm-based  
89 predation experiments using two canopy-dwelling species that are abundant in the  
90 eelgrass beds of southern California, the mesopredatory juvenile giant kelpfish  
91 *Heterostichus rostratus* and one of its common prey species, the epifaunal grass shrimp  
92 *Hippolyte californiensis*.

93  
94

### 95 **3. Materials and Methods**

#### 96 *3.1 Study species*

97           We chose juvenile giant kelpfish (hereafter “kelpfish”) and *H. californiensis*  
98 (hereafter “grass shrimp”) for our study species due to their high abundance (reaching  
99 densities of ca. 2 and 2000 individuals m<sup>-2</sup> in southern California eelgrass habitat,  
100 respectively: Moore & Hovel 2010) and their strong trophic linkage. Though the most  
101 abundant epifaunal prey item found in the guts of juvenile giant kelpfish are amphipods,  
102 grass shrimp are a common component of the diet, composing up to 20% of the biomass  
103 in kelpfish guts (Moore & Hovel 2010). These two species also represent groups of  
104 vertebrate mesopredators and invertebrate grazers that may exert strong top-down control  
105 on seagrass growth and abundance via their predator-prey interaction (Valentine & Duffy  
106 2006). Kelpfish are active predators that swim slowly within the eelgrass canopy  
107 searching for epifaunal prey such as grass shrimp, which consume epiphytic algae on  
108 eelgrass blades (KAH, personal observation).

109           We collected kelpfish (80-120 mm fork length (FL)) with a beach seine and  
110 collected grass shrimp by dip netting within shallow subtidal seagrass habitat within San  
111 Diego Bay, California. Kelpfish and grass shrimp were held in a recirculating seawater  
112 system at the SDSU Coastal and Marine Institute Laboratory in San Diego before use in  
113 experiments. Kelpfish were fed grass shrimp *ad libitum* for six days while in captivity  
114 and were starved for 2 d before being used in trials. Organisms were not held more than  
115 10 d and were not reused in experiments.

116

117 *3.2 Experimental design and procedure*

118           We conducted experiments within glass mesocosms (122 x 61 x 61 cm) filled to a  
119 depth of 8 cm with clean beach sand and then filled with recirculating seawater to a depth  
120 of 45 cm. We varied structural complexity within mesocosms by transplanting eelgrass  
121 from San Diego Bay to create six shoot densities, each randomly assigned to one  
122 mesocosm: 20, 40, 80, 160, 250, or 320 shoots m<sup>-2</sup>, which represent low to moderate  
123 levels for San Diego Bay. Pilot experiments revealed that we were able to reliably  
124 observe prey and predator behaviors at shoot densities as high as 320 shoots m<sup>-2</sup>. To  
125 examine the relative effects of varying prey density and varying structural complexity on  
126 prey survival, encounter rates, foraging behavior of predators, and predator avoidance  
127 behavior by prey, we conducted two experiments, one in which grass shrimp density was  
128 held constant across the six levels of structural complexity, and one in which grass  
129 shrimp density increased with structural complexity. We used a density of 20 shrimp per  
130 mesocosm in the constant prey density experiment, and in the variable prey density  
131 experiment we increased shrimp density proportionally with shoot density to maintain an  
132 approximate ratio of one grass shrimp for every 2 -3 shoots (Table 1). Our prey densities  
133 are lower than what typically is found in seagrass patch interiors, but are comparable with  
134 grass shrimp densities along the edges of seagrass patches in San Diego Bay (Moore &  
135 Hovel 2010). Using these prey density levels allowed us to recover 100% of grass  
136 shrimp at the conclusion of trials with minimum disturbance to transplanted eelgrass.

137           Before transplantation, intact eelgrass shoots were rinsed to remove sediment,  
138 macroalgae, and large organisms, and then were soaked in freshwater for 30 min to

139 remove remaining epifauna from the blades. Shoots were added to mesocosms by tying  
140 rhizomes to randomly selected points on a plastic grid buried beneath the sediment.  
141 Blades then were trimmed to be flush with the water's surface. Shoots began to decay  
142 after approximately two weeks, at which point mesocosms were randomly assigned a  
143 new shoot density treatment and all shoots within each mesocosm were replaced with  
144 fresh shoots from San Diego Bay. To minimize disturbance by observers during  
145 predation trials, we covered three sides with opaque white plastic sheeting, and placed a  
146 mesh blind over the remaining side. Mesocosms were illuminated by two fluorescent  
147 Coralife<sup>®</sup> aquarium bulbs during trials.

148         Prior to the start of a trial, the experimental tanks were cleaned of any seagrass  
149 detritus and detached seagrass blades, and replacement shoots, if necessary, were  
150 haphazardly placed in mesocosms. Grass shrimp then were added to an aquarium and  
151 were allowed to acclimate for 30 min, after which time one kelpfish was measured (FL)  
152 and placed in a plastic mesh container floating within the mesocosm. After 15 min of  
153 acclimation to the mesocosm the kelpfish was released by gently inverting the basket  
154 which began a trial. For each 75 min trial, one observer recorded kelpfish behaviors and  
155 one observer recorded grass shrimp behaviors using voice recorders (see *Predator and*  
156 *prey behaviors* below). After 75 min, we removed kelpfish from mesocosms and  
157 collected all surviving shrimp within mesocosms by dipnetting for 15 min, which was  
158 100% effective at recovering grass shrimp in pilot experiments using up to 80 grass  
159 shrimp and no kelpfish. At the conclusion of each trial, kelpfish were placed in plastic  
160 containers without seagrass in which they were offered an additional five "post-trial"  
161 grass shrimp for 1 h, after which time we counted the number of post-trial grass shrimp

162 consumed. This was done to determine whether grass shrimp survival rates and kelpfish  
163 behaviors could be influenced by satiation as well as structural complexity and prey  
164 density, particularly at low levels of structural complexity or high levels of prey density  
165 (see *Statistical analysis* below).

166 We conducted four replicate trials for each structural complexity treatment in the  
167 constant shrimp density treatment, and six replicate trials for each shoot density in the  
168 variable shrimp density treatment between March and October 2009 (N = 60 trials).

169 Trials were discarded if fish did not attempt to hunt or eat shrimp for the entire 75 min.

170

### 171 *3.3 Predator and prey behaviors*

172 We quantified several distinct components of predator-prey interactions that  
173 affect predator foraging efficiency and that may be influenced by structural complexity or  
174 prey density (Ryer 1988; Table 2). First, the number of predator-prey encounters during  
175 a trial served a measure of the ability of kelpfish to detect their prey. We defined  
176 predator-prey encounters as an obvious fixation of both eyes of the fish on a shrimp,  
177 accompanied by a halt in motion (Ryer 1988). In addition to counting the number of  
178 encounters per trial, we divided the number of predator-prey encounters by the starting  
179 number of prey to serve as a measure of the probability that an individual grass shrimp  
180 would be detected by kelpfish. Second, after detecting prey, predators must choose  
181 whether to attack, and attacks may or may not be successful. We therefore calculated the  
182 proportion of encounters that resulted in attacks by kelpfish and the proportion of attacks  
183 that were successful. Though we also counted the number of unsuccessful attacks that  
184 were followed by a pursuit of prey by kelpfish, there were too few pursuits to conduct

185 statistical analysis. Third, we quantified the total number of seconds kelpfish spent in  
186 motion, and calculated proportional kelpfish activity by dividing the number of seconds  
187 spent in motion by the total number of seconds in a trial (4500). High rates of activity  
188 suggest predators are engaging in active hunting, whereas low rates of activity suggest a  
189 sit-and-pursue strategy (Savino & Stein 1982, Michel & Adams 2009). Finally, predator  
190 foraging efficiency also may depend on the tendency of prey to detect predators and  
191 attempt to flee from them, and we therefore calculated the proportion of encounters that  
192 resulted in escape attempts by grass shrimp prey (before an attack or after an  
193 unsuccessful attack), and the number of times shrimp switched sides of seagrass blades  
194 (“side switching”). Side switching was used by the grass shrimp *Tozeuma carolinense* to  
195 avoid being detected or pursued by predators (Main 1987) and we observed *H.*  
196 *californiensis* performing this behavior in pilot experiments. To record side switching,  
197 we haphazardly selected individual shrimp to observe for 5 min intervals, during which  
198 we recorded the number of times an individual moved to the other side of a seagrass  
199 blade. The total number of times side switching was observed during a trial was divided  
200 by the number of shrimp observed to yield an average frequency per five minute interval.

201

### 202 *3.4 Statistical analysis*

203 We calculated grass shrimp proportional survival by dividing the number of  
204 surviving grass shrimp by the number of grass shrimp placed in the mesocosm at the start  
205 of a trial. Our satiation trials revealed, however, that there was an inverse relationship  
206 between structural complexity and the number of post-trial grass shrimp consumed by  
207 kelpfish in the variable prey density experiment ( $df = 1, 32, F = 12.1, P = 0.001, r^2 =$

208 0.25), suggesting that kelpfish may become satiated at high prey densities. To ensure that  
209 this did not result in artificially inflated rates of survival at high levels of grass shrimp  
210 density (e.g. if kelpfish could consume only a fraction of available prey), we also  
211 calculated an adjusted grass shrimp proportional survival for our highest density  
212 treatment by dividing the number of surviving grass shrimp by the maximum number of  
213 shrimp a fish was observed to eat over 75 min in pilot experiments (= 49 shrimp). Trends  
214 were qualitatively similar between adjusted and unadjusted proportional survival, and we  
215 therefore conducted statistical analyses using unadjusted proportional survival.

216 We used linear regression, non-linear regression, and a comparison of slopes  
217 procedure (Zar 2009) to test whether the influence of structural complexity on grass  
218 shrimp proportional survival, as well as all behavioral variables, differed between the two  
219 grass shrimp experiments (constant vs. variable prey density). We originally included  
220 fish fork length as an independent variable in our analyses, but removed it from final  
221 analyses as did not contribute significantly to statistical models. For each dependent  
222 variable (Table 2), we first ran separate least-squares linear regressions to obtain best-fit  
223 lines and residuals for each experiment. If data appeared strongly heteroscedastic across  
224 structural complexity treatments and included one or more extreme outliers (i.e.  
225 standardized residual  $\geq 3.0$ ), we used least-trimmed squares robust regression rather than  
226 linear regression to generate best-fit lines (Gotelli & Ellison 2004). If upon visual  
227 inspection residuals from both regressions were random, we then tested whether effects  
228 of structural complexity on the dependent variable differed between the constant and  
229 variable shrimp treatments using a *t*-test for equality of slopes (Zar 2009). If the residuals  
230 from one or both initial regressions appeared non-random, we used quadratic regression

231 to test for a non-linear relationship between the dependent variable and seagrass  
232 structural complexity. We assumed the relationship to be non-linear if the quadratic  
233 regression was significant and explained a larger proportion of the variance in the  
234 dependent variable than did the linear regression (Zar 2009).

235         Several outcomes were possible for each dependent variable examined in our  
236 experiments. First, significant relationships between structural complexity and the  
237 dependent variable may be similar (i.e. have equal slopes) between the two experiments.  
238 This would suggest that structural complexity, but not prey density, influences the  
239 dependent variable. Second, significant relationships between the dependent variable and  
240 structural complexity may be dissimilar between the two experiments, which would  
241 suggest that structural complexity influences the dependent variable, but variable prey  
242 density modifies this relationship. Third, a significant relationship between the  
243 dependent variable and structural complexity may exist only for one of the experiments.  
244 For instance, if a relationship between the dependent variable and structural complexity  
245 exists only when prey density increases with structural complexity, this would suggest  
246 that (i) only prey density influences the dependent variable, or (ii) the effects of structural  
247 complexity and prey density are additive. We were not able to distinguish between these  
248 two possibilities because we did not vary prey density while standardizing structural  
249 complexity. We did not include such an experiment because we were interested in  
250 whether variability in prey density would alter the relationship between structural  
251 complexity and each dependent variable. Fourth, lack of a significant relationship  
252 between the dependent variable and structural complexity in both experiments would

253 suggest that neither structural complexity nor prey density influence the dependent  
254 variable.

255

## 256 **4. Results**

### 257 *4.1 Grass shrimp survival*

258 Relationships between seagrass structural complexity and grass shrimp  
259 proportional survival differed between experiments; proportional survival was correlated  
260 with structural complexity only when prey density increased with structural complexity  
261 (Table 2, Figure 1), suggesting that grass shrimp density, rather than structural  
262 complexity, influenced proportional survival, or that the effects of the two independent  
263 variables on survival were additive. For variable grass shrimp density, linear regressions  
264 generated non-random residuals and a quadratic regression improved model fit, with the  
265 best-fit line suggesting a hyperbolic relationship. Proportional grass shrimp survival  
266 therefore increased with grass shrimp density and structural complexity relatively rapidly  
267 at low to moderate grass shrimp densities, with proportional survival leveling off  
268 thereafter (Figure 1).

269 As noted above, for the variable prey density experiment the number of post-trial  
270 shrimp consumed by kelpfish was inversely correlated with grass shrimp density.  
271 However, for the constant prey density experiment there was no relationship between  
272 structural complexity and the number of post-trial grass shrimp consumed by kelpfish ( $df$   
273  $= 1, 22, F = 2.2, P = 0.14, r^2 = 0.05$ ). This suggests that grass shrimp survival rates were  
274 not inflated by kelpfish satiation at low levels of structural complexity.

275

276 *4.2 Components of predator efficiency*

277 Both structural complexity and prey density influenced the total number of  
278 encounters during a trial, as well as the number of encounters per prey (Table 2, Figure  
279 2). Encounters per trial decreased linearly with structural complexity when prey density  
280 was held constant, but there was a parabolic relationship between encounters and  
281 structural complexity when prey density varied. Thus, increasing prey density from low  
282 to moderate levels increased encounter rates despite increases in structural complexity,  
283 but encounter rates decreased from moderate to high levels of structural complexity  
284 despite increases in prey density (Figure 2). In contrast, the probability that an individual  
285 grass shrimp prey would be detected by kelpfish (= encounters per prey) decreased both  
286 for constant shrimp density and variable shrimp density, though the relationship was  
287 linear for constant shrimp density and non-linear for variable shrimp density (Table 2,  
288 Figure 2). Though similar trends between the two experiments would suggest that  
289 structural complexity alone influences encounters per prey, we conclude that both  
290 structural complexity and prey density influence encounters per prey because varying  
291 prey density with structural complexity altered the nature of the relationship. Low prey  
292 density increased the probability that a grass shrimp would encounter a kelpfish at very  
293 low structural complexity, but grass shrimp density appeared to have little influence on  
294 the probability of encounter at moderate to high levels of structural complexity.

295 Attack probability decreased linearly with structural complexity only when  
296 shrimp density increased with structural complexity, suggesting that prey density, but not  
297 structural complexity, influenced the probability that kelpfish would attack prey after  
298 detecting them (Table 2, Figure 3). Though this could result from additive effects of the

299 two independent variables, we conclude that this is unlikely because the slope of the best-  
300 fit line for attack probability vs. structural complexity was nearly zero. Kelpfish attacked  
301 detected prey 100% of the time at very low prey densities, but on average attacked ca.  
302 75% of the time at the highest prey density. In contrast, neither structural complexity nor  
303 prey density influenced proportional attack success by kelpfish (Table 2, Figure 3). On  
304 average, kelpfish were successful on approximately 66% percent of attacks when prey  
305 density was held constant, and successful on 72% of attacks when prey density varied.

306 We found relatively strong evidence that the relationship between proportional  
307 kelpfish activity and seagrass structural complexity differed between the two experiments  
308 ( $P$  for comparison of slopes = 0.06; Table 2, Figure 4). However, there was little  
309 evidence for a correlation between proportional activity and structural complexity for  
310 either experiment. The results therefore suggest that kelpfish foraging activity is not  
311 strongly influenced by structural complexity or by prey density at the levels we used in  
312 our study, but that kelpfish activity levels are somewhat increased by high prey densities  
313 (Figure 4).

314

### 315 *4.3 Prey behaviors*

316 Overall, grass shrimp attempted to escape on 46.8 % ( $\pm$  4.7% SE) of encounters  
317 with kelpfish, with approximately 80% of escapes coming after a kelpfish had initiated an  
318 attack. Structural complexity, and not prey density, influenced prey escape attempts: the  
319 proportion of encounters on which grass shrimp attempted to escape decreased with  
320 structural complexity regardless of whether prey density was held constant or varied  
321 (Table 2, Figure 5). Both relationships were non-linear, precluding a comparison of

322 slopes between treatments, but relationships were similar enough to conclude that prey  
323 density had little effect on the tendency for prey to attempt escape. We found no  
324 evidence that structural complexity or prey density influenced the frequency that grass  
325 shrimp switched sides of seagrass blades (Table 2, Figure 5).

326

## 327 **5. Discussion**

328         A primary conclusion from our experiments is that variability in prey density may  
329 influence survival and the behavioral mechanisms involved in predator-prey interactions  
330 as much as, or more than may variability in structural complexity, at least at the low to  
331 moderate levels of structural complexity used in our experiments. Specifically, we found  
332 that prey survival only increased with seagrass structural complexity when prey density  
333 also increased with structural complexity, and that prey density modified the effects of  
334 structural complexity on several components of predator-prey interactions, including  
335 encounter rates and decisions by predators to attack prey. Our results suggest that  
336 mechanisms by which habitat structure appears to influence predator-prey interactions  
337 should not be taken for granted, and that it is important to consider factors that often co-  
338 vary with habitat structure in nature, such as organismal densities and behaviors, when  
339 assessing the outcomes of predator-prey interactions in structurally complex habitats  
340 (Savino & Stein 1982, Ryer 1988, Mattila et al. 2008, Stoner 2009).

341

### 342 *5.1 Prey survival, prey density, and structural complexity*

343         Habitat structure and prey density both strongly influence prey survival in  
344 terrestrial and marine habitats. Though a variety of studies have addressed how

345 variability in habitat structure influences relationships between prey density and prey  
346 survival (e.g., effects of habitat on predator functional response: Lipcius & Hines 1986,  
347 Sponaugle & Lawton 1990, Moksnes et al. 1997, Seitz et al. 2001) far fewer studies have  
348 addressed the converse (i.e., how variable prey density influences effects of habitat  
349 structure on prey survival: Mattila et al. 2008; but see Gotceitas & Colgan 1990, Corona  
350 et al. 2000). In one of the few studies that tested relative effects of structural complexity  
351 and prey density on predator foraging efficiency, Gotceitas & Colgan (1990) found that  
352 rates of predator (bluegill sunfish) consumption of damselfly nymph prey were higher in  
353 simulated aquatic vegetated habitat with high levels of prey density, even when high prey  
354 density patches had five-fold higher stem density than low prey density patches,  
355 suggesting that positive effects of prey density on predator consumption rates offset  
356 negative effects of structural complexity on consumption rates. Our results were similar  
357 in that prey density had a strong influence on prey survival, but in our study system  
358 predator consumption rates decreased rather than increased with prey density. In contrast  
359 to our study and to Gotceitas & Colgan (1990), consumption of epibenthic amphipods by  
360 the predatory pink shrimp *Farfantepenaeus duorarum* in Gulf of Mexico seagrass beds  
361 decreased with habitat structural complexity, but did not vary with amphipod density  
362 (Corona et al. 2000).

363         Complex relationships between prey density, predator density, and habitat  
364 structure may influence patterns of prey survival with structural complexity (Crowder &  
365 Cooper 1982, Gotceitas & Colgan 1990, Mattila et al. 2008), and may lead to differences  
366 among studies, species, and even ontogenetic stages in the effects of structural  
367 complexity on predator-prey relationships. For instance, high levels of seagrass (*Zostera*

368 *marina*) structural complexity enhanced relative survival of large juvenile blue crabs  
369 (*Callinectes sapidus*), but reduced relative survival of small juvenile blue crabs due to  
370 high abundances of larger, cannibalistic conspecifics in dense seagrass (Schulman 1996).  
371 Similarly, prey (grass shrimp *Palaemonetes pugio*) survival did not increase with  
372 simulated seagrass (*Thalassia testudinum*) structural complexity in laboratory  
373 experiments in which prey and predator (pinfish *Lagodon rhomboides*) densities were  
374 increased with structural complexity (Mattila et al. 2008, Canion & Heck 2009). These  
375 results led Mattila et al. (2008) and Canion & Heck (2009) to suggest that high levels of  
376 structural complexity may not enhance prey survival as commonly as believed, because  
377 prey and predator densities often increase with structural complexity in naturally  
378 occurring seagrass habitat. Our results support their important findings that effects of  
379 seagrass habitat structure on prey survival depend on organismal densities as well as on  
380 structural complexity. However, we suggest that relationships between epifaunal density,  
381 predator density, and seagrass habitat structure are highly variable among locations and  
382 taxa, and thus it is important to test for relative effects of structural complexity and prey  
383 density on prey survival. In San Diego Bay, for instance, preferences for components of  
384 seagrass structural complexity (e.g. dense shoots vs. tall shoots vs. total biomass) differed  
385 among epifaunal species (Sirota & Hovel 2006), and relationships between seagrass  
386 structural complexity and epifaunal (prey) density were modified by proximity to patch  
387 edges for some taxa (e.g. amphipods) and by predator presence for other taxa (e.g. grass  
388 shrimp) (Moore & Hovel 2010). Habitat selection also may differ among predator  
389 species, particularly organisms like juvenile fishes and invertebrates (mesopredators) that  
390 are vulnerable to higher-order predators. Mesopredators dwelling in complex habitats

391 may select areas of intermediate complexity to trade off foraging efficiency with  
392 mortality risk (Crowder & Cooper 1982, Werner et al. 1983), or may switch to highly  
393 complex patches only when threats from higher-order predators are introduced (Gotceitas  
394 & Colgan 1990). Alternatively, mesopredator habitat selection may depend more on  
395 epifaunal biomass than on structural complexity (Sirota & Hovel 2006).

396         Adding to the variability among studies and taxa in the effects of structural  
397 complexity on predator-prey interactions is the fact that variability in structural  
398 complexity may involve differences in the density, heterogeneity, and morphology of  
399 structural elements (McCoy & Bell 1991), each of which may interact with the  
400 morphology and behavior of prey and predatory organisms to dictate the outcome of  
401 predatory encounters (Warfe & Barmuta 2004). For instance, relationships between  
402 seagrass biomass and amphipod survival upon exposure to pinfish predators varied  
403 among seagrass species with different architectures (Stoner 1982), and predation rates by  
404 the omnivorous fish *Acanthaluteres spilomelanurus* on amphipods residing in algae were  
405 higher within diffusely branching algae than within more compact algae (Edgar 1983). In  
406 laboratory experiments involving Pacific halibut (*Hippoglossus stenolepus*) preying upon  
407 newly settled red king crabs (*Paralithodes camtschaticus*), crab survival increased both  
408 with the amount of artificial structure and the heterogeneity of structure in experimental  
409 arenas (Stoner 2009). Elements of habitat structure at landscape scales, including  
410 proximity to edges and patchiness, also have strong potential to mediate relationships  
411 between prey survival and structural complexity. Seagrass patchiness altered  
412 relationships between juvenile blue crab (*Callinectes sapidus*) relative survival and  
413 seagrass shoot density (the habitat-survival function) in Back Sound, North Carolina

414 (Hovel & Fonseca 2005) and newly settled red king crabs exhibited higher survival rates  
415 when refuge habitat was available in patchy vs. uniform configurations, due to lower  
416 predation rates in patch interiors by predatory Pacific halibut (Stoner 2009). Seagrasses  
417 and other coastal marine habitats (e.g., kelp forest, salt marsh, coral reefs, and oyster  
418 reefs) often are found in patchy configurations and more information is needed on the  
419 interactive effects of habitat structure at multiple spatial scales on ecological interactions.

420

#### 421 *5.2 Behavioral components of predator-prey interactions*

422       Though studies documenting relationships between prey survival and habitat  
423 structure are common in marine systems, relatively few studies have examined the  
424 specific mechanisms by which habitat structure influences predator-prey interactions (but  
425 see Ryer 1988, Ryer et al. 2004, Stoner 2009) and none that we are aware of have  
426 examined the relative effects of habitat structure and prey density on these mechanisms in  
427 structured marine habitats (but see e.g. Manatunge et al. 2000 for an example of this  
428 approach with freshwater macrophytes). There are several components to predator-prey  
429 interactions, each of which may be influenced by structural complexity and prey density  
430 (Ryer 1988): (i) prey detection by predators, (ii) decisions by predators to attack prey,  
431 (iii) predator success in capturing prey, and (iv) decisions by predators to pursue prey in  
432 the event they are unsuccessful. In addition, habitat structure and prey density may  
433 influence (v) the ability of prey to detect threats from predators and to take action to  
434 avoid attacks (Savino & Stein 1982, Ryer et al. 2004). By examining each of these  
435 behavioral components, the mechanisms structuring relationships between prey survival  
436 (or conversely predator foraging success) and habitat structure can be elucidated.

437           Our results suggest that seagrass structural complexity and prey density drive  
438 patterns of prey survival primarily through variability in rates of prey detection by  
439 predators, and that variability in prey density plays an important role in determining per  
440 capita encounter rates for prey. We found an inverse correlation between seagrass  
441 structural complexity and per capita encounter rates regardless of whether prey density  
442 increased with seagrass structure or remained constant. However, per capita encounter  
443 rates decreased quickly to a lower plateau when prey density increased with structural  
444 complexity, but decreased only slightly (though significantly) with structural complexity  
445 when prey density was held constant. Concomitantly, prey survival rates increased  
446 quickly to an upper plateau as prey density and structural complexity increased, but  
447 increased only slightly (and non-significantly) with structural complexity when prey  
448 density was held constant. Decisions by predators to attack detected prey also may have  
449 played a role in the outcome of our experiments. A moderate decrease in attack  
450 probability as prey density increased may have strengthened the relationship between  
451 survival and prey density, thereby contributing to differences in survival between our two  
452 experiments.

453           Prey behavior also may have influenced patterns of prey survival. The decrease  
454 in grass shrimp escape attempts with structural complexity is likely due to reduced ability  
455 of grass shrimp to detect approaching and attacking predators. Though there were similar  
456 patterns between the two experiments, differences among levels of structural complexity  
457 in the ability of grass shrimp to detect predators appeared to be somewhat larger when  
458 prey density was held constant than when prey density varied. This suggests that the lack  
459 of a positive effect of structural complexity alone on grass shrimp survival may have

460 been partially due to decreased ability of grass shrimp to detect threats as structural  
461 complexity increased. Though it is unclear why increasing prey density with structural  
462 complexity would slightly modify this effect, one possibility is that grass shrimp observe  
463 more escape attempts from conspecifics when prey density is high, and therefore are  
464 more vigilant. Regardless of whether prey density increased with structural complexity  
465 or remained constant, the overall frequency of prey escape attempts was relatively small,  
466 suggesting that prey behavior played less of a role than predator behavior in structuring  
467 prey survival. We suggest, however, that theories on effects of habitat structure of prey  
468 survival should incorporate the concept that increasing habitat structure may work to  
469 conceal foraging predators as well as vulnerable prey (Griesser & Nystrand 2009) .

470         Reduced predator-prey encounter rates in highly complex habitats commonly is  
471 caused by interference of structural elements with predator vision. For instance,  
472 largemouth bass (*Micropterus salmoides*) detection of prey (bluegill sunfish *Lepomis*  
473 *macrochirus*) decreased with increasing density of artificial plant stems, though  
474 differences in prey behavior among stem densities also influenced predation success  
475 (Savino & Stein 1982). Pipefish (*Syngnathus fuscus*) detection rates of amphipod prey  
476 were lower in structurally complex artificial seagrass than in structural simple artificial  
477 seagrass (Ryer 1988), and detection of *Daphnia pulex* by the topmouth gudgeon  
478 (*Pseudorasbora parva*) decreased with increasing densities of artificial macrophyte stems  
479 (Manatunge et al. 2000). In contrast, sponge habitat structure did not decrease detection  
480 rates of juvenile rock sole (*Lepidopsetta polyxstra*) and age-0 Pacific halibut  
481 (*Hippoglossus stenolepis*) by predatory age-2 Pacific halibut in laboratory experiments;  
482 rather, sponges served as a barrier to predator movement, thus interfering with predator

483 search and capture (Ryer et al. 2004). A simplified scheme for the effects of habitat  
484 structure on predator-prey relationships was devised by Bartholomew et al. (2000), who  
485 created dimensionless indices that quantify two aspects of habitat structure that may  
486 independently influence prey survival: (i) the relative amount of habitat cover that  
487 interferes with a predator's ability to see its prey, and (ii) the extent to which habitat  
488 structure interferes with a predator's ability to move. In accordance with their theory and  
489 similar to results from Ryer et al. (2004), Bartholomew et al. (2000) found that predators  
490 (killifish *Fundulus heteroclitus*) became less efficient at capturing amphipod prey as  
491 increasingly narrow spaces between structural elements restricted their ability to move  
492 through the habitat, but that the effects of cover on the ability of *F. heteroclitus* to detect  
493 amphipod prey were more equivocal. One commonality between Ryer et al. (2004) and  
494 Bartholomew (2000) was that experimental habitat consisted of rigid structures, which  
495 may be expected to restrict predator movement more than would flexible structures such  
496 as seagrass blades. For instance, kelpfish were able to freely move among seagrass  
497 blades in our study, and we found no effect of structural complexity on proportional  
498 attack success for kelpfish. Similar non-effects of habitat structure on proportional attack  
499 success exist in other marine predator-prey systems (e.g. Pacific halibut preying upon  
500 juvenile red king crabs: Stoner 2009) as well as in freshwater systems (e.g. the predatory  
501 fish *P. parva* preying on zooplankton: Manatunge et al. 2004; see also Anderson 1984).  
502 More research is needed on the effects of different types of habitat structure on  
503 components of predator-prey interactions.

504 In contrast to many studies, we did not find effects of seagrass habitat structure on  
505 predator activity levels. Predator activity levels often decrease with habitat structure as

506 predators switch from active searching to sit-and-pursue predation (Savino & Stein 1982,  
507 Ryer 1988, Michel & Adams 2009) which may help reduce the negative effects of  
508 structural complexity on foraging efficiency. Predatory beetle (*Dytiscus* spp.) larvae  
509 switched from actively foraging to a sit-and-pursue foraging strategy as structural  
510 complexity increased, resulting in similar rates of prey capture among levels of structural  
511 complexity (Michel & Adams 2009) as was true for lined seahorses (*Hippocampus*  
512 *erectus*) feeding on grass shrimp (*Hippolyte zostericola*) in simulated seagrass habitat  
513 (James & Heck 1994). We observed a weak trend for kelpfish to decrease activity levels  
514 with increasing structure when prey density was held constant, but not when prey density  
515 increased with structural complexity. This trend may have been stronger if we had used  
516 higher levels of structural complexity; in fact, in follow-up experiments using simulated  
517 seagrass within mesocosms, kelpfish activity was significantly reduced at a higher shoot  
518 density (600 m<sup>-2</sup>) than used herein (KAH, unpublished data).

519 We also did not observe changes in prey behaviors with habitat structure that  
520 minimize encounter rates with predators. We predicted that side switching by grass  
521 shrimp, which puts an opaque barrier between predator and prey, would be more frequent  
522 at low levels of structural complexity, but this was not observed. In contrast, grass  
523 shrimp *Tozeuma carolinense* exhibited strong reaction to predators by moving around  
524 seagrass blades and reducing time spent in motion (i.e. walking on blades; Main 1987).  
525 Changes in prey behavior with habitat structure were observed for bluegill sunfish in  
526 experimental pools: sunfish schooled for protection from largemouth bass at low artificial  
527 stem densities and dispersed among stems at high stem densities (Savino & Stein 1982).  
528 Juvenile Pacific halibut were more likely to remain motionless when approached by a

529 predator within structured habitat than within open sand (Ryer et al. 2004) and juvenile  
530 red king crabs associate with structure to a greater degree when predators are present than  
531 when they are absent (Stoner 2009).

532

### 533 *5.3 Conclusions*

534        Though structural complexity often varies substantially within and among patches  
535 and habitats, biotic and abiotic factors that covary with complexity may strongly  
536 influence predator-prey interactions. We demonstrated that prey density modifies the  
537 effects of seagrass structural complexity on predation, and that different components of  
538 predator-prey interactions respond to variability in prey density in different ways.  
539 Caveats of our study include the fact that we used relatively low levels of seagrass  
540 densities and prey densities in our experiments, as well as only one pair of predator-prey  
541 species. Our results should be extrapolated to other, denser seagrass habitats and to other  
542 species cautiously, and more research is needed for other seagrass habitats and species  
543 that may include higher levels of structural complexity and prey density. Our work also  
544 took place in a controlled laboratory setting in which organisms were not able to choose  
545 among habitats or levels of structural complexity. In naturally occurring seagrass habitat,  
546 abiotic factors such as currents (that bend seagrass blades and affect swimming ability),  
547 turbidity (that influences detection ranges for predators and prey), water depth,  
548 temperature, and proximity to alternative patches and habitats (that allow prey an  
549 alternative means of avoiding predators) may interact with structural complexity and prey  
550 density to mediate predator-prey interactions. The presence of higher-order predators  
551 that represent a threat to mesopredators such as kelpfish also may strongly influence

552 foraging behaviors and survival rates of epifaunal prey. Further research on the effects of  
553 structural complexity in marine systems and elsewhere should consider how factors that  
554 covary with habitat structure may add complexity to simple relationships between habitat  
555 structure and predation.

556

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564

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724

Table 1. Structural complexity and prey density values per  $\text{m}^{-2}$  used in the constant prey density experiment (C) and in the variable prey density experiment (V). Numbers in parentheses represent the number of shoots or grass shrimp per mesocosm.

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Structural complexity (no. shoots $\text{m}^{-2}$ or mesocosm $^{-1}$ )	<u>Prey density (C)</u> (no. grass shrimp $\text{m}^{-2}$ or mesocosm $^{-1}$ )	<u>Prey density (V)</u> (no. grass shrimp $\text{m}^{-2}$ or mesocosm $^{-1}$ )
20 (14)	28 (20)	7 (5)
40 (29)	28 (20)	14 (10)
80 (67)	28 (20)	28 (20)
160 (114)	28 (20)	56 (40)
250 (129)	28 (20)	87 (63)
320 (220)	28 (20)	111 (80)

---

Table 2. Results of linear and non-linear regressions and slopes comparisons for relationships between seagrass structural complexity vs. grass shrimp survival, kelpfish behaviors, and grass shrimp behaviors. *P* values < 0.1 are in bold.

Variable	Prey density constant				Prey density variable				Slopes different?			Interpretation <sup>†</sup>	
	df	F	<i>P</i>	<i>r</i> <sup>2</sup>	df	F	<i>P</i>	<i>r</i> <sup>2</sup>	df	<i>t</i>	<i>P</i>	SC	PD
Prop. prey survival	1, 22	0.61	0.44	0.0	2, 30	12.3	< <b>0.001</b>	0.41		na <sup>§</sup>		no	yes
No. encounters	1, 18	3.86	<b>0.06</b>	0.13	2, 31	3.17	<b>0.05</b>	0.12		na <sup>§</sup>		yes	yes
Encounters prey <sup>-1</sup>	1, 22	9.75	<b>0.005</b>	0.28	2, 31	15.4	< <b>0.001</b>	0.46		na <sup>§</sup>		yes	yes
Attack probability	1, 22	0.00	0.93	0.0	1, 32	6.42	<b>0.02</b>	0.14	56	2.8	<b>0.03</b>	no	yes
Prop. success	1, 17	0.44	0.84	0.0	1, 29	0.94	0.34	0.0	46	0.0	1.0	no	no
Prop. activity	1, 22	2.3	0.14	0.05	1, 32	0.01	0.95	0.0	54	1.94	<b>0.06</b>	no	no
Escapes encounter <sup>-1</sup>	2, 21	11.1	< <b>0.001</b>	0.46	2, 31	3.9	<b>0.03</b>	0.15		na <sup>§</sup>		yes	no
Switch sides	1, 15	0.99	0.34	0.0	1, 24	0.36	0.56	0.0	39	1.58	0.12	no	no

<sup>†</sup>For each dependent variable, whether combined results suggest an effect of structural complexity (SC) or prey density (PD).

<sup>§</sup>No slope comparison possible due to nonlinearity for one or both experiments, for which a quadratic regression was used.

## List of figures

Figure 1. *Hippolyte californiensis*. Relationship between seagrass shoot density and grass shrimp proportional survival in mesocosm experiments in which shrimp density increased as seagrass shoot density increased (V, black circles) or remained constant as shoot density increased (C, white circles). Dashed lines represent non-significant regressions and are shown to illustrate results for slopes comparison.

Figure 2. *Hippolyte californiensis* and *Heterostichus rostratus*. Relationship between seagrass shoot density and (A) total number of encounters, and (B) number of encounters per prey for mesocosm experiments in which shrimp density increased as seagrass shoot density increased (V, black circles) or remained constant as shoot density increased (C, white circles).

Figure 3. *Heterostichus rostratus*. Relationship between seagrass shoot density and (A) total number of attacks by juvenile giant kelpfish, and (B) proportional attack success for juvenile giant kelpfish in mesocosm experiments in which shrimp density increased as seagrass shoot density increased (V, black circles) or remained constant as shoot density increased (C, white circles). Dashed lines represent non-significant regressions and are shown to illustrate results for slopes comparison.

Figure 4. *Heterostichus rostratus*. Relationship between seagrass shoot density and the proportion of trial time that juvenile giant kelpfish spent in motion in mesocosm experiments in which shrimp density increased as seagrass shoot density increased (V, black circles) or remained constant as shoot density increased (C, white circles). Dashed

lines represent non-significant regressions and are shown to illustrate results for slopes comparison.

Figure 5. *Hippolyte californiensis*. Relationship between seagrass shoot density and (A) the proportion of encounters with juvenile giant kelpfish that resulted in grass shrimp escape attempts, and (B) the mean number of times that grass shrimp switched sides of seagrass blades per five minute interval in mesocosm experiments in which shrimp density increased as seagrass shoot density increased (V, black circles) or remained constant as shoot density increased (C, white circles). Dashed lines represent non-significant regressions and are shown to illustrate results for slopes comparison.

Figure 1

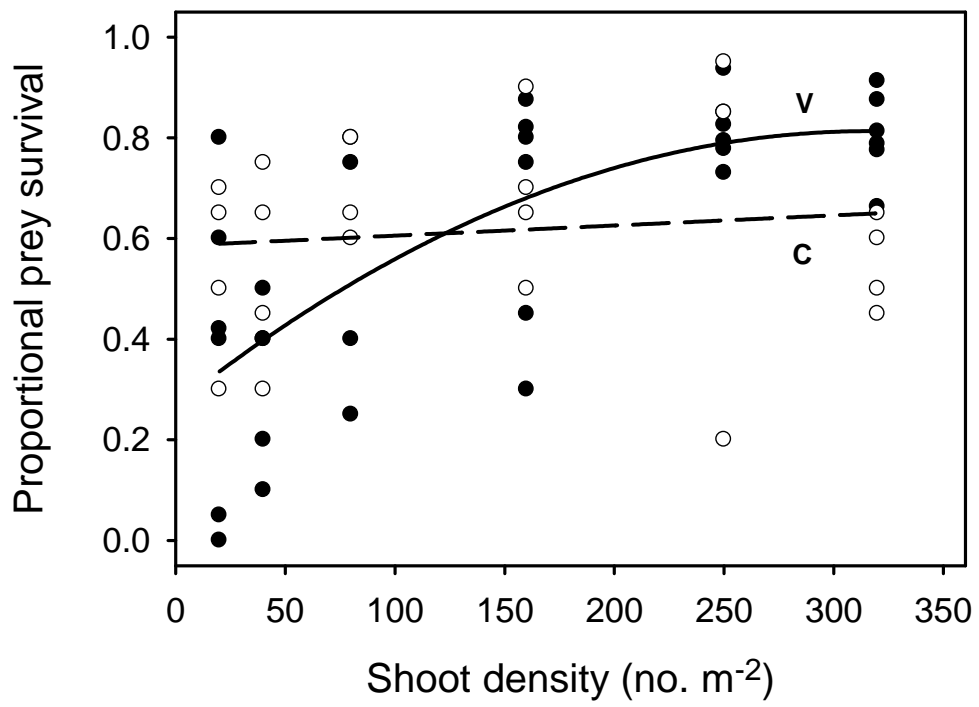


Figure 2

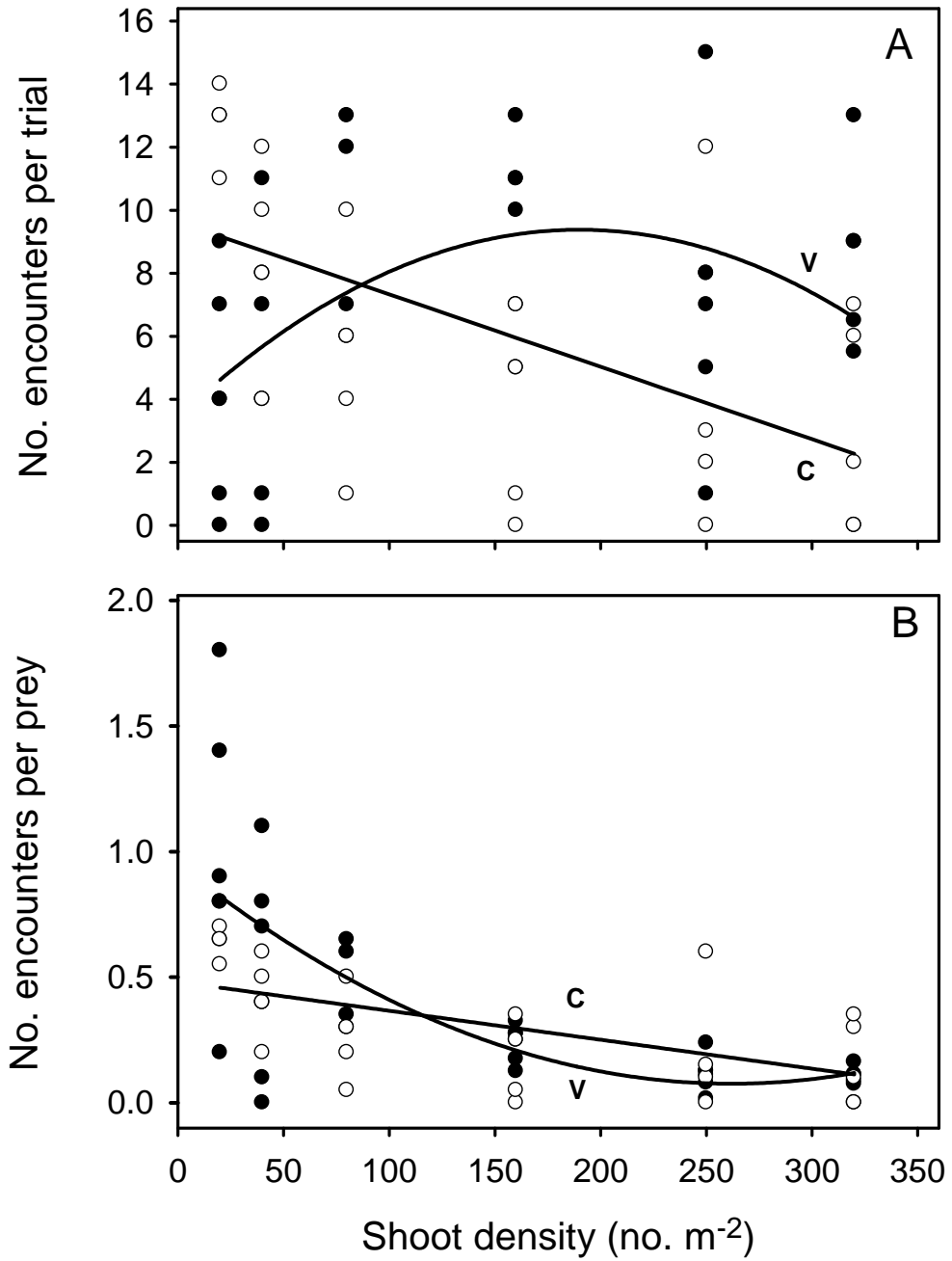


Figure 3

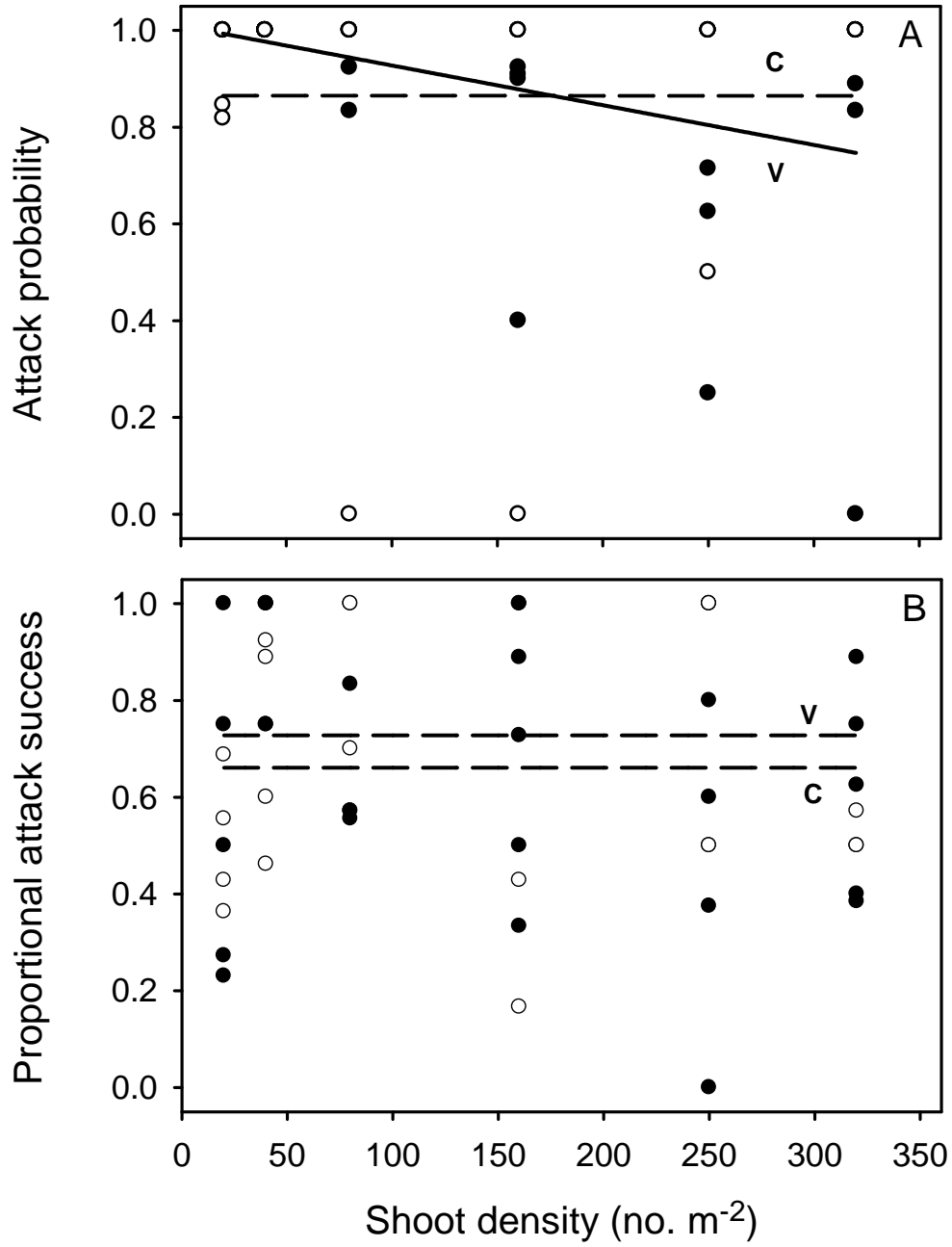


Figure 4

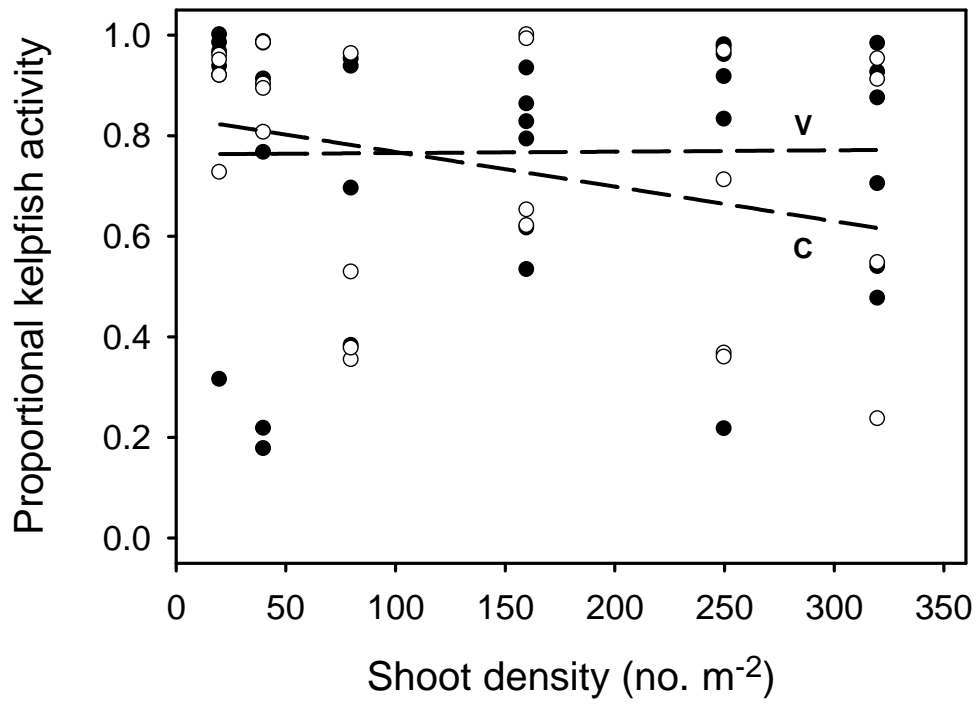


Figure 5

