



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.

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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 (*Tautoglabrus 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 km² 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 m² (high), 600 shoots m² (medium), and 0 shoots m² (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 m³ 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 center-line 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

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