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Disentangling fine- and broad- scale effects of habitat on predator–prey interactions

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ABSTRACT

Predator–prey interactions can be influenced by habitat at different spatial scales. In seagrass systems, blade density can provide refugia for prey at fine scales, which are further embedded within broad-scale features such as variation in biotic (e.g., predator assemblages) and abiotic attributes (e.g., turbidity, salinity). Fine-scale effects of seagrass habitats on predator–prey interactions involving invertebrates have been well studied while less is known about their effects on fish as prey. A field experiment was conducted in Tampa Bay, Florida, USA to examine and separate the effects of habitat across fine and broad scales on the relative predation rates of tethered pinfish (*Lagodon rhomboides*). Artificial seagrass units (ASUs) were used at three levels of blade density and deployed in different locations within the seascape. Predation rates on pinfish decreased with increasing seagrass blade density. The effects of blade density were consistent across locations, but overall mortality was higher in the lower Bay, where the water was less turbid, higher in salinity, and characterized by a different suite of predators compared to the mid Bay. Using controlled-laboratory experiments, it was found that pinfish reduced their activity levels in more turbid water as well as in response to the presence of a common predator in both clear and more turbid waters. Thus, predation rates were influenced by the combined effects of refugia (fine scale), variation in prey behavior (broad scale), and detection by predators (both scales). This study demonstrates the strong influence habitat can have at different spatial scales in mediating predator–prey interactions of mobile species in estuarine environments.

1. Introduction

The strength of ecological processes, such as predation, can be contextual upon location, thus requiring a landscape perspective for their study. In the marine environment, seagrass beds are appropriate for using a broad-scale approach because they cover extensive areas of coastal habitats (Robbins and Bell, 1994; Bell et al., 2006), support an abundant and diverse community of fishes and invertebrates (Hemminga and Duarte, 2000; Gillanders, 2006; Stallings et al., 2015), and can have high levels of heterogeneity (Bell et al., 1995; Bowden et al., 2001; Baltestri et al., 2003). Broad-scale studies in seagrass beds have mainly focused on assessing faunal responses to geomorphic and geospatial habitat features such as patchiness, fragmentation, configuration, and proximity to other habitats (Bell and Hicks, 1991; Bell et al., 2001; Healey and Hovel, 2004; Bell et al., 2006; Heck and Orth, 2006; Larkum et al., 2006; Carroll and Peterson, 2013).

Other ecological (e.g., predator communities) and environmental features (e.g., water turbidity) can also vary across the seascape in seagrass beds, with potential effects on predator–prey dynamics. These variations in the seascape often result in discrepancies observed when experiments are repeated at different locations in the field. For example, both survival and recolonization of mussels were contextual upon the spatial scale and location in the rocky intertidal where identically-designed experiments were conducted (Menge et al., 1994). Similarly, Menge (1976) observed several aspects of community structure (such as abundance of predators and species richness) to vary across six areas of intertidal communities in Maine and Massachusetts spanning a wave exposure gradient.

Embedded within these broad-scale features, fine-scale variation in the complexity of seagrass habitats (e.g., blade density) can further influence predator–prey dynamics. Structurally complex habitats can provide physical and visual barriers that can reduce predation risk (Stoner and Lewis, 1985; Wahle and Steneck, 1991; Beukers and Jones, 1998; Pirtle et al., 2012) and this has been a rich area of study in seagrass systems (Irlandi, 1994; Murphey and Fonseca, 1995; Irlandi, 1997; Hovel and Fonseca, 2005). At fine spatial scales the survival of organisms varies with the presence, density, or biomass of seagrass blades (Heck and Crowder, 1991; Orth, 1992; Irlandi, 1994; Rooker et al., 1998; Hovel and Fonseca, 2005). Most of these studies, however, have been conducted in controlled-laboratory settings or have largely focused on invertebrates in the field (Heck and Thoman, 1981; Orth et al., 1984; Main, 1987; Gotceitas, 1990; Heck and Crowder, 1991; Hovel and Lipcius, 2002; Heck et al., 2003).

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Fishes are an important component of seagrass bed communities, both as predators and prey (Heck and Orth, 2006) and thus may also be influenced by complex seagrass habitats. In the laboratory, Gotceitas et al. (1997) observed that the survival of Atlantic Cod (*Gadus morhua*) increased with eelgrass density only after a threshold of seagrass density was reached. Harris et al. (2004) found that refuge from predation for Tautog (*Tautoga onitis*), Cunners (*Tautogolabrus adspersus*), and Silversides (*Brevoortia tyrannus*) can be modeled as an asymptotic function of plant density. Others have found no differences in mortality between vegetated and unvegetated habitat types (Laurel and Brown, 2006; Horinouchi, 2007a). Additionally, macrophyte complexity in littoral zones of lakes has been identified as an important factor in reducing predation and altering behavior in predator–prey interactions among fishes (Savino and Stein, 1982; Gotceitas, 1990). While most of these studies suggest that seagrass complexity may influence the survival of fishes, the results are equivocal. Furthermore, few studies have focused on how blade density may directly affect mortality of fishes in the field (Horinouchi, 2007b; Schultz and Kruschel, 2010), thus requiring further research *in situ* to better understand generalities.

Tampa Bay is a large, shallow embayment with approximately 12,000 ha of seagrass coverage (Greening et al., 2011). Because of its large size, it has a great potential for variation in biotic and abiotic factors over multiple spatial scales. These features present a suitable opportunity to evaluate the integration of broad- and fine- scale effects of seagrass habitats on predator–prey interactions. This study examined the broad-scale effects of location and fine-scale effects of seagrass complexity (via blade density) on predation rates of a common marine fish. Specifically, a field experiment was used to examine 1) the broad-scale effects of distinct locations of the Bay and 2) the fine-scale effects of seagrass blade density (high, medium, and none) on the relative mortality rates on pinfish (*Lagodon rhomboides*; Family Sparidae). A laboratory experiment was also used to examine how the behavior of pinfish varied with exposure to different biotic and abiotic features. By manipulating fine-scale complexity of seagrass habitats deployed in locations embedded in broad-scale seascapes, it was sought to provide insight on how ecological processes can be affected by habitat over multiple spatial scales.

2. Materials and methods

2.1. Study organism

The pinfish inhabits coastal waters from the Yucatan Peninsula of Mexico eastward through the Gulf of Mexico and up to Massachusetts, USA (Hoese and Moore, 1977; Darcy, 1985; Nelson, 2002; Harter and Heck, 2006). Pinfish are an ecologically important species for several reasons. First, they are commonly the most abundant vertebrate found in seagrass beds (Nelson et al., 2013; Stallings et al., 2015). Second, juveniles feed on a suite of invertebrates influencing entire assemblages of benthic macrofauna (Young et al., 1976; Young and Young, 1977; Nelson, 1978; Stoner, 1980; Nelson, 2002). Third, pinfish are an important link between primary and secondary production due to their consumption of plant matter (Stoner, 1982; Weinstein et al., 1982; Nelson, 2002). Because all life stages are preyed upon by other fishes (Kjelson and Johnson, 1976; Seaman and Collins, 1983; Nelson, 2002; Stallings, 2010; Stallings et al., 2010; Hall-Scharf and Stallings, 2014; Hall-Scharf et al., 2016) they also serve as an important linkage to offshore food webs (Nelson et al., 2013).

In Florida, adult pinfish spawn in offshore waters from late fall to early winter and have peak larval settlement in February and March (Tabb and Manning, 1961; Chacin, 2014). Post-larval pinfish settle in a variety of habitats including shallow and vegetated flats where juveniles remain most of their first year. These vegetated flats (mostly composed of seagrass beds) are nearshore habitats often located in estuarine environments, where biotic and abiotic factors can be highly variable.

2.2. Study region

This study was conducted in Tampa Bay, Florida, USA (Fig. 1), during the months of July through September 2013. Tampa Bay is a large, open-water estuary with a surface area of ~1000 km^2 and mean water depth of ~4.0 m (Chen et al., 2007). Two locations of the Bay were selected for this study, the middle-west and south-west, which we hereafter refer to as "mid Bay" and "lower Bay," respectively. These two locations were chosen because they have the highest densities of pinfish observed in the Bay (Chacin, 2014). Tethering experiments were deployed at each location.

2.3. Field experiment — study design

An orthogonally designed field experiment was used to test whether pinfish experienced different predation rates under different habitat complexities (via three blade density levels) cross-factored with different locations of the Bay. Artificial seagrass units (ASUs) were used to control for the density of seagrass blades, which were constructed on plastic mesh (0.5 m × 0.5 m squares) with 1500 shoots m^2 (high), 600 shoots m^2 (medium), and 0 shoots m^2 (none); these values were meant to simulate *Thalassia testudinum* densities found in Tampa Bay (Meyer and Bell, 2010). Each shoot was composed of two 30 cm long blades made with 1 cm wide green polypropylene ribbon tied to the plastic mesh. Pinfish (size range standard length (SL): 50–80 mm) were tethered using a 0.25 m microfilament braided line (18.1 kg test) connected to a 2 m long microfilament braided line attached to the center of the ASUs (Fig. 2). A small plastic float was attached on the other end of the 2 m braided line to keep it vertical in the water column. Although the sizes of the ASUs were small, they allowed for replication and experimental control to determine mechanism, and were large enough to allow the pinfish space to swim both horizontally and vertically in a 0.39 m^3 cylinder. Pinfish used for the study were collected using seine and cast nets, and immediately tethered after capture. All fishes other than the study species were released instantly upon capture.

The deployment of the ASUs required three steps. First, the plot was fixed to the substrate with metal stakes (one in each corner) on the edge of the natural and continuous seagrass bed. By retaining a constant edge position, rather than confounding with interior habitat locations, it was assumed that if edge effects occurred, they were consistent across trials. Second, the tether line was secured to a pinfish by inserting it through the mouth and out the opercular opening to form a loose loop forward of its snout. The entire process was fairly rapid (~10–15 s) and the tethered pinfish was quickly returned to the water without the need for recovery from anesthesia, which could have artificially inflated mortality. This same approach was previously used to tether pinfish in Biscayne Bay, Florida, USA (Hammerschlag et al., 2010) and is advantageous over more invasive methods (e.g., running tether through soma) as it minimizes tissue damage and the release of body fluids, which could increase detection by predators. Last, the tether was secured to the centerline using a loose loop, allowing pinfish to move in a vertical cylinder with a radius of 0.25 m (Fig. 2) but preventing it from accessing adjacent habitats. If bending of the line occurred despite the preventions used, it was assumed it occurred equally across all treatments.

During each tethering event, fifteen plots were deployed with five replicates for each blade density (high, medium, none) randomly arranged at the seagrass edges to avoid potential confounding effects of predation differences between edge and interior locations (Peterson et al., 2001). Deployments were always positioned at the shoreward edge to avoid potential predation differences due to variation in fish abundances known to occur at shoreward versus seaward edges (Smith et al., 2008) and were conducted at both locations throughout the experimental months.

Although tethering studies cannot produce estimates of *absolute* mortality rates, given the potential artifacts of the approach, they are

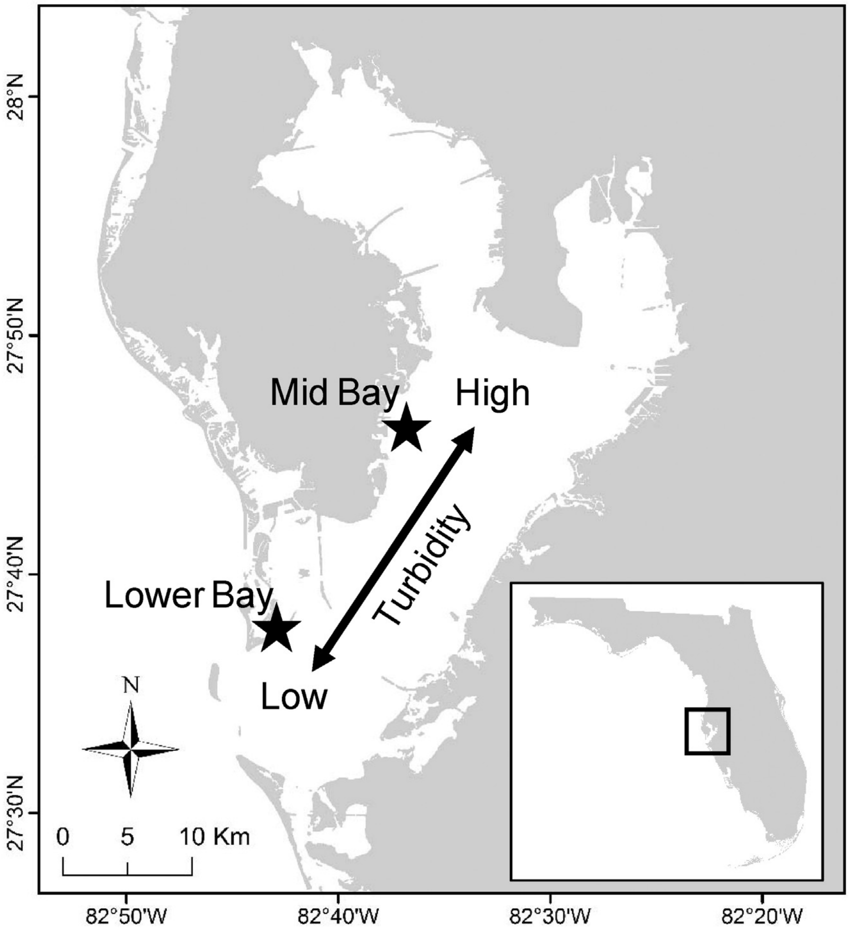

Fig. 1. Map of Tampa Bay, Florida, USA, showing the general turbidity gradient and the study locations (stars).

powerful tools for comparing relative mortality among experimental treatments. Pilot deployments were video recorded and analyzed for potential alterations of pinfish behavior caused by tethering and artificial seagrass units. Pinfish swimming behavior was not altered; they readily swam both horizontally and vertically through the water column. It was concluded that although the distance pinfish could swim was restricted, the tether did not hamper their hiding and swimming behaviors. No losses from pinfish breaking free from the tether during the pilot deployments (five per seagrass blade density level) were observed, nor were there any entanglements during either the pilot trials or when tethers were retrieved. Therefore, it was assumed that any losses in tethered fish were due to predation events.

A series of pilot deployments were conducted to determine optimal experimental time. It was found that 10-h deployments were sufficiently long given the observed mortality rates while also short enough to avoid potential confounding effects of increased predation during crepuscular periods. Deployments began two hours after sunrise and ended two hours before sunset (0800-1800). Deployments were replicated a minimum of 15 times for each ASU density $*$ location combination, with one tethered fish per individual deployment. The absence of the pinfish or the presence of an injured fish at the conclusion of the deployment was counted as a predation event.

2.4. Field experiment — data analysis

Differences in mortality rates were compared separately across 1) seagrass density (three levels) and 2) location (two levels) using non-parametric analysis of variance (npANOVA). The non-parametric ANOVAs were permutation-based and distribution-free, due to data not meeting assumptions of normality and to avoid concerns about zero inflations; this method is equivalent to a univariate PERMANOVA. Pair-wise comparisons were included for the tests involving seagrass densities. For all analyses, a dissimilarity matrix was produced for the response variable (mortality) based on Euclidean distance using Fathom toolbox for Matlab (Jones, 2014). A two-way npANOVA was conducted to test for the interactions between seagrass density with location on mortality. A one-way ANOVA was used (in addition to the two-way) to perform the pairwise comparisons among seagrass densities and also because one of the factors is kept constant when a two-way ANOVA is performed, yielding inaccurate *F*-statistics. The level of significance for all tests was based on an alpha value of 0.05.

2.5. Exploration of other abiotic and biotic variables

Because differences in pinfish mortality were observed between study locations (see Results), potential correlated biotic and abiotic variables that could have contributed to the results were explored. Seagrass habitats were chosen at both study locations that were dominated by *T. testudinum*, with lower and similar compositions of *Syringodium filiforme* and *Halodule wrightii.* Canopy heights of the beds were 25–35 cm. Both locations contained continuous seagrass cover, with a bed area ~ 600 m^2 and had an average depth of 1.9 m. Locations also had similar adjacent land habitat (thin sand/vegetation mix set in an urban area). Other variables, however, that could have influenced the results of the experiments, such as turbidity, temperature, salinity, and predatory assemblage were explored.

The experiments were restricted to the summer season in Tampa Bay, when a turbidity gradient is the strongest with higher values in the upper and mid Bay and lower values in the lower Bay. It was assumed that since juvenile pinfish remain in the same relative area

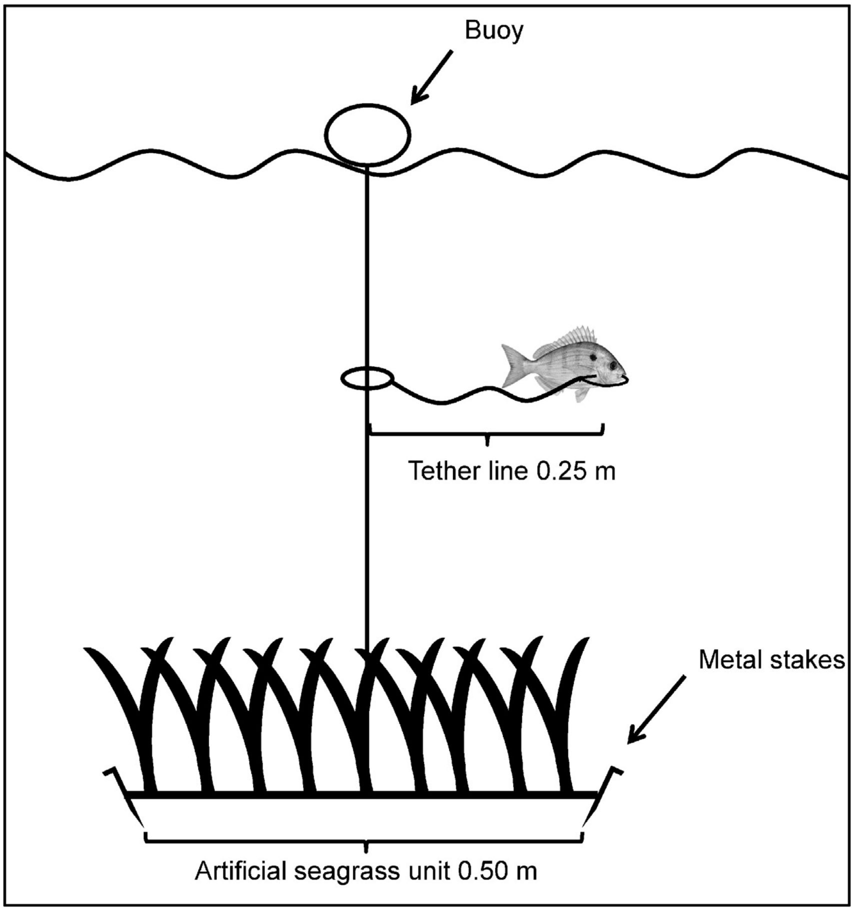

Fig. 2. Diagram of the tethering setup on an Artificial Seagrass Unit. The diagram shows a tethered pinfish on a high density ASU. Pinfish illustration was kindly provided with permission by Diane R. Peebles.

prior to egress, they experienced consistently different turbidities depending on which general location of the Bay they occupied. Turbidity levels during the study were quantified with data provided by the Environmental Protection Commission of Hillsborough County's (EPCHC) Tampa Bay water quality monitoring program. Water samples were collected at mid depth of a station if it was over 3 m in depth, otherwise surface water samples were collected. Turbidity of water samples was measured with Hach® Model 2100N Turbidimeter. Turbidity values were then averaged over the summer months (corresponding to the months when experiments were conducted) and were compared using paired *t*-tests to determine if turbidity varied between study locations.

The remaining variables explored were obtained from Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute (FWRI). The state agency's Fishery Independent Monitoring Program (FIM) conducts sampling trips each month throughout Tampa Bay (and other locations in Florida) and thus can provide the most extensive database for determining spatial dynamics in the assemblages of pinfish predators as well as environmental variables at their sampling locations (e.g., temperature, salinity). The FIM data were collected with a 6.1 m otter trawl, towed over an area of 4120 m^2. All data used for the analyses were collected at the same locations and time period of the tethering experiment. Since predation is one of the primary drivers of juvenile fish mortality, it was explored whether there were differences in the predatory assemblages that could have influenced the patterns observed between the study locations. Although there was no direct way to determine which species consumed the tethered pinfish, all fishes with reported evidence of piscivory that were ≥180 mm (SL) as a conservative size due to gape limitation were included. These characteristics narrowed the analysis to include predators that most likely consume pinfish. Since the predator data were zero-inflated and did not meet assumptions of normality, a permutation-based two-tailed *t*-test was conducted to determine whether species richness and density of predators differed between study locations. Additionally, predator assemblage composition was compared between the study locations using a permutation-based MANOVA followed by a Canonical Analysis of Principal Coordinates (CAP) to create a bi-plot and correlation vector plot to visualize which species, if any, were driving the observed differences. Salinity and temperature values were averaged over the summer months (similarly to turbidity) and compared with paired *t*-tests.

2.6. Laboratory experiment — study organisms

Previous studies on fishes have suggested that turbidity levels below 10 NTUs may not influence behaviors and interactions (Meager and Batty, 2007; Meager et al., 2006; De Robertis et al., 2003). It is possible that turbidity effects on behavior could be species dependent. Although turbidity was <5 NTU during the study, it was statistically different between regions of the Bay (see Results), and the potential effects it may have had on anti-predatory behaviors of the visually-oriented pinfish were intriguing. Therefore, in addition to the field experiment, two laboratory experiments were conducted to examine the behavior of pinfish 1) under two turbidity levels (low and high) and 2) in response to visual cues from a common predator under different levels of turbidity.

The predatory species used was Spotted Seatrout (*Cynoscion nebulosus*). Spotted Seatrout is an inshore fish found in coastal waters from the Yucatan Peninsula of Mexico to the Chesapeake Bay, USA. They inhabit the same vegetated areas as pinfish (e.g., seagrass beds) and a substantial portion of their diets include pinfish (FWRI-FIM, unpublished data; Hall-Scharf and Stallings, 2014; Hall-Scharf et al., 2016).

Pinfish and Spotted Seatrout were collected using seine nets. They were placed in 40-l holding tanks containing aerated seawater and were transported to the aquarium laboratory at the University of South Florida, College of Marine Science. Once in the lab, pinfish were held in 621-l tanks and Spotted Seatrout in 1200-l tanks until the time of the experimental trials. Each tank was supplied with flow-through water from Tampa Bay, with aerators to maintain constant oxygenation (DO ≥ 6.5 mg/l) and heaters to ensure a constant temperature (26.7–28.3 °C).

2.7. Laboratory experiment — study design

Turbidity treatments were prepared by mixing artificial seawater (ASW; from Instant Ocean ® Sea Salt product) with Kaolin powder clay in trial tanks. Two turbidity levels were produced: low (0 g Kaolin per liter) and high (0.13 g Kaolin per liter). The turbidity measurements were not represented in Nephelometric Turbidity Units (NTU) since Kaolin is formed by particles of similar size and reflectivity and therefore would differ from the field where the presence of varying suspended particles will influence the NTUs. It is recognized that this is a limitation in the study and caution must be exerted when comparing to field settings. Nevertheless, valuable insights could be gained from further examination of mechanisms in such relative conditions. Thus, the low turbidity level was meant to simulate areas where water turbidity is the lowest in Tampa Bay (e.g., lower Bay) while the high level was meant to simulate areas such the upper and mid regions of the Bay. After the turbidity preparation, individual pinfish (size range SL: 56–90 mm) were moved into the trial tanks for a 1-h acclimation period. Lightning conditions were kept constant before, during, and among experimental trials.

Behavioral observations were conducted in rectangular, 38-l tanks filled with 19 l ASW to a water depth of 20 cm. A 15 cm × 9 cm plot of artificial seagrass was submerged in the center of the tank (Fig. 3A). The plot was used to provide a small shelter for the pinfish to associate, whether hiding inside or adjacent to it, as are common anti-predatory behaviors. While the sizes of the tank and seagrass plots were small, pinfish behavior did not appear to be affected. The fish were observed swimming while foraging around the tank or using the plot as shelter by hiding in it. Sixteen food pellets were evenly scattered across the bottom of the tank to encourage foraging. An air diffuser was placed at the corner of the tank to maintain constant oxygenation. A grid with dimensions 5 cm × 5 cm was placed under the trial tanks to provide a framework for measuring activity level, recorded as the number of times the experimental pinfish crossed a line of the grid per minute (Fig. 3B). Trials were recorded with a downward-looking video camera to reduce observer effects on fish behavior.

In the first laboratory experiment, 70 10-min trials were conducted to measure pinfish behavior between the low ($n = 35$) and high ($n = 35$) turbidity levels in the absence of any visual cues. In the second laboratory experiment, turbidity (low vs. high) and visual cues from a predator were crossed. As controls for the predator treatment, a non-predatory conspecific (a large pinfish) and an empty tank filled with ASW-only (i.e., no fish) were used. The order of the trials was randomized and trials were conducted during the day between 1200 and 1600. Preparation of visual cues consisted of placing the Spotted Seatrout (size range SL: 230–310 mm), the large pinfish (SL: 140–150 mm), or ASW-only into a separate tank (with the same dimensions of the trial tank) adjacent to the trial tank prior the start of the experiment (Fig. 3B). The visual cue tank was filled with ASW with no Kaolin powder present. A black barrier was placed between the trial and visual cue tanks (Fig. 3B). After a 10-min observational period, the barrier was removed exposing the experimental pinfish to the visual cue tank. The movements of the large pinfish and Spotted Seatrout used as visual cues were restricted with a mesh barrier placed to guarantee they remained near the experimental tank; this was done to ensure that the experimental pinfish had full view of the visual cue in the adjacent tank. Observations of activity levels were recorded for 10 additional minutes after the barrier was removed. Thirty-six 20-min trials were completed (6 replicates for each turbidity ∗ visual cue combination).

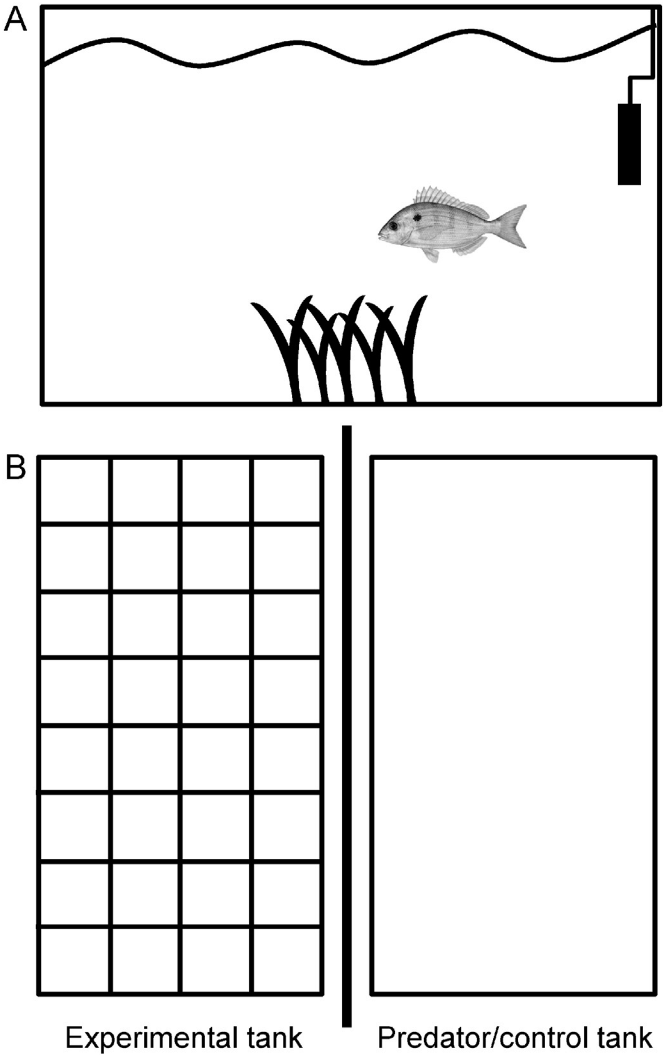

Fig. 3. Laboratory experimental setup from both a side view (A) and a top view (B). Note the grid shown in (B), used to quantify behavior of pinfish. The dark line between the experimental tank containing the pinfish and the predator/control tank represents the visual barrier, which was removed after the 10-min pre-stimulus period. Pinfish illustration was kindly provided with permission by Diane R. Peebles.

2.8. Laboratory experiment — data analysis

For the controlled laboratory experiments, the number of lines crossed per minute measured between turbidity levels (experiment 1) was compared using a two-sample *t*-test. Additionally, line crosses per minute before and after the visual stimuli (experiment 2) were compared using a paired *t*-test. Data were log transformed to meet the assumption of homoscedasticity and the level of significance for all tests was based on an alpha value of 0.05.

3. Results

In total, 136 tethering deployments were conducted across the mid and lower regions of the Bay (Table 1). There was a significant effect of seagrass density on relative mortality rates of pinfish ($F_{2,\ 26} = 4.41$, $p = 0.021$). The posteriori, permutation-based, pair-wise comparisons indicated that the relative mortality rates in seagrass plots with zero and medium densities of blades were not statistically different from

Table 1
Number of pinfish preyed upon over tethering deployments conducted at each study location and by seagrass density treatment.

Study location	Seagrass density		
	Low	Medium	High
Mid Bay	3/22	2/20	0/22
Lower Bay	20/23	14/25	5/24

Table 2
Non-parametric one-way and two-way analysis of variance tests for main effects and interactions between seagrass density with location effects on relative mortality rates of pinfish. Values in bold indicate significant differences.

Source	df	SS	MS	*F*	p
Location	1	1.448	1.448	18.746	**0.0002**
Residual	27	2.085	0.077		
Total	28	3.533			
Seagrass density	2	0.895	0.447	11.284	**0.0006**
Location	1	1.448	1.448	36.513	**0.0002**
Seagrass density × location	2	0.278	0.139	3.511	0.0546
Residual	23	0.912	0.040		
Total	28	3.533			

each other ($t = 0.96$, $p = 0.340$). Relative mortality rates in seagrass plots with high blade density were lower than those with both zero ($t = 2.99$, $p = 0.009$) and medium blade densities ($t = 2.17$, $p = 0.042$, Fig. 4).

Relative mortality was higher for deployments made in the lower Bay ($F_{1,\,27} = 18.75$, $p < 0.001$). Although not significant at the alpha 0.05 level, there was marginal support of an interaction between seagrass density and location ($F_{2,\,23} = 0.69$, $p = 0.055$, Table 2, Fig. 4), suggesting that habitat structure may have been less critical under higher turbidity conditions.

During the summer months, Tampa Bay experienced a turbidity gradient with higher levels in the upper and mid regions of the Bay (3.74 ± 0.19 Nephelometric Turbidity Units; NTU ± SE) compared to the lower Bay (2.17 ± 0.15 NTU, 2000–2009, $t_{29} = 8.18$, $p = 0.03$). Temperature was similar between locations (mid Bay = 29.6 ± 0.20 °C and lower Bay = 30.2 ± 0.16 °C, $t_{36} = 2.76$, $p = 0.109$) and salinity was higher in the lower Bay (32.5 ± 2.17 ppt) than the mid Bay (26.1 ± 0.70 ppt, $t_{36} = 14.2$, $p = 0.001$).

There were no differences in either the abundance ($t_{40} = 0.77$, $p = 0.258$, Fig. 5A) or species richness of predators ($t_{40} = 0.86$, $p = 0.226$ Fig. 5B) between mid and lower locations of the Bay from FWRI—FIM data collected during the field experiment. The assemblage composition, however, varied between the two locations ($F_{1,\,40} = 4.00$, $p = 0.001$, Fig. 6) with Common Snook (*Centropomus undecimalis*) and Red Drum (*Sciaenops ocellatus*) driving the patterns in the mid Bay while Gulf Flounder (*Paralichthys albigutta*) and Inshore Lizardfish (*Synodus foetens*) did so in the lower Bay.

In the behavioral study, pinfish were typically observed swimming and foraging around the tank, which it was interpreted as an indication of normal behavior in the absence of anti-predatory responses; this occurred mainly in the low turbidity treatments. Pinfish tended to associate more closely with the ASU (either inside or directly adjacent) in the high turbidity trials, and reduced their activity levels compared to low turbidity trials ($t_{68} = 2.67$, $p = 0.010$, Fig. 7A). Pinfish also reduced their activity after the predator visual cue was presented in both turbidity levels (low $t_5 = 2.64$, $p = 0.046$ and high $t_5 = 2.81$, $p = 0.038$, Fig. 7B), but not in the conspecific control (low $t_5 = 1.58$, $p = 0.175$ and high $t_5 = 1.27$, $p = 0.260$), or ASW-only trials lacking fish (low $t_5 = 0.26$, $p = 0.808$ and high $t_5 = 0.38$, $p = 0.721$).

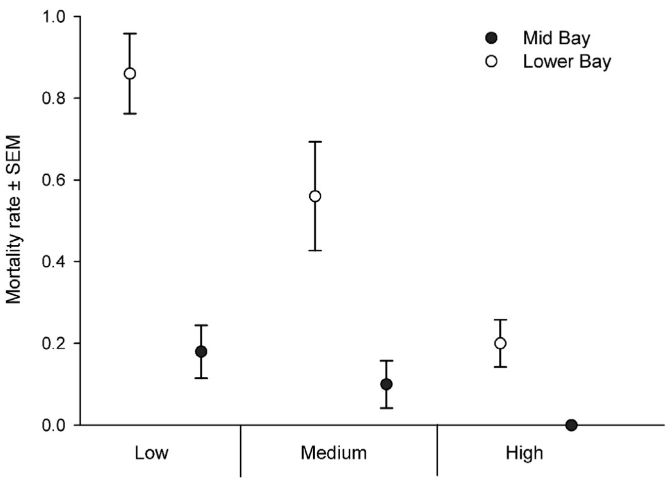

Fig. 4. Mean ± standard error of relative predation rates of pinfish across the three blade densities of seagrass and two study locations.

4. Discussion

Using an experimental approach in the field, it was observed that predation rates differed strongly among treatment levels at two habitat scales. The effects of habitat at the fine scale (blade density) on mortality were consistent between locations in Tampa Bay but overall mortality differed at broader scales (between locations). The locations where deployments were conducted were similar in many habitat-related aspects but also had broad-scale differences in turbidity, salinity, and predator assemblage that could have influenced the observed results.

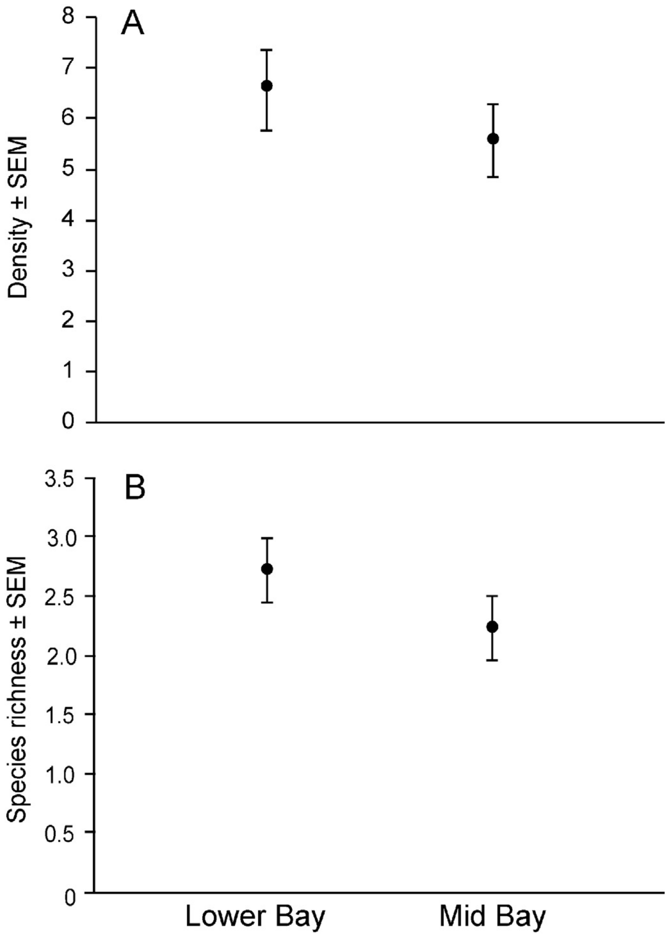

Fig. 5. Mean ± standard error density (A) and richness (B) of pinfish predators per sample trawl tow (per hectare) in the two sections of the Bay where tethering experiments were conducted.

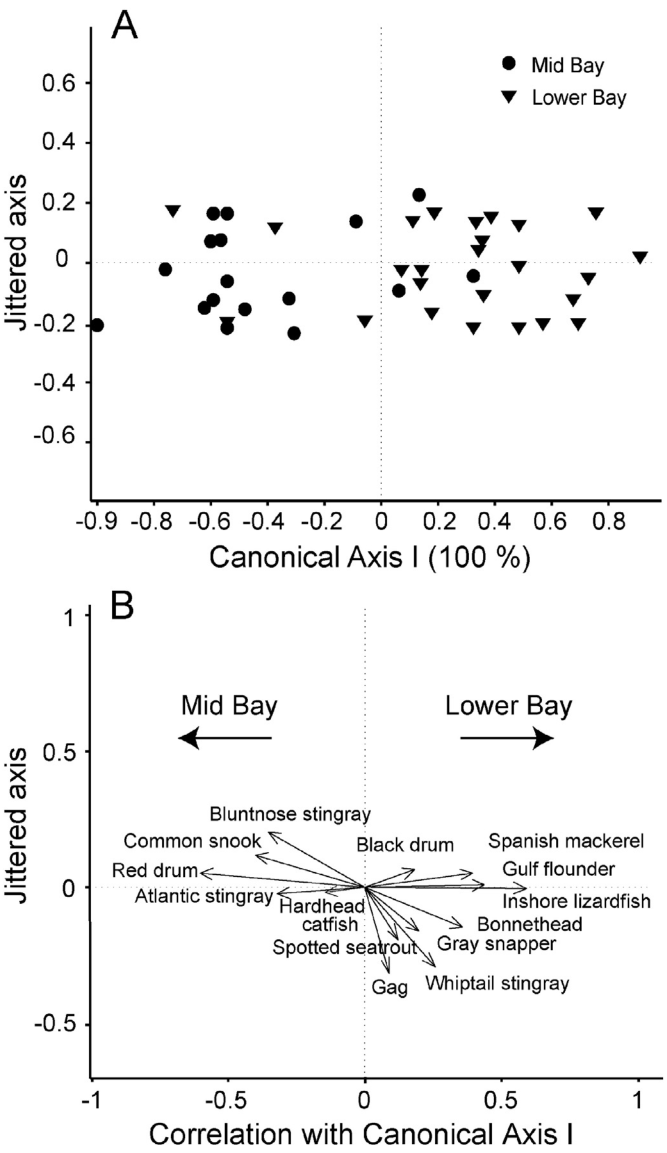

Fig. 6. CAP plot of pinfish predator assemblage structure (A). Circles represent data points in the mid Bay and upside down triangles the lower Bay. The Y-axis data are jittered to ease visual assessment of the patterns. Species vectors pointing to the right were the drivers in the lower Bay while those pointing to the left were drivers in the mid Bay (B).

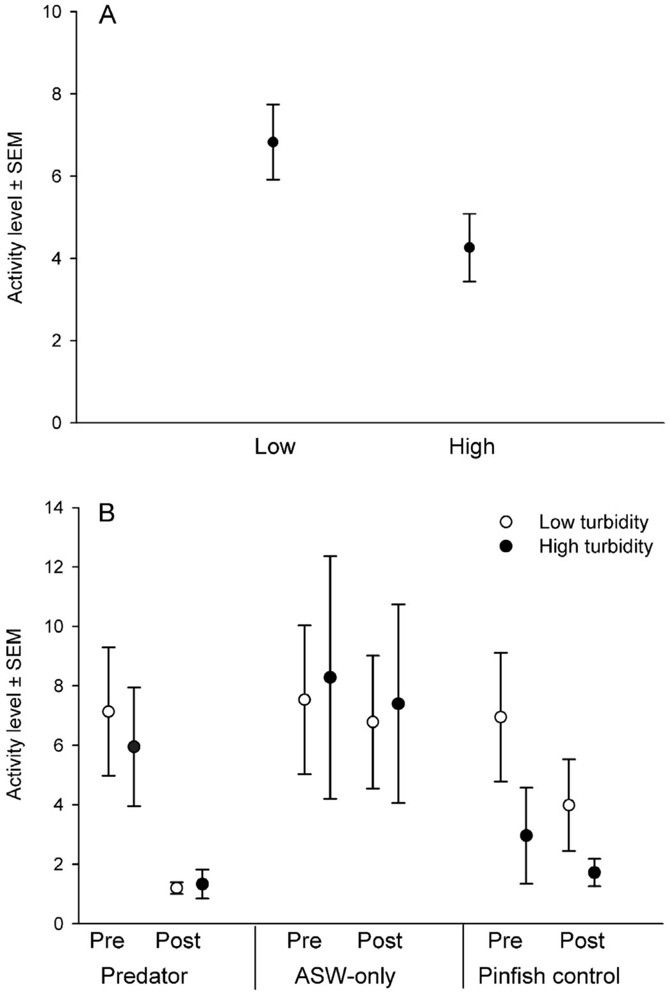

Fig. 7. Activity of pinfish in two turbidity levels (A) and in response to a cross-factored turbidity ∗ predator cue experiment (B).

Additionally, through controlled-laboratory experiments it was observed that pinfish activity levels decreased as water turbidity increased as well as when they detected the presence of a common predator. Therefore, predation rates were likely influenced by the combined effects of refugia (fine scale), variation in prey behavior (broad scale), and detection and feeding of predators with different predatory tactics (both scales).

At the fine scale of seagrass habitats that were used in this study, relative predation rates of pinfish were lowest on ASU plots with a high density of seagrass blades, consistent with previous studies using invertebrate macrofauna as prey and fishes as predators (Nelson, 1978; Heck and Thoman, 1981; Crowder and Cooper, 1982; Stoner, 1982; Orth et al., 1984; Heck and Crowder, 1991; Hovel and Lipcius, 2002; Heck et al., 2003). Thus, increased density of seagrass blades appeared to have provided pinfish with protection from their predators likely due to the dense structure inhibiting efficient foraging as it has been observed in other studies (e.g., Crowder and Cooper, 1982). This study is among the few (e.g., Horinouchi, 2007a; Schultz and Kruschel, 2010) that have examined the effects of seagrass blade density on relative mortality rates of mobile fish prey in situ. Interestingly, predation rates were equally high in low (no blades) and medium complexity habitats, suggesting that the presence alone of seagrass blades was not enough to provide protection. These results corroborate laboratory studies that involved fish as prey. In their examination of foraging efficiency of 3-year old Atlantic Cod (*G. morhua*) on age-0 cod, Gotceitas et al. (1997) found that there was no difference in mortality among the lower densities of seagrass patches, but did find a significant reduction in mortality in high density patches. Harris et al. (2004) found that the mortality of three prey fishes in *Zostera marina* declined at a low-blade density but did not continue to decrease with increased densities of the seagrass. Since the field experiment in this study was only composed of three levels of blade density, it is difficult to conclude whether a complexity threshold existed. Additional levels of blade density would be required to determine the functional response, as has been reported in other studies (Gotceitas, 1990; Nelson and Bonsdorff, 1990; Harris et al., 2004). In contrast, others have found mortality to either decrease in a linear manner or have no relationship with increased seagrass complexity (e.g., Harris et al., 2004; Horinouchi, 2007b). Notably, studies that have shown predation to decrease with an increase in plant density have observed this relationship primarily with predators that use chase-and-attack foraging tactics in the laboratory (Horinouchi, 2007a, Horinouchi et al., 2009). Conversely, the experiment in this study was conducted in the field, thereby exposing experimental pinfish to the natural suite of predators that would normally prey upon them.

Pinfish mortality was higher in the lower Bay compared to the mid Bay. These results were not surprising since Tampa Bay experiences environmental and biological differences from the innermost to outermost locations of the Bay. The turbidity gradient observed at broader scales in the Tampa Bay seascape may have been one responsible factor. It is known that turbidity in Tampa Bay is influenced by a combination of organic matter, phytoplankton, and suspended solids resulting mainly from wind-driven bottom resuspension and riverine input (Johansson, 1991; Janicki and Wade, 1996; Chen et al., 2007). This is especially true in the mid and innermost regions of the Bay during the summer, which is highly influenced by river discharges. Turbidity resulting from dissolved organic matter, suspended solids, and plankton can absorb and scatter light and hence decrease the visual capacities of fishes (Gregory and Northcote, 1993; Gregory, 1993; Abrahams and Kattenfeld, 1997; Vogel and Beauchamp, 1999; Meager et al., 2006). Turbidity has been shown to influence predator–prey interactions by altering foraging efficiency, anti-predator responses, habitat preference, prey searching activity, and consumption (Boehlert and Morgan, 1985; Miner and Stein, 1993, 1996; Gregory and Levings, 1998; De Robertis et al., 2003, Meager et al., 2006; Meager and Utne-Palm, 2007). Although differences in the suspended particles used to manipulate turbidity in the simulated conditions in the laboratory prevented a direct quantitative comparison to turbidity levels in the field, the relative water turbidities had interesting effects on pinfish behaviors. In the lab, pinfish behavior did not seem affected by the small dimensions of the tank. They were observed swimming and foraging when no turbidity was present in the water. Pinfish reduced their activity levels (swimming), stopped foraging, and became more closely associated with the ASUs when the water was more turbid. It is possible that pinfish employed these anti-predatory behaviors in both laboratory and field settings to compensate for the reduction of vision used to detect the threat of predators in more turbid waters. In addition, increased turbidity has been shown to interfere with the foraging of predators by making it more difficult for them to locate prey (Meager and Batty, 2007). By reducing their activity levels and remaining closer to the seagrass refugia, pinfish might have been less visible to predators, hence decreasing the risk of capture and consumption and lowering the predation rates observed in the mid Bay compared to the lower Bay. Pinfish have been shown to change their selection of habitat and behavior based on the presence of predators (Jordan et al., 1996), which can result in the use of suboptimal foraging habitats and slower growth (Harter and Heck, 2006). This can serve as further support that alteration of pinfish behavior is possible and could have influenced the observed predation differences between locations. Compared to other studies where turbidity acts as an ecological constraint on predator recognition and hampers anti-predatory responses (Ferrari et al., 2010; Becker and Gabor, 2012), pinfish in the laboratory experiments in this study were able to detect predators even at higher turbidity levels, suggesting they may have a visual advantage over some predators as turbidity increases. This speculation may be further supported by the observation that pinfish can exist at incredibly high densities, including a wide range of individual sizes, across variable levels of turbidity (Chacin, 2014; Stallings et al., 2015) and are visual feeders (Luczkovich, 1988).

Furthermore, marginal support for the presence of an interaction between seagrass complexity and location was found. This could indicate that differences in mortality between sites were stronger when habitat structure was absent compared to when it was more complex. Assuming that the mortality patterns were due to the difference in turbidity between locations, then habitat structure may have been less important for fish predation risk in high turbidity versus low turbidity conditions. To fully clarify this relationship, however, further experiments involving several levels of turbidity and habitat structure must be conducted.

The locations where experiments were conducted also differed in distance to the mouth of the Bay, which is likely responsible for the variation observed in salinity which in turn might have influenced the structure of the predator assemblages. The predator assemblage composition could have been another factor that influenced mortality rates between locations. While the abundance and species richness of predators was similar between the lower and mid Bay, assemblage structure differed between locations. Thus, species identity may have been an important factor contributing to differences in mortality (e.g., Stallings, 2009) potentially due to differences in foraging mode (Huey and Pianka, 1981). Gulf flounder (*P. albigutta*) and Inshore Lizardfish (*S. foetens*) drove the patterns in the lower Bay. These fishes are voracious, lie-and-wait predators and it is possible that less turbid conditions benefited their type of foraging and behavior. For example, in water where visibility is higher, predators that are mainly stationary on the bottom (and thus non-conspicuous) may have a foraging advantage over conspicuous species. Additionally, fishes in lower turbidity waters have longer reactive distances and thus larger search volumes and higher prey encounter rates (Bret and Groot, 1963; Vinyard and O'Brien, 1976; Gerkin, 1994; Benfield and Minello, 1996). Hence, it is likely that predators at the less turbid location, the lower Bay, were able to locate pinfish more efficiently compared to the mid Bay where the water was more turbid. In the mid Bay, Red Drum (*Sciaenops ocellatus*) and Common Snook (*Centropomus undecimalis*) were key piscivores driving the assemblage patterns. These species are more active and ambush their prey; this feeding strategy could have been beneficial in water where visibility was lower. By being more active, predators can increase their encounter rates with prey. It is probable that the increased scattering of light due to higher turbidity in the mid Bay may have reduced their reactive distance and encounter rates yielding the lower predation rates of pinfish that were observed.

Other studies have reported similar results in that ecological responses (e.g., survival, recruitment) from identically designed, replicated, and controlled field experiments have yielded different outcomes when conducted at multiple sites along environmental gradients (Menge, 1976; Menge and Sutherland, 1987). The existence of such experiments (also termed "comparative experimental approach") allows scientists to understand the importance and generality of factors varying along environmental gradients in the seascape (Dayton, 1975; Menge, 1976; Lubchenco and Menge, 1978; Menge et al., 1994). This study suggests that moderately turbid seagrass environments can have important refuge value for an ecologically important species. Although eutrophication can be a major cause of seagrass loss (Burkholder et al., 2007), moderate nutrient input (usually correlated with higher turbidity) can stimulate epiphytic algal growth, which can support increased secondary productivity. Embracing the nursery function (e.g., Beck et al., 2001; Dahlgren et al., 2006), it is possible that more turbid seagrass habitats (to some extent) could contribute a considerable number of recruits to the adult population, via reduced mortality rates (as observed in this study). It is not being implied that low turbidity seagrass habitats are less essential, but it is an attempt to emphasize the importance of accounting for more turbid habitats that may be considered less "aesthetically" appealing by human observers.

In this study it was determined that both fine-scale effects of seagrass blade density and broad-scale effects of locations varying in turbidity and predator assemblage can influence relative predation rates on pinfish. This study may serve as a baseline for continuing investigations on how these and other effects of habitat may mediate predator–prey interactions across spatial scales. Extensive declines in the presence and abundance of seagrass habitats have occurred worldwide in recent years, often with associated changes in blade densities, turbidity levels, and fish assemblages (Blaber and Blaber, 1980; Cyrus and Blaber, 1987; Breitburg, 1988; Shepherd et al., 1989; Hauxwell et al., 2003; Orth et al., 2006; Horinouchi, 2007b; Horinouchi et al., 2009; Waycott et al., 2009). In response to the continuing and accelerating changes to coastal marine ecosystems, often as a consequence of anthropogenic activities (Jackson et al., 2001), different species will experience positive, negative, and null effects. Thus, there is a need to better understand generalities to allow for a more predictive framework that can be used to inform conservation and management efforts.

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