

# Mesopredator foraging success in eelgrass (*Zostera marina* L.): Relative effects of epiphytes, shoot density, and prey abundance



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## ABSTRACT

In seagrass habitats, structural complexity influences predator foraging success and prey survival by moderating encounter rates and behaviors of predators and prey. Studies of the effects of structural complexity on predator–prey interactions typically vary seagrass shoot density, biomass, or architecture. Filamentous epiphytic algae commonly grow on seagrass blades and add structure to seagrasses, but the effect of epiphytes on the outcome of predator–prey interactions has rarely been explored. This study determined the relative effects of simulated seagrass epiphytes, eelgrass (*Zostera marina*) shoot density, and prey density on the foraging behaviors of a common predator, the juvenile giant kelpfish *Heterostichus rostratus* (Girard, 1854) and on escape responses of their prey, grass shrimp *Hippolyte californiensis* (Holmes, 1895). Juvenile giant kelpfish hunted for grass shrimp in a laboratory experiment in which two levels of grass shrimp density were crossed with three levels of structural complexity (low density artificial eelgrass, low density artificial eelgrass with artificial epiphytes, and high density artificial eelgrass). Increased structural complexity had variable effects on juvenile kelpfish activity levels, but enhanced their success at catching prey after detection, resulting in no net effect of structural complexity on the total number of prey captured. Grass shrimp made fewer escape attempts in high vs. low structural complexity, which may have enhanced kelpfish foraging success because kelpfish rarely pursued fleeing prey. Prey density did not influence kelpfish behaviors or the total amount of prey they consumed. These results suggest that it is important to consider how different forms of habitat complexity affect the mechanisms by which predators hunt for prey in structured marine habitats.

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## 1. Introduction

Predator–prey interactions, and the concomitant effects of predation on population dynamics and community structure, are strongly influenced by habitat structural complexity (Heck and Crowder, 1991; Orth et al., 1984). Structural complexity represents the amount and spatial distribution of the structural elements of habitats such as seagrass, rocky reefs, coral reefs, kelp forests, and oyster reefs. These complex habitats may serve as nursery habitats by promoting the survival and growth of juvenile fishes and invertebrates (McCoy and Bell, 1991). Laboratory experiments and field tethering experiments in these habitats have suggested that increasing structural complexity often limits the ability of predators to find and capture their prey, resulting in a reduction in predator efficiency and an increase in prey survival (Bartholomew et al., 2000; Gotceitas and Colgan, 1989; Johns and Mann, 1987; Minello and Zimmerman, 1983; Stoner, 1982). Experiments testing for effects of structural complexity on foraging success do not often account for two important concepts, however: (i) there are several components to predator–prey interactions (e.g., foraging

mode, detection of prey, and probability of successful attack), each of which may be influenced by structural complexity in different ways (Ryer, 1988); and (ii) prey (and sometimes predator) densities typically increase with increasing structural complexity (Canion and Heck, 2009; Mattila et al., 2008). Because structural complexity and organismal density both may strongly influence predator–prey interactions, experiments designed to measure predator foraging success in structured habitats should consider the potential interactive effects of these variables on the ability of predators to find and capture their prey.

Habitat structural complexity and prey density may influence predator foraging success in a variety of ways. Structural elements of habitat and prey abundance both may influence the ability of predators to detect prey (Bartholomew et al., 2000; Michel and Adams, 2009), but similarly, prey may have a harder time detecting approaching predators when habitats are dense (Catano et al., 2015). The structure of the habitat and the proximity of other potential prey items also may influence a predator's decision to attack prey after detection, as well as the likelihood that the attack will be successful (Ryer, 1988). Lastly, structural complexity and prey density may influence predator foraging mode, e.g., whether they actively hunt throughout the habitat or sit-and-wait for prey to approach (Michel and Adams, 2009; Savino and Stein, 1982). Many studies have quantified the end result of these interactions

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by measuring prey survival after exposure to predators, but fewer have determined the specific behavioral mechanisms by which structural complexity or prey density may influence predator–prey interactions (see Ryer, 1988; Toscano and Griffen, 2013). This is important information for gauging how structured habitats contribute to ecosystem function (e.g., the transfer of nutrients and energy among trophic levels) as well as to nursery habitat function.

Seagrasses are widespread in shallow marine and estuarine systems (Hemminga and Duarte, 2000), house a diverse assemblage of vertebrate and invertebrate organisms (Williams and Heck, 2001), and have served as effective experimental model systems for testing how habitat structure influences predator foraging success and prey survival (e.g. Heck and Thoman, 1981; James and Heck, 1994; Stoner, 1982). Seagrass habitats such as eelgrass (*Zostera marina*), one of the world's most widespread marine macrophytes, exhibit high variability in structural complexity and patchiness over relatively small spatial scales (Irlandi, 1997; Robbins and Bell, 1994). Likewise, the density of common epifaunal prey (e.g., amphipods, isopods, grass shrimp, small blue crabs) often is correlated with habitat structure at local (Heck and Crowder, 1991) and landscape (Hovel and Lipcius, 2001) scales. Shoot density, length, and biomass per unit area are common measures of structural complexity in seagrass habitats. Many species of seagrass, however, serve as substrate for filamentous algae that add structural complexity and that may influence the ability of predators to detect and capture prey (and perhaps the ability of prey to detect and escape from predators). Seagrass blades with epiphytic algae are preferred over non-epiphytized blades by many epifaunal taxa, though this may be due to the fact that epiphytes are a common source of food in seagrass habitat (Bologna and Heck, 1999; Boström and Mattila, 1999) as well as to reducing predation risk or simply the addition of habitat (Hall and Bell, 1988). Epiphytic algae compete with seagrasses for light and nutrients, and many recent studies have focused on the ability of crustacean and molluscan mesograzers to control epiphytic algal abundance and consequently the growth and abundance of seagrass (Duffy et al., 2001; Myers and Heck, 2013; Whalen et al., 2013). Understanding the other side of this feedback loop, that is, how epiphytes influence the ability of predators to detect and capture mesograzers, is important for forming a complete picture of the complex interactions between grazers, predators, seagrasses, and epiphytes.

The overall goal of this study was to determine the interactive effects of structural complexity and prey density on the foraging success of an abundant mesopredator (juvenile giant kelpfish *Heterostichus rostratus*; hereafter, kelpfish) in Southern California *Z. marina* habitat. Specifically, a laboratory experiment was conducted to quantify how variability in eelgrass shoot density and the presence of epiphytic algae influenced kelpfish behavior and their ability to detect and also successfully capture prey (grass shrimp *Hippolyte californiensis*; hereafter, grass shrimp), and whether these functions were influenced by prey density.

## 2. Methods

### 2.1. Study species and experimental setup

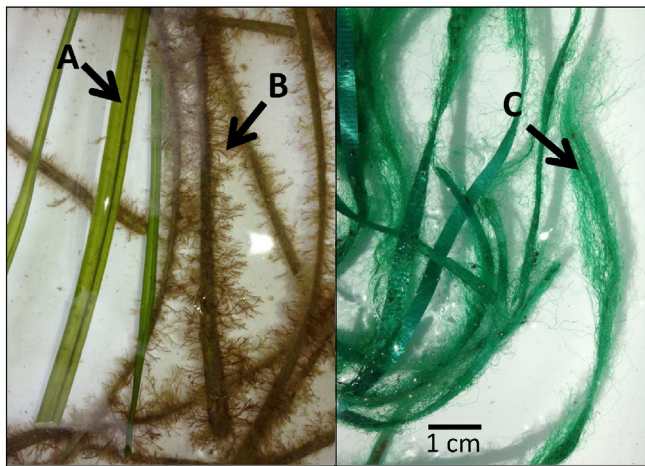
Kelpfish and grass shrimp are abundant predator and prey organisms in Southern California eelgrass habitat, with densities of approximately 0.5–1 m<sup>-2</sup> and 100–500 m<sup>-2</sup> in San Diego Bay eelgrass, respectively. Grass shrimp compose up to 20% of the biomass in kelpfish guts (Moore and Hovel, 2010). Kelpfish are active, diurnal and visually oriented predators that swim slowly within the eelgrass canopy searching for epifaunal prey such as grass shrimp, which are often found clinging to eelgrass blades where they consume epiphytic algae. Kelpfish (80–120 mm fork length [FL]) and grass shrimp (approx. 15–20 mm total length, a size range commonly found in kelpfish guts; Moore and Hovel, 2010) were collected by seining and dipnetting in eelgrass beds located just offshore of Shelter Island in San Diego Bay, California. Kelpfish (about 20 at any given time) were held in a 500 l

aquarium with recirculated seawater kept at a constant temperature of 17 °C at the San Diego State University Coastal and Marine Institute Laboratory. Kelpfish were held for a minimum of five days prior to experimentation, were fed ad libitum on a diet of grass shrimp, and starved for two days before being used in experimental trials. Grass shrimp were held in a 100 l aquarium and allowed to feed on epiphytic algae growing on fresh *Z. marina* shoots.

Experimental trials were conducted in 400 l glass mesocosms (122 cm × 56 cm × 60 cm) filled with clean beach sand to a depth of 8 cm and seawater to a depth of 45 cm. Artificial seagrass units (ASUs) consisting of green polypropylene ribbon affixed to a plastic grate buried beneath the sand served as experimental habitat and was used to vary structural complexity. Artificial seagrass has been used extensively in field and laboratory settings to mimic naturally occurring eelgrass (e.g., Bologna and Heck, 1999; Boström and Bonsdorff, 2000; Virstein and Curran, 1986) as it allows for precise control and standardization of structural complexity among experimental units. Artificial seagrass shoots were 40 cm high × 1 cm in width, similar to the dimensions of naturally occurring shoots in the shallow subtidal zone of San Diego Bay, and covered the entire extent of the mesocosm bottom. A total of four mesocosms were used to conduct trials and treatments were randomly rotated among mesocosms through time. Lighting was provided by two fluorescent Coralife® aquarium bulbs hung over each mesocosm. To reduce potential effects of observers on fish, mesocosms were surrounded by tarps to minimize disturbances, and observers moved as little as possible when recording data during experiments. All trials for the experiment were conducted between May and September 2011.

### 2.2. Experimental procedure

Structural complexity (artificial eelgrass shoot density and the presence of simulated epiphytes) and prey density were factorially varied to determine how these factors jointly influence kelpfish foraging behavior and efficiency, as well as escape attempts by grass shrimp. The three levels of structural complexity were (1) low shoot density (150 shoots m<sup>-2</sup>), (2) low shoot density with artificial epiphytes, and (3) high shoot density (400 shoots m<sup>-2</sup>), which were crossed with two levels of grass shrimp density (75 per mesocosm = 110 shrimp m<sup>-2</sup>, and 300 per mesocosm = 440 shrimp m<sup>-2</sup>) to create six treatments. Using an epiphyte vs. non-epiphyte treatment of the same shoot density allowed the determination of whether adding structure in the form of artificial epiphytes has a similar effect on fish foraging as does adding structure in the form of denser shoots. Eelgrass densities in San Diego Bay range from approximately 150–1200 shoots m<sup>-2</sup>, and average about 400 shoots m<sup>-2</sup>; thus, shoot densities in the field may take on higher values than the high shoot density treatment. The upper range of shoot density in the experiment was limited to 400 shoots m<sup>-2</sup> because (i) in pilot experiments, kelpfish ceased swimming and foraging at shoot densities ≥600 shoots m<sup>-2</sup> (see also Lannin and Hovel, 2011), and (ii) higher shoot densities made it difficult to observe animal behaviors. Epiphytic algal growth on eelgrass blades was simulated by gluing 2 cm long pieces of frayed green macramé cord (Pepperell 6 mm Bonnie Macramé Craft Cord®) onto artificial eelgrass using spray adhesive, which resulted in approximately 1 cm of intertwined, filamentous structure on either side of artificial blades (Fig. 1). The final effect of this was for artificial epiphytes to fill about half of the empty space among shoots, leaving spaces of approximately 3 cm between adjacent blades, similar to spacing between artificial shoots at the high shoot density. Artificial eelgrass and epiphytes were soaked in running seawater for one week before being used in experiments, after which simulated epiphytes remained firmly glued to shoots. To control for any possible effects of the adhesive on behaviors, shoots used for non-epiphyte treatments also were sprayed with adhesive and soaked in running seawater before use.



**Fig. 1.** Blades of eelgrass from the subtidal region of Shelter Island, San Diego Bay. (A) epiphyte-free blade; (B) blade heavily fouled with chain-forming diatoms; (C) artificial eelgrass covered with artificial epiphytes used in the experiment.

To conduct a trial of this experiment, at 0900–1000 h the appropriate amount of grass shrimp were added to the mesocosm and were allowed to acclimate for 30 min. Two kelpfish then were acclimated to the mesocosm by placing them in a floating plastic container filled with seawater for 15 min. The plastic container then was gently overturned to release kelpfish, which were allowed to forage on grass shrimp for 30 min while two observers recorded kelpfish and shrimp behaviors (see below). Two kelpfish were used in each trial because pilot experiments revealed that single kelpfish often did not actively swim or feed. At the conclusion of a trial, both fish were removed from the tank and measured to the nearest millimeter [FL]. Shrimp were retrieved by repeated dipnetting until three consecutive sweeps produced zero shrimp. Water was drained from mesocosms and new water was added before the next trial, and fish and shrimp were not reused and were released back into San Diego Bay at the conclusion of trials. There were  $n = 6$  trials for each treatment combination.

The experiment quantified several distinct components of predator–prey interactions that affect predator foraging efficiency and that may be influenced by structural complexity or prey density (Ryer, 1988; Table 1). First, a stopwatch was used to quantify the proportion of time kelpfish spent in motion (as opposed to resting on the bottom or remaining motionless). High rates of activity suggest predators are engaging in active hunting, whereas low rates of activity suggest that predators might be engaged in sit-and-wait hunting (Michel and Adams, 2009; Savino and Stein, 1989). Second, the number of detections was enumerated, which were defined as an obvious fixation of both eyes of the kelpfish on a grass shrimp accompanied by a sudden halt in swimming (sensu Ryer, 1988). Third, after detecting prey, predators

**Table 1**

Results of two-way ANOVAs testing for the effects of structural complexity and prey density on juvenile giant kelpfish (*Heterostichus rostratus*) behavior and foraging success, and grass shrimp (*Hippolyte californiensis*) behavior in the lab experiment. Numbers in parentheses are degrees of freedom for each factor.  $P$  values < 0.05 are bolded.

Variable	Structural complexity	Prey density	Structural complexity * prey density
	(2, 30)	(1, 30)	(2, 30)
	F, P	F, P	F, P
Time swimming (%)	4.1, <b>0.02</b>	1.1, 0.31	0.50, 0.61
No. detections	4.4, <b>0.02</b>	1.7, 0.20	0.35, 0.70
Detections resulting in strikes (%)	1.6, 0.22	0.94, 0.34	0.73, 0.49
Strike success (%)	6.5, <b>0.005</b>	0.43, 0.52	0.43, 0.66
Escape attempts (%)	4.3, <b>0.02</b>	0.01, 0.97	0.21, 0.81
No. prey consumed	1.7, 0.21	2.8, 0.11	0.60, 0.56

must choose whether to attack, and attacks may or may not be successful. Therefore the proportion of encounters that resulted in attacks by kelpfish was recorded, as well as the proportion of attacks in which grass shrimp were successfully consumed. Fourth, predator foraging efficiency also may depend on the tendency of prey to detect predators and attempt to flee from them, and thus the proportion of encounters that resulted in escape attempts by grass shrimp prey was calculated.

Before analysis, data were summed for the two fish used in each mesocosm because they were non-independent, yielding one data point for each dependent variable from each trial. Effects of structural complexity and grass shrimp density on each dependent variable were tested with separate two-way analyses of variance (ANOVAs) followed by Student–Newman–Keuls (SNK) post-hoc tests where appropriate. Kelpfish FL was included in initial ANOVA models, but was dropped from final models because it never approached significance and model fit (as measured by AIC values) always was improved without this term. Before analyses were performed, the data were tested for normality using a KS test and tested for homogeneity of variances using Cochran's test, and data were log transformed where necessary to meet the assumptions of ANOVA for this and all subsequent tests (Underwood, 1997). To determine how effective grass shrimp escape attempts were at preventing predation, a linear regression was used to test for a correlation between the proportion of detections by kelpfish that resulted in grass shrimp escape attempts and the proportion of successful kelp fish strike attempts.

### 3. Results

Overall, structural complexity had moderate to strong effects on most kelpfish and shrimp behaviors, whereas prey density did not affect any behaviors or the total number of prey consumed by kelpfish. There were no interactive effects of structural complexity and prey density on any variable. The proportion of time kelpfish spent in motion was lower when artificial epiphytes were attached to shoots than when shoots were bare at both low and high shoot densities (Table 1, Fig. 2A). Structural complexity also influenced the ability of kelpfish to detect prey (Table 1, Fig. 2B). The mean number of prey detections by kelpfish was higher in low shoot density eelgrass vs. eelgrass with artificial epiphytes and high shoot density eelgrass. In contrast there was no effect of structural complexity on decisions to attack prey after detection, with kelpfish choosing to attack prey on average 71% of the time regardless of treatment (Fig. 2C). Proportional strike success was higher in eelgrass with artificial epiphytes and in high density eelgrass than in low density eelgrass (Fig. 2D). Structural complexity also affected grass shrimp escape attempts: grass shrimp attempted to escape attacking kelpfish more often in low density eelgrass than in high density eelgrass (Table 1, Fig. 2E). There was no effect of structural complexity on the number of prey consumed by kelpfish (Fig. 2F).

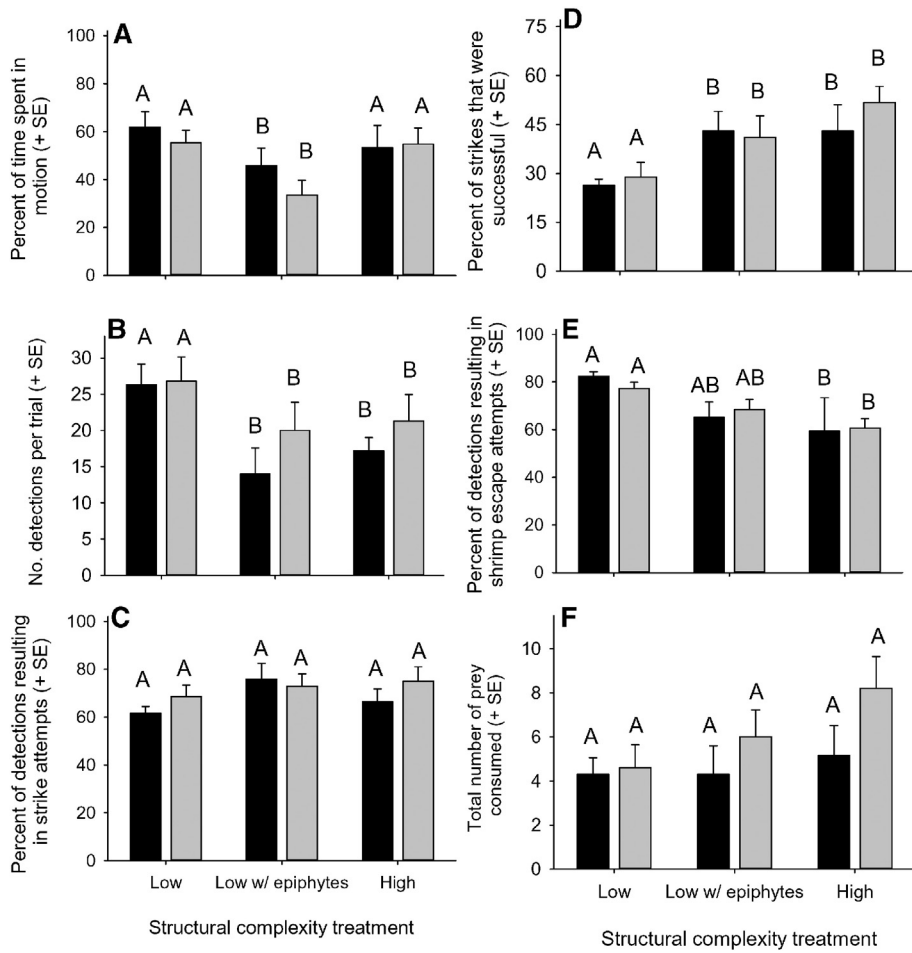
Grass shrimp escape attempts generally were effective at preventing predation; there was a strong inverse correlation between the proportion of detections that resulted in escape attempts and the proportion of successful strikes within trials (linear regression:  $df = 1, 33$ ,  $F = 104.8$ ,  $P < 0.001$ ,  $r^2 = 0.75$ ; Fig. 3). Very few kelpfish were observed pursuing grass shrimp that had fled from seagrass blades.

### 4. Discussion

#### 4.1. Structural complexity and components of foraging

Structural complexity influenced different components of the kelpfish–grass shrimp predator–prey interaction in different ways. First, adding epiphytes to eelgrass decreased the proportion of time that kelpfish spent actively hunting prey. Increasing structural complexity may result in decreased predator foraging activity when predators shift to a sit-and-wait mode of hunting (Michel and Adams, 2009; Savino and Stein, 1982) or if structure simply impedes predator



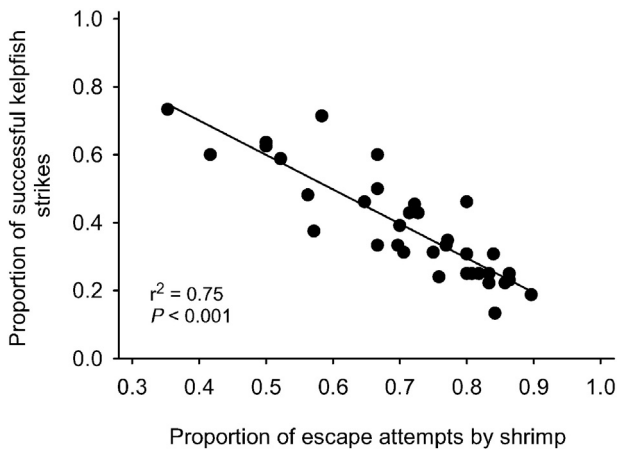


**Fig. 2.** Results of the laboratory experiment in which juvenile giant kelpfish fed upon grass shrimp. Black bars = low grass shrimp density; gray bars = high grass shrimp density. Means are shown for (A) the percent of time per trial in which kelpfish were actively swimming; (B) the number of grass shrimp detected by kelpfish per trial; (C) the percent of detections after which kelpfish decided to strike at grass shrimp; (D) the percent of strikes in which kelpfish successfully captured grass shrimp; (E) the percent of detections in which grass shrimp tried to escape from kelpfish by fleeing; and (F) the total number of grass shrimp consumed by kelpfish during a trial. Unlike letters above bars denote means that were significantly different in Student–Newman–Keuls (SNK) post-hoc tests.

movement during attempts at active foraging (Bartholomew et al., 2000; Ryer et al., 2004). Predator avoidance also may be a motivation for kelpfish to alter their behavior as structural complexity increases; for instance, if kelpfish feel safer in high complexity seagrass, they may reduce activity levels to remain there. Kelpfish appeared to shift to sit-and-wait hunting in the experimental mesocosms: when

epiphytes were present, kelpfish often remained motionless near the bottom of the mesocosm and attempted to capture grass shrimp that were in close proximity. Lined seahorses (*Hippocampus erectus*) shifted from active hunting to sit-and-wait hunting when artificial seagrass was added to experimental arenas, and sit-and-wait hunting allowed them to capture prey with equal efficiency across several levels of structural complexity (James and Heck, 1994). The same was true for predatory beetles (*Dytiscus* spp.) feeding on *Hyla versicolor* tadpoles in freshwater mesocosms (Michel and Adams, 2009). Similarly, Horinouchi et al. (2009) found that ambush predators became more efficient at capturing prey when structural complexity increased. In contrast, pygmy perch *Nannoperca australis* adopted a sit-and-wait foraging mode in low macrophyte density, but actively foraged in high macrophyte density, likely because they are vulnerable to large piscivorous predators in low structural complexity but are too small to be impeded by high structural complexity (Warfe and Barmuta, 2004). Though in the present study increasing artificial eelgrass shoot density did not reduce kelpfish activity to the same extent as adding epiphytes, in previous experiments with kelpfish larger increases in eelgrass shoot density (to 600 m<sup>-2</sup>) resulted in reduced kelpfish activity levels, either because shoots physically restrict kelpfish swimming or because sit-and-wait predation is less energetically costly for fish when structural complexity is high (Lannin and Hovel, 2011).

Adding structural complexity, in both the form of epiphytes and additional shoots, reduced the ability of kelpfish to detect grass shrimp prey. Interference with a predator's field of vision and ability to find



**Fig. 3.** Relationship between the proportion of kelpfish detections that resulted in grass shrimp escape attempts and the proportional success of kelpfish strikes.

prey is commonly cited as a primary mechanism by which structurally complex habitats reduce predator foraging efficiency and increase prey survival (Bartholomew, 2012; Manatunge et al., 2000). Kelpfish were less active in the artificial epiphyte treatment, which at least in part resulted in fewer detections. Kelpfish swimming activity was similar between low and high shoot density treatments however, suggesting that fewer detections in high shoot densities likely were due to visual barriers formed by artificial shoots. Though slower movement in dense shoots also could account for fewer detections, kelpfish are slow “cruisers” even in sparse seagrass (Tait and Hovel, 2012) and there were no obvious differences in the distances traveled by kelpfish over the course of a trial between low and high shoot density treatments. Relatively few studies have quantified the independent effects of habitat structure on predators' abilities to detect prey vs. predators' abilities (or willingness) to move through habitat. Manatunge et al. (2000) quantified predator (cyprinid fish *Pseudorasbora parva*) behaviors as they fed on *Daphnia* prey in laboratory mesocosms, and concluded that the primary effect of increasing macrophyte stem density was to impede the ability of fish to detect prey. In contrast, reduced maneuverability of killifish (*Fundulus heteroclitus*) predators through dense artificial stems was the primary mechanism by which structural complexity enhanced amphipod prey survival (Bartholomew et al., 2000).

After detecting prey, predators must decide whether to attack. Predators may limit their attack rate on prey in situations in which the chances of capturing prey are reduced, for instance, when high structural complexity may limit their maneuverability or increase the probability of escape by prey (Savino and Stein, 1982). This may be particularly true when pursuing prey is energetically expensive for predators; however, there was no effect of structural complexity (or prey density) on the probability that kelpfish would attack grass shrimp (see also Lannin and Hovel, 2011). In contrast, predatory beetles attempted 69% fewer strikes at tadpoles as structural complexity increased in freshwater aquaria (Michel and Adams, 2009), and the probability that largemouth bass would attack bluegill sunfish decreased with macrophyte stem density (Savino and Stein, 1982). It is possible that kelpfish readily pursued prey when structural complexity was high because their success rate (probability of capturing prey after attacking) increased, and escape attempts by grass shrimp decreased with structural complexity. In fact, the strongest trend in the study was the increase in the probability of successful attack with an increase in structural complexity. The addition of artificial epiphytes to shoots, and increases in shoot density both resulted in a higher probability that kelpfish would be able to consume grass shrimp once they decided to strike. This trend was surprising because structural complexity typically has stronger effects on the ability of predators to detect prey than to capture prey after detection (Anderson, 1984; Dionne and Folt, 1991; Manatunge et al., 2000; Savino and Stein, 1982). This may in part be a consequence of prey behavior, because grass shrimp escape attempts declined with increases in structural complexity (see also Lannin and Hovel, 2011), and grass shrimp escape attempts had a high success rate. Grass shrimp may not have been able to detect approaching kelpfish as easily in the presence of artificial epiphytes or when shoot density was high, resulting in fewer escape attempts and more shrimp that remained motionless on blades. High complexity also may impede prey movement and escape attempts (Bartholomew, 2012). Grass shrimp movement did not appear to be hindered by epiphytes or high shoot densities, however, and we suspect that fewer grass shrimp escape attempts in high vs. low shoot density were due to shrimp not detecting kelpfish, or shrimp perceiving that they were safer by remaining motionless. Kelpfish rarely pursued fleeing grass shrimp and seemed to focus their efforts on shrimp that remained on blades.

Because structural complexity reduced predator detection rates, but increased proportional strike success, there was no net difference among habitat treatments in the total number of grass shrimp consumed. Similarly, diving water beetle (*Dytiscus* spp.) predators were equally successful at foraging on tadpole prey among simulated

structural complexity treatments, because detection rates decreased with structure, but capture probability increased with structure (Michel and Adams, 2009). These results contrast a large number of studies in aquatic vegetated systems indicating that vegetation structural complexity reduces predator foraging efficiency and increases prey survival (see reviews by Heck and Crowder, 1991; Horinouchi, 2007; Orth et al., 1984). Two factors that help explain contrasting effects of structural complexity on predator–prey interactions are (i) prey and predator behavior, and (ii) prey and predator density. Increasing structural complexity may have contrasting effects on the efficiency of actively swimming predators vs. sit-and-wait predators, with high levels of structural complexity often favoring less active, ambush predators (Horinouchi, 2007; Horinouchi et al., 2009). This corresponds to observations that kelpfish reduced swimming and relied more on ambush in high structural complexity treatments. Because prey and predator densities may be positively correlated with structural complexity, experiments that use fixed levels of prey or predator density may incorrectly conclude that structural complexity enhances prey survival (Cannon and Heck, 2009). Two studies manipulating the complexity of the seagrass *Thalassia testudinum* along with the densities of predatory fish and invertebrate prey found no influence of seagrass complexity on prey survival when the ratio of predator density to prey density was similar among complexity treatments (Cannon and Heck, 2009; Mattila et al., 2008). Lannin and Hovel (2011) found that variable prey (grass shrimp) density influenced the relationship between kelpfish foraging success and eelgrass structural complexity (shoot density), primarily by increasing the probability that kelpfish would attack prey. It was therefore surprising to find negligible effects of prey density on predator–prey interactions in the present study.

#### 4.2. Epiphytes and structural complexity

Epiphytes are rarely considered when assessing the effects of seagrass structural complexity on predator–prey interactions, yet they may add a substantial amount of structure to the seagrass canopy where many mesopredatory fishes forage. Though the biomass of epiphytic algae may be small in comparison to above-ground seagrass structure (Frankovitch and Fourqurean, 1997; van Montfrans et al., 1984), their effect on foraging via obstruction of predator and prey vision may be substantial, particularly for filamentous algal taxa. This may in part be why natural and artificial seagrass with epiphytic algae are preferred over bare seagrass blades by many epifaunal taxa (e.g., copepods, nematodes, and polychaetes: Hall and Bell, 1988; tanaids, amphipods, midges, and gastropods: Schneider and Mann, 1991; isopods: Boström and Mattila, 1999). Epifauna may be attracted to seagrass blades with epiphytic algae to seek refuge from predation, to use epiphytic algae as a food source, or simply due to an increase in living space, all of which are not mutually exclusive. Copepod abundance increased with the cover of artificial seagrass epiphytes in Florida, suggesting that the positive associations between copepods and epiphyte biomass observed in naturally occurring seagrass in this area are due to an increase in habitat structure, rather than food availability (Hall and Bell, 1988). In contrast, Bologna and Heck (1999) found far higher epifaunal abundance on naturally occurring vs. structurally similar artificial epiphytes in experimental seagrass habitat in St. Joseph Bay, Florida, illustrating the important trophic role of epiphytes for seagrass epifauna.

An interesting result was that the addition of artificial epiphytes to shoots had a similar effect on predator foraging as did increasing shoot density. Admittedly, this result likely depends on the choice of experimental shoot densities and the way in which epiphytes are simulated. Increasing shoot density beyond 400 shoots  $m^{-2}$  may result in a much larger effect of shoot density on predator foraging than epiphytes, due to the strong effect of shoot density on predator maneuverability (Bartholomew et al., 2000) as well as field of vision. Indeed, an upper shoot density of 400 shoots  $m^{-2}$  was designated in part because in

earlier experiments, higher shoot densities resulted in many fish ceasing all movement for the duration of a trial. The artificial epiphytes used in the experiment simulated moderate to heavy epiphytic cover in San Diego Bay (Fig. 1). Epiphytic algal cover takes on a range of values in nature, however, from being nearly absent when mesograzers abundance is high or nutrient levels are low, to prolific growth that can smother eelgrass under eutrophic conditions or in the absence of mesograzers (Frankovitch and Fourqurean, 1997). Future experiments on the refuge value of epiphytes should involve a range of epiphyte cover.

#### 4.3. Conclusion

In conclusion, structural complexity had contrasting effects on different components of mesopredator foraging behavior. Adding epiphytes and adding shoots to low density eelgrass reduced the ability of fish to detect prey, but increased their ability to capture prey, resulting in no net effect of structural complexity on the total number of prey captured by mesopredators. Moreover, the addition of artificial epiphytes to eelgrass shoots had comparable effects on mesopredator foraging as did increasing shoot density to moderate levels. Lastly, prey density did not influence foraging behavior or the total number of prey captured by mesopredators. Though crustacean mesograzers like grass shrimp may have substantial effects on the abundance of epiphytic algae (Duffy et al., 2001; Myers and Heck, 2013; Whalen et al., 2013), epiphytic algae can conversely influence components of predator–prey interactions involving these key mesograzers. More information is needed on the effect of seagrass epiphytes on the abundance and mortality risk of mesograzers.

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#### References

- Anderson, O., 1984. Optimal foraging by largemouth bass in structured environments. *Ecology* 65, 851–861.
- Bartholomew, A., 2012. Space size relative to prey width and total cover in an area both influence the habitat choices of freshwater angelfish *Pterophyllum scalare* in mesocosms. *Mar. Freshw. Behav. Physiol.* 45, 29–43.
- Bartholomew, A., Diaz, R.J., Cicchetti, G., 2000. New dimensionless indices of structural habitat complexity: predicted and actual effects on a predator's foraging success. *Mar. Ecol. Prog. Ser.* 206, 45–58.
- Bologna, P.A.X., Heck Jr., K.L., 1999. Differential predation and growth rates of bay scallops within a seagrass habitat. *J. Exp. Mar. Biol. Ecol.* 239, 299–314.
- Boström, C., Bonsdorff, E., 2000. Zoobenthic community establishment and habitat complexity – the importance of seagrass shoot-density, morphology and physical disturbance for faunal recruitment. *Mar. Ecol. Prog. Ser.* 205, 123–138.
- Boström, C., Mattila, J., 1999. The relative importance of food and shelter for seagrass-associated invertebrates: a latitudinal comparison of habitat choice by isopod grazers. *Oecologia* 120, 162–170.
- Canion, C.R., Heck Jr., K.L., 2009. Effect of habitat complexity on predation success: re-evaluating the current paradigm in seagrass beds. *Mar. Ecol. Prog. Ser.* 393, 37–46.
- Catano, L.B., Rojas, M.C., Malossi, R.J., Peters, J.R., Heithaus, M.R., Fourqurean, J.W., Burkepile, D.E., 2015. Reefscapes of fear: predation risk and reef heterogeneity interact to shape herbivore foraging behavior. *J. Anim. Ecol.* <http://dx.doi.org/10.1111/1365-2656.12440>.
- Dionne, M., Folt, C.L., 1991. An experimental analysis of macrophyte growth forms as fish foraging habitat. *Can. J. Fish. Aquat. Sci.* 48, 123–131.
- Duffy, J.E., MacDonald, K.S., Rhode, J.M., Parker, J.D., 2001. Grazer diversity, functional redundancy, and productivity in seagrass beds: an experimental test. *Ecology* 82, 2417–2434.
- Frankovitch, T.A., Fourqurean, J.W., 1997. Seagrass epiphyte loads along a nutrient availability gradient, Florida Bay, USA. *Mar. Ecol. Prog. Ser.* 159, 37–50.
- Gotceitas, V., Colgan, P., 1989. Predator foraging success and habitat complexity: quantitative test of the threshold hypothesis. *Oecologia* 80, 158–166.
- Hall, M.O., Bell, S.S., 1988. Response of small motile epifauna to complexity of epiphytic algae on seagrass blades. *J. Mar. Res.* 46, 613–630.
- Heck Jr., K.L., Crowder, L.B., 1991. Habitat structure and predator–prey interactions in vegetated aquatic systems. In: Bell, S.S., McCoy, E.D., Mushinsky, H.R. (Eds.), *Habitat Structure: The Physical Arrangement of Objects in Space*. Chapman and Hall, London, pp. 281–299.
- Heck Jr., K.L., Thoman, T.A., 1981. Experiments on predator–prey interactions in vegetated aquatic habitats. *J. Exp. Mar. Biol. Ecol.* 53, 125–134.
- Hemminga, M.A., Duarte, C.M., 2000. *Seagrass Ecology*. Cambridge University Press, Cambridge.
- Horinouchi, M., 2007. Review of the effects of within-patch scale structural complexity on seagrass fishes. *J. Exp. Mar. Biol. Ecol.* 350, 111–129.
- Horinouchi, M., Mizuno, N., Jo, Y., Fujita, M., Sano, M., Suzuki, Y., 2009. Seagrass habitat complexity does not always decrease foraging efficiencies of piscivorous fishes. *Mar. Ecol. Prog. Ser.* 377, 43–49.
- Hovel, K.A., Lipcius, R.N., 2001. Habitat fragmentation in a seagrass landscape: patch size and complexity control blue crab survival. *Ecology* 82, 1814–1829.
- Irandi, E.A., 1997. Seagrass patch size and survivorship of an infaunal bivalve. *Oikos* 78, 511–518.
- James, P.L., Heck Jr., K.L., 1994. The effects of habitat complexity and light intensity on ambush predation within a simulated seagrass habitat. *J. Exp. Mar. Biol. Ecol.* 176, 187–200.
- Johns, P.M., Mann, K.H., 1987. An experimental investigation of juvenile lobster habitat preference and mortality among habitats of varying structural complexity. *J. Exp. Mar. Biol. Ecol.* 109, 275–285.
- Lannin, R., Hovel, K.A., 2011. Variable prey density modifies the effects of seagrass habitat structure on predator–prey interactions. *Mar. Ecol. Prog. Ser.* 442, 59–70.
- Manatunge, J., Asaeda, T., Priyadarshana, T., 2000. The influence of structural complexity on fish-zooplankton interactions: a study using artificial submerged macrophytes. *Environ. Biol. Fish.* 58, 425–438.
- Mattila, J., Heck Jr., K.L., Millstein, E., Miller, E., Gustafsson, C., Williams, S.L., Bryon, D., 2008. Increased habitat structure does not always provide increased refuge from predation. *Mar. Ecol. Prog. Ser.* 361, 15–20.
- McCoy, E.D., Bell, S.S., 1991. Habitat structure: the evolution and diversification of a complex topic. In: Bell, S.S., McCoy, E.D., Mushinsky, H.R. (Eds.), *Habitat Structure: The Physical Arrangement of Objects in Space*. Chapman and Hall, London, pp. 3–27.
- Michel, M.J., Adams, M.M., 2009. Differential effects of structural complexity on predator foraging behavior. *Behav. Ecol.* 20, 313–317.
- Minello, T.J., Zimmerman, R.J., 1983. Fish predation on juvenile brown shrimp, *Penaeus aztecus* Lves: the effect of simulated *Spartina* structure on predation rates. *J. Exp. Mar. Biol. Ecol.* 72, 211–231.
- Moore, E.C., Hovel, K.A., 2010. Relative influence of habitat complexity and proximity to patch edges on seagrass epifaunal communities. *Oikos* 119, 1299–1311.
- Myers, J.A., Heck Jr., K.L., 2013. Amphipod control of epiphyte load and its concomitant effects on shoalgrass *Halodule wrightii* biomass. *Mar. Ecol. Prog. Ser.* 483, 133–142.
- Orth, R.J., Heck Jr., K.L., van Montfrans, J., 1984. Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator–prey relationships. *Estuaries* 7, 339–350.
- Robbins, B.D., Bell, S.S., 1994. Seagrass landscapes: a terrestrial approach to the marine subtidal environment. *Trends Ecol. Evol.* 9, 301–304.
- Ryer, C.H., 1988. Pipefish foraging: effects of fish size, prey size, and altered habitat complexity. *Mar. Ecol. Prog. Ser.* 48, 37–45.
- Ryer, C.H., Stoner, A.W., Titgen, R.H., 2004. Behavioral mechanisms underlying the refuge value of benthic habitat structure for two flatfishes with differing anti-predator strategies. *Mar. Ecol. Prog. Ser.* 268, 231–243.
- Savino, J.F., Stein, R.A., 1982. Predator–prey interaction between largemouth bass and bluegills as influenced by simulated, submersed vegetation. *Trans. Am. Fish. Soc.* 11, 255–266.
- Savino, J.F., Stein, R.A., 1989. Behavioral interactions between fish predators and their prey: effects of plant density. *Anim. Behav.* 37, 311–321.
- Schneider, F.I., Mann, K.H., 1991. Species specific relationships of invertebrates to vegetation in a seagrass bed. II. Experiments on the importance of macrophyte shape, epiphyte cover and predation. *J. Exp. Mar. Biol. Ecol.* 145, 119–139.
- Stoner, A.W., 1982. The influence of benthic macrophytes on the foraging behavior of pinfish, *Lagodon rhomboides* (Linnaeus). *J. Exp. Mar. Biol. Ecol.* 58, 271–284.
- Tait, K.J., Hovel, K.A., 2012. Do predation risk and food availability modify prey and mesopredator microhabitat selection in eelgrass (*Zostera marina*) habitat? *J. Exp. Mar. Biol. Ecol.* 426, 60–67.
- Toscano, B.J., Griffen, B.D., 2013. Predator size interacts with habitat structure to determine the allometric scaling of the functional response. *Oikos* 122, 454–462.
- Underwood, A.J., 1997. *Experiments in Ecology: Their Logical Design and Interpretation Using Analysis of Variance*. Cambridge University Press, Cambridge.
- van Montfrans, J., Wetzel, R.L., Orth, R.J., 1984. Epiphyte-grazer relationships in seagrass meadows: consequences for seagrass growth and production. *Estuaries* 7, 289–309.
- Virnstain, R.W., Curran, M.C., 1986. Colonization of artificial seagrass versus time and distance from source. *Mar. Ecol. Prog. Ser.* 29, 279–288.
- Warfe, D.M., Barmuta, L.A., 2004. Habitat structural complexity mediates the foraging success of multiple predator species. *Oecologia* 141, 171–178.
- Whalen, M.A., Duffy, J.E., Grace, J.B., 2013. Temporal shifts in top-down vs. bottom-up control of epiphytic algae in a seagrass ecosystem. *Ecology* 94, 510–520.
- Williams, S.L., Heck Jr., K.L., 2001. Seagrass communities. In: Bertness, M.D., Gaines, S.D., Hay, M.E. (Eds.), *Marine Community Ecology*. Sinaur Press, Sunderland, MA, pp. 317–337.