



## Risk of predation affects habitat selection by the pinfish *Lagodon rhomboides* (Linnaeus)

Frank Jordan<sup>a,b,\*</sup>, Mark Bartolini<sup>b,c</sup>, Christine Nelson<sup>b</sup>, Paula E. Patterson<sup>b,c</sup>,  
Heather L. Soulen<sup>b</sup>

<sup>a</sup>Department of Zoology and Florida Cooperative Fish and Wildlife Research Unit, National Biological Service, 117 Newins-Ziegler Hall, University of Florida, Gainesville, FL 32611, USA

<sup>b</sup>Department of Biology and Marine Science, Jacksonville University, 2800 University Boulevard North, Jacksonville, FL 32211, USA

<sup>c</sup>Department of Fisheries and Aquatic Sciences, University of Florida, Gainesville, FL 32611, USA

Received 31 July 1995; revised 11 December 1995; accepted 24 May 1996

---

### Abstract

Estuarine fishes are generally much more abundant in structurally-complex seagrass beds than in nearby sand flats. We tested for this pattern by comparing trawl catches from adjacent seagrass beds and sand flats within Turkey Point Shoal, a shallow estuarine system in the northern Gulf of Mexico. Fish abundance in seagrass beds (primarily *Thalassia testudinum* Konig) was significantly (760%) higher than in sand flats. Pinfish *Lagodon rhomboides* (Linnaeus) accounted for much of this difference. Laboratory experiments in behavioral arenas were performed to determine whether this difference was due to habitat selection. In the absence of predators, pinfish used seagrass and sand equally. Additionally, groups of pinfish swam about freely within the water column. Therefore, habitat preference alone does not likely explain the patterns observed in the field. We then tested the hypothesis that observed habitat use patterns were due in part to predator-mediated habitat selection. Pinfish tended to avoid non-vegetated sections of behavioral arenas after predatory southern flounder *Paralichthys lethostigma* Jordan and Gilbert were introduced. Qualitative observations indicated that pinfish also reduced their use of the upper water column in the presence of these predators. Therefore, behaviorally mediated predator avoidance may help explain observed patterns of differential habitat use within estuarine mosaics of sand and seagrass habitats.

**Keywords:** Antipredator behavior; Habitat selection; *Lagodon rhomboides*; Microhabitat use; *Paralichthys lethostigma*; Risk of predation; Seagrass ecology

---

\*Corresponding author.

## 1. Introduction

Habitat structure plays an important role in determining habitat-specific assemblage structure, often by mediating the outcome of predator–prey interactions (e.g. Huffaker, 1958). Structurally-complex habitats tend to support more individuals and species than do adjacent, structurally-simple habitats. For example, estuarine seagrass beds commonly support orders of magnitude more fishes and invertebrates than do adjacent sand flats (Orth and Heck, 1980; Stoner, 1983; Heck et al., 1989; Ferrell and Bell, 1991; Heck and Crowder, 1991; Sogard and Able, 1991; reviewed by Orth et al., 1984). Reduced risk of predation, increased microhabitat availability, and enhanced diversity and abundance of prey all contribute to this difference in habitat use. Predation likely plays a predominant role in generating habitat specific patterns, either directly by the removal of prey species, or indirectly by influencing habitat selection in vulnerable prey species (reviewed by Lima and Dill, 1990).

Stoner (1983) found that fish abundance was positively correlated ( $R = 0.998$ ) with seagrass biomass and hypothesized that differential predation (i.e. harvesting) was likely causing this pattern. However, predator-mediated habitat selection is a viable alternative to this hypothesis (e.g. Main, 1987). Few studies of seagrass fishes have tried to distinguish between these two competing hypotheses. Bell and Westoby (1986) found that a gobiid fish (*Bathygobius krefftii*) emigrated away from cropped patches of seagrass even in the absence of predators. Sogard and Olla (1993) showed that juvenile walleye pollock (*Theragra chalcogramma*) preferred unstructured-habitat over seagrass, but reversed this preference in the presence of a predator mimic. These studies indicate that seagrass fishes make active decisions about habitat use and that these decisions incorporate information about the relative risk of predation. Clearly, more research is needed to evaluate the general importance of behaviorally mediated habitat selection by seagrass fishes.

The pinfish *Lagodon rhomboides* (Linnaeus) is a numerically dominant member of the near-shore ichthyofauna of southern Atlantic and Gulf of Mexico coasts of the United States (Hoese and Moore, 1977). It is an important omnivorous predator (Stoner, 1980; Stoner and Livingston, 1984; Luczkovich, 1987) within seagrass beds and often comprises a significant portion of the community biomass in these systems (Adams, 1976a,b). Previous research indicates that pinfish are significantly more abundant in vegetated sites than in non-vegetated sites of the Gulf of Mexico (Kilby, 1955; Caldwell, 1957; Livingston, 1975; Stoner, 1983). In this study, we tested the hypothesis that enhanced abundance of pinfish in seagrass beds reflects their behavioral responses to elevated risk of predation in adjacent non-vegetated habitats. Specifically, we examined use of seagrass beds and sand flats by fishes (especially pinfish) to verify published patterns of differential habitat use for our study area. Then we examined habitat use by groups of pinfish swimming in 1200-l behavioral arenas that were evenly divided into sand and seagrass patches. Finally, we examined how relative use of these habitats was affected by addition of piscivorous southern flounder *Paralichthys lethostigma* Jordan and Gilbert to the behavioral arenas.

## 2. Methods

### 2.1. Study animals and local study area

We compared the abundance of fishes from adjacent seagrass beds and sand flats in our local study area to confirm published observations of differential habitat use. Fishes were collected during August 1994 from two seagrass beds and two sand flats within Turkey Point Shoal, which lies approximately 2.5 km offshore of the Florida State University Marine Laboratory (Franklin County, Florida, northern Gulf of Mexico). The sampling area was generally less than 3-m deep and was comprised of seagrass meadows interspersed with stretches of sand and mud. Vegetated sites were mixed stands of turtlegrass *Thalassia testudinum* König and manatee grass *Syringodium filiforme* Kütz., whereas non-vegetated sites were primarily comprised of sand. Sites were separated from one another by about 0.5–1.0 km. Five replicate, 2-min trawls (5 m otter trawl; 20 mm mesh wing; 6 mm mesh liner) were made at a speed of about 2 km/h within each site. All fishes were immediately identified, enumerated, and released unharmed. Since trawls were not independent of one another (i.e. they were subsamples), we used nested analysis of variance (ANOVA) to test for differences in fish abundance between seagrass beds and sand flats (Underwood, 1981). To avoid pseudoreplication, the fixed effect Habitat was tested using the mean square error associated with the nested Trawl effect as the denominator of the *F*-test. An *F*-max test and residual analysis indicated that data transformation was unnecessary. Taxonomic authorities for all fishes listed in Section 3 are after Robins et al. (1991).

### 2.2. Habitat selection experiment

Pinfish and flounder were collected from seagrass beds within Turkey Point Shoal. Predators and prey were immediately brought to the laboratory and maintained separately in several large tanks provided with flow-through seawater and air diffusers. Individual pinfish (45–115 mm standard length; mean and SD =  $67.7 \pm 8.1$  mm) were held for at least 24 h without food, used in an experiment once, and then released. We were only able to capture and maintain six southern flounders (245–384 mm standard length), therefore it was necessary to reuse them in different trials.

Habitat selection experiments were carried out in a rectangular tank (Fig. 1) subdivided with plywood partitions into three behavioral arenas (inside dimensions  $200 \times 120$  cm). Fresh seawater flowed (9 l/m) into one end of the tank, through small holes drilled into the partitions, and out a standpipe at the opposite end of the tank. Water level was maintained at 50 cm and an airstone was placed into the center of each of the arenas. The bottom of the tank was covered with 4–5 cm of clean sand to provide a natural substratum.

We manipulated seagrass cover within each of the three arenas. In one half of an arena, we left barren sand to mimic a sandflat. In the other half, we anchored strips of dark plastic ( $390 \times 14$  mm) into the sand substratum to mimic a bed of turtlegrass. Grass blades were stocked at a density of  $331/\text{m}^2$ , which is representative of an average

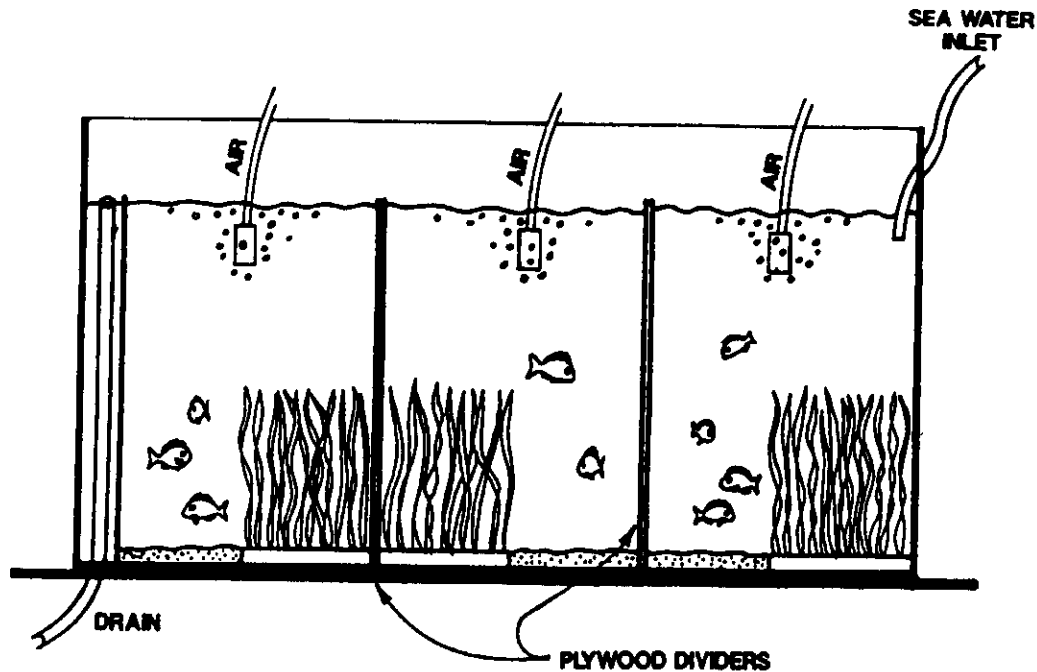


Fig. 1. Schematic diagram of experimental arenas. See Section 2 for tank dimensions and additional details concerning construction materials. The position of artificial seagrass was switched in between trials.

seagrass bed in the region (Zimmerman and Livingston, 1979; Stoner, 1983). Artificial seagrass was used to avoid confounding predator avoidance with differential prey abundance (i.e. omnivorous pinfish feed both on epiphytic organisms and seagrass blades; Stoner, 1980; Stoner and Livingston, 1984; Luczkovich, 1987).

Control and Predator trials were started by adding 10 pinfish into the center of each arena. We used groups of 10 because this species is a group forager (Luczkovich, 1987). Pinfish were allowed to acclimate for 30 min. We then counted the number of individuals that were swimming in the non-vegetated portion of each arena (Before-Predator period). Care was taken to ensure that any buried pinfish were also counted. Counts were repeated every 20 min for a 1-h observation period. A predator was added to the center of the tank (Predator trials) or we simply approached the tank to mimic adding a predator (Control trials). Pinfish were allowed to acclimate for another 30 min, and three more counts of pinfish swimming in the non-vegetated portion of each arena were made (After-Predator period). The numbers of pinfish counted in the non-vegetated portion of each arena were totalled separately for the Before-Predator and After-Predator periods and converted to proportions. Additionally, the proportion of pinfish swimming in the vegetated sections was determined by subtraction.

Each arena was an independent replicate since the pinfish and flounder in different arenas were unable to see and interact with one another. However, Control and Predator trials were run separately because pinfish are responsive to chemical stimuli (Luczkovich, 1988). Therefore, either three Control or three Predator replicates were run simultaneously during each trial. Control and Predator treatments were replicated nine and twelve times, respectively. The vegetated and non-vegetated portions of each arena

were switched between trials, and the arenas were drained and refilled between trials. All pinfish were captured and counted at this time to determine whether any had been eaten during the trial.

To test for habitat selection in the absence of predation risk, the proportions of pinfish found in the seagrass and sand sections during the Before-Predator observation period in both Predator and Control trials were compared using a two-tailed *t*-test. We then subjected the proportion of pinfish swimming over open sand to a repeated measures ANOVA, testing for the effects of Predator presence and Observation period. Inspection of residual plots and an *F*-max test indicated that the assumptions for this analysis were met and that data transformation was unnecessary. A priori contrasts were used to test for differences among relevant pairs of means. First, we tested whether the proportion of pinfish swimming over open sand in the Predator trials changed after the addition of a predator (contrast 1). Second, we tested whether the proportion of pinfish swimming over open sand in the After-Predator period differed between the Predator and Control trials (contrast 2).

### 3. Results

#### 3.1. Trawl survey

The density of fishes in seagrass beds was significantly higher than in adjacent sand flats ( $F_{1,2} = 146.2$ ,  $p = 0.0068$ ). Much of this difference was attributable to the abundant pinfish, which comprised 51 and 12% of the fish assemblages found in seagrass beds and sand flats, respectively. A total of 185 individuals (26 species) were collected from sand flats, whereas 1408 individuals (17 species) were collected from seagrass beds (Table 1).

#### 3.2. Habitat selection experiment

There were obvious differences in the behavior of pinfish exposed to predators. During the Before-Predator observation period, pinfish in both treatments swam about freely inspecting the sand and seagrass portions of the arenas. The relative abundance of pinfish observed in the sand section (44%) did not differ statistically ( $t_{20} = -1.27$ ,  $p = 0.22$ ) from that observed in the seagrass section (56%). In the absence of predators (i.e. during Control trials and the first half of Predator trials), pinfish spent much of the time in the water column and moved about freely. However, pinfish appeared to be much more alert when swimming over sand. That is, they tended to form larger, more cohesive aggregations and darted about furtively.

Pinfish exposed to predators behaved quite differently than did non-threatened pinfish. Movement between vegetated and non-vegetated portions decreased, and fish seldom ventured into the water column. Pinfish that did venture into the non-vegetated section displayed two characteristic behaviors. First, some pinfish would congregate at the top of the water column in the corner of the arena farthest from the predator. Second, individual pinfish would burrow sideways beneath the sand with only one eye exposed

Table 1  
Total numbers of fishes collected in August 1994 from seagrass beds (SG) and sand flats (SF) within Turkey Point Shoal

Species	Common name	SF	SG
<i>Dasyatis sabina</i>	Atlantic stingray	4	0
<i>Anchoa mitchilli</i>	bay anchovy	14	0
<i>Harengula jaguana</i>	scaled sardine	1	0
<i>Bagre marinus</i>	gafftopsail catfish	3	0
<i>Synodus foetens</i>	inshore lizardfish	2	0
<i>Opsanus beta</i>	gulf toadfish	1	6
<i>Syngnathus louisianae</i>	chain pipefish	2	112
<i>Syngnathus scovelli</i>	gulf pipefish	0	8
<i>Centropristis striata</i>	black sea bass	0	32
<i>Diplectrum formosum</i>	sand perch	0	3
<i>Mycteroperca microlepis</i>	gag	0	1
<i>Chloroscombrus chrysurus</i>	Atlantic bumper	5	0
<i>Eucinostomus gula</i>	silver jenny	2	0
<i>Orthopristis chrysoptera</i>	pigfish	9	149
<i>Diplodus holbrooki</i>	spottail pinfish	0	7
<i>Lagodon rhomboides</i>	pinfish	23	720
<i>Pagrus pagrus</i>	red porgy	0	1
<i>Bairdiella chrysoura</i>	silver perch	24	250
<i>Cynoscion arenarius</i>	sand seatrout	51	0
<i>Leiostomus xanthurus</i>	spot	15	0
<i>Menticirrhus americanus</i>	southern kingfish	11	0
<i>Hypsoblennius hentz</i>	feather blenny	0	1
<i>Chaetodipterus faber</i>	Atlantic spadefish	1	0
<i>Peprilus burti</i>	gulf butterfish	1	0
<i>Ancylosetta quadrocellata</i>	oscillated flounder	1	0
<i>Etropus crossotus</i>	fringed flounder	6	0
<i>Paralichthys albigutta</i>	gulf flounder	1	1
<i>Trinectes maculatus</i>	hogchoker	2	0
<i>Symphurus plagiusa</i>	blackcheek tonguefish	2	0
<i>Monacanthus hispidus</i>	planehead filefish	1	56
<i>Lactophrys quadricornis</i>	scrawled cowfish	1	22
<i>Sphoeroides nephelus</i>	southern puffer	1	5
<i>Chilomycterus schoepfi</i>	striped burrfish	1	34
Total		185	1408

Ten trawls were collected from within each habitat type; see text for specific sampling details. Taxonomic authorities for species listed in this table are after Robins et al. (1991).

( $n = 3$ ). These fish would remain motionless for a period of 5–10 min. Flounder exhibited consistent behavior during the experiment. They usually remained buried beneath the sand at the interface between the vegetated and non-vegetated portions of the tank, with only their eyes exposed. However, one flounder left this position long enough to eat a pinfish.

Overall, pinfish reduced the amount of time spent swimming in the open portion of the arena between observation periods (significant Predator effect; Table 2). However, this result is somewhat misleading in light of the significant Predator  $\times$  Observation

Table 2

Results of repeated measures ANOVA. Response variable is the proportion of pinfish observed swimming over open sand before and after a predator was introduced

Source	df	MS	F	P
Predator	1	8750.0	13.9	0.0014
Subject (Group)	19	629.7		
Observation period	1	607.5	2.7	0.1164
Observation period*Predator	1	1703.8	7.6	0.0126
Observation period*Subject (Group)	19	224.5		

period interaction (Table 2, Fig. 2). This interaction arose because pinfish that were not exposed to flounder behaved similarly between observation periods, whereas pinfish in the Predator trials reduced their use of the non-vegetated portion of the arenas by about 20%. Fig. 2 suggests that pinfish in the Predator trials used sand less than those in the Control trials before the addition of predators. However, these values are not statistically different and likely reflect random variation in pinfish behavior or test conditions between trials.

The presence of a predator resulted in a significant decrease in the relative amount of time spent in the non-vegetated portion of the arenas (Table 2 and Fig. 2). This pattern is more clearly understood by examining the a priori defined contrasts comparing relevant means. Pinfish in the Predator trials spent considerably more time in the non-vegetated portion of the arenas during the Before-Predator period than during the After-Predator period (contrast 1;  $F = 5.94$ ,  $p = 0.0196$ ). Additionally, during the After-Predator observation period, pinfish in Control trials spent significantly more time in the non-vegetated sections than did pinfish in the Predator trials (contrast 2;  $F = 21.28$ ,  $p = 0.0001$ ).

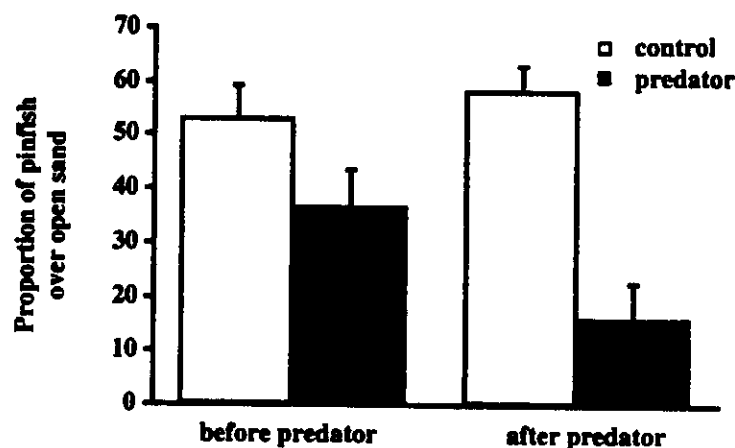


Fig. 2. Mean proportion of pinfish (+ 1 SE) observed swimming over open sand before and after the addition of a predatory southern flounder. A predator was added during the second observation period in Predator trials, but not in Control trials.

#### 4. Discussion

Previous researchers of aquatic systems have found higher numbers of individuals and species of fishes and macroinvertebrates in vegetated habitats relative to nearby unvegetated habitats (freshwater: Gerking, 1957; Hall and Werner, 1977; Crowder and Cooper, 1982; marine: Orth and Heck, 1980; Stoner, 1983; Orth et al., 1984; Heck et al., 1989; Ferrell and Bell, 1991; Sogard and Able, 1991). This pattern is also apparent from our survey of fishes within Turkey Point Shoal in the northern Gulf of Mexico, where fishes were 760% more abundant in seagrass beds than in adjacent sand flats. As in this study, pinfish have been shown to be numerically dominant members of the seagrass ichthyofaunas throughout their range (e.g. Kilby, 1955; Caldwell, 1957; Stoner, 1983). These opportunistic omnivores contribute appreciably to overall secondary production and play significant roles in the food web dynamics of seagrass systems (Adams, 1976a,b; Darcy, 1985).

Although between-habitat differences in food availability (McIvor and Odum, 1988; Rozas and Odum, 1988) and recruitment rates (Bell et al., 1987) can contribute significantly to heterogeneous habitat use patterns, predation is possibly the predominant structuring factor affecting mobile fishes in shallow marine environments. Seagrass beds and sand flats in the study area support a variety of piscine predators that eat pinfish (Ryan, 1981; references in Darcy, 1985), including: Atlantic sharpnose sharks (*Rhizoprionodon terraenovae*), ladyfish (*Elops saurus*), hardhead catfish (*Arius felis*), gafftopsail catfish (*Bagre marinus*), inshore lizardfish (*Synodus foetens*), southern hake (*Urophycis floridana*), gulf toadfish (*Opsanus beta*), black sea bass (*Centropristis striata*), gag grouper (*Mycteroperca microlepis*), crevalle jack (*Caranx hippos*), sand seatrout (*Cynoscion arenarius*), spotted seatrout (*Cynoscion nebulosus*), red drum (*Sciaenops ocellata*), and southern flounder. We collected many of these species during qualitative trawl and gill net surveys performed in conjunction with this study (unpublished data). Indeed, stomachs of hardhead catfish and gag grouper that we examined contained pinfish remains (unpublished data). Tethering studies within Turkey Point Shoal indicated that 24-h predation rates on pinfish were 97%, although no consistent differences between habitats were noted (unpublished data). Predation rates may have been overestimated in seagrass beds because highly agile pinfish can generally flee predators by hiding within dense seagrass cover (Minello, 1993). Direct removal of pinfish by predators probably did not account for the large difference in abundance observed between habitats.

Our experimental results show that pinfish used seagrass and sand equally in the absence of a predator. Pinfish in Control trials initially fled into the seagrass when we approached them (i.e. an acute disturbance), but increased their use of open sand to previous levels by the beginning of the After-Predator period (i.e. < 30 minutes). In contrast, addition of a predator caused a significant and persistent decrease in use of the non-vegetated portion of the experimental arenas. The pinfish likely perceived a change in risk of predation and modified their behavior accordingly (i.e. only one pinfish was eaten during the experiments). When pinfish were in the open portion of the arenas in the presence of a predator, they either buried or swam along the wall at the far end of the tank. Therefore, pinfish could simply be swimming as far away from the predator as

possible and not seeking cover in seagrass *per se*. Pinfish do tend to occupy predator-free areas of aquaria that lack any protective cover (J.J. Luczkovich, pers. comm.). This alternative cannot, however, wholly account for our results because most of the predators remained buried in the center of the arenas. Pinfish should have congregated at the far ends of the behavioral arenas in equal proportions if they were simply moving as far away as possible from predators positioned in the center of the arenas. Habitat use by pinfish in the field and contrast 1 do not support this contention. Other researchers have found that prey fishes will remain in the cover of seagrass even when predators are found therein (e.g. Savino and Stein, 1989; Sogard and Olla, 1993). In preliminary trials using gag grouper, both pinfish and grouper remained in vegetated portions of our behavioral arenas (pers. obser.). Additional research is needed to compare the relative responses of seagrass fishes to larger predatory and non-predatory fishes.

Persistent variation in habitat-specific foraging rates suggests that there is likely strong selection for the evolution of antipredator behaviors (Kerfoot and Sih, 1987; Bell et al., 1987). Reductions in predator foraging efficiency translate into reductions in prey vulnerability and should result in enhanced evolutionary fitness of prey. Structurally-complex habitats reduce the foraging efficiency of visually-oriented predators by restricting vision and manoeuvrability (e.g. Glass, 1971; Vince et al., 1976; Nelson, 1979; Heck and Thoman, 1981; Savino and Stein, 1982; Coull and Wells, 1983; Minello and Zimmerman, 1983; Diehl, 1988; Gotceitas and Colgan, 1989). Habitat complexity also interacts with predator size, such that larger predators suffer greater reductions in foraging efficiency due to their inability to manoeuvre among structural elements such as seagrass blades, crevices, and submerged logs (Stoner, 1982; Ryer, 1988). Therefore, in the absence of other anti-predatory adaptations prey fishes should select more complex habitats when predators are nearby. Predator mediated shifts in habitat use are common in aquatic prey (Lima and Dill, 1990), although few seagrass fishes have been tested as prey (e.g. Bell et al., 1987; Sogard and Olla, 1993). Numerous researchers in other systems have documented behavioral responses of fishes to their predators (e.g. Werner et al., 1983; Gilliam and Fraser, 1987; Power, 1987; Savino and Stein, 1989; Harvey, 1991; Harvey and Stewart, 1991; Gotceitas and Brown, 1993; Christensen and Persson, 1993). Risk of predation appears to be a pervasive force structuring aquatic communities, including marine fishes in seagrass beds and adjacent sand flats.

One caveat concerning our experimental design relates to scale and edge effects. Due to the size of behavioral arenas (1200 l), pinfish could never venture more than one meter away from the seagrass refuge. Therefore, use of non-vegetated sections may more accurately reflect edge behavior of pinfish: i.e. constant movement across the sand-vegetation interface and vertically within the water column in order to explore alternative foraging opportunities. It is likely that use of available sand habitat would decrease with increasing distance from seagrass cover (Ferrell and Bell, 1991). Interestingly, the observed sideways burrowing with one eye exposed may be an antipredator behavior (e.g. Main, 1987) employed by nomadic pinfishes moving across open sand patches in between seagrass beds. Coen et al. (1981) also noted this burrowing behavior.

In conclusion, our results indicate that use of estuarine habitat mosaics can be partially explained by predator-mediated habitat selection. Fishes are actively selecting structural-

ly complex seagrass beds in response to the increased risk of predation in nearby non-vegetated sand and mud flats. Although we found that non-threatened pinfish used open sand and seagrass patches equally within our experimental arenas, this pattern would not likely hold with increasing distance from the vegetated refuge (e.g. Ferrell and Bell, 1991). As our trawl results indicate, pinfish do occur in structurally-simple environments, albeit in low numbers (Darcy, 1985). These nomadic individuals are likely in transit between more structured habitats, but may also represent “spillover” from densely populated seagrass patches. Therefore, the mosaic of habitats found within shallow estuarine systems may be profitably envisioned as a collection of demographic sources and sinks (Pulliam, 1988; Pulliam and Danielson, 1991). Moreover, the process of active habitat selection (and avoidance) results in a profoundly different demographic profile than does differential predation rates among adjacent habitat patches (Holt, 1987). Finally, more research is needed to clarify the relative importance of seagrass beds with respect to reduced predation risks and increased foraging opportunities (e.g. Werner et al., 1983; McIvor and Odum, 1988; Rozas and Odum, 1988).

### Acknowledgments

This research was carried out as part of an undergraduate experimental design course entitled The Ecology of Seagrass Habitats that was offered by Jacksonville University. Special thanks go to our fellow seagrass conspirators: G. Burr, J. Croop, M. Gallagher, L. Holton, M. Kwiatkowski, J. VanVuren and S. Williams. J. Jimeian and M. Hubbard assisted in the field during the trawl surveys. Special thanks to K. Babbitt, J. Luczkovich, A. Stoner and several anonymous reviewers for reading earlier versions of this paper. This work would not have been possible without the excellent support of J. Hitron and the staff of the Florida State University Marine Laboratory.

### References

- Adams, S.M., 1976a. The ecology of eelgrass, *Zostera marina* (L.), fish communities. I. Structural analysis. *J. Exp. Mar. Biol. Ecol.*, Vol. 22, pp. 269–291.
- Adams, S.M., 1976b. The ecology of eelgrass, *Zostera marina* (L.), fish communities. II. Functional analysis. *J. Exp. Mar. Biol. Ecol.*, Vol. 22, pp. 293–311.
- Bell, J.D. and M. Westoby, 1986. Abundance of macrofauna in dense seagrass is due to habitat preference, not predation. *Oecologia*, Vol. 68, pp. 205–209.
- Bell, J.D., M. Westoby and A.S. Steffe, 1987. Fish larvae settling in seagrass: do they discriminate between beds of different leaf density? *J. Exp. Mar. Biol. Ecol.*, Vol. 111, pp. 133–144.
- Caldwell, D.K., 1957. The biology and systematics of the pinfish, *Lagodon rhomboides* (Linnaeus). *Bull. Florida State Museum, Biol. Sci.*, Vol. 2, pp. 77–173.
- Christensen, B. and L. Persson, 1993. Species-specific antipredatory behaviors: effects on prey choice in different habitats. *Behav. Ecol. Sociobiol.*, Vol. 32, pp. 1–9.
- Coen, L.K., K.L. Heck and L.G. Abele, 1981. Experiments on competition and predation among shrimps of seagrass meadows. *Ecology*, Vol. 62, pp. 1484–1493.
- Coull, B.C. and J.B.J. Wells, 1983. Refuges from fish predation: experiments with phytal meiofauna from the New Zealand rocky intertidal. *Ecology* Vol., 64, pp. 1599–1609.

- Crowder, L.B. and W.E. Cooper, 1982. Habitat structural complexity and the interaction between bluegills and their prey. *Ecology*, Vol. 63, pp. 1802–1813.
- Darcy, G.H., 1985. Synopsis of biological data on the pinfish, *Lagodon rhomboides* (Pisces: Sparidae). NOAA Technical Report, Vol. NMFS 23, pp. 1–32.
- Diehl, S., 1988. Foraging efficiency of three freshwater fishes: effects of structural complexity and light. *Oikos*, Vol. 53, pp. 207–214.
- Ferrell, D.J. and J.D. Bell, 1991. Differences among assemblages of fish associated with *Zostera capricorni* and bare sand over a large spatial scale. *Mar. Ecol. Prog. Ser.*, Vol. 72, pp. 15–24.
- Gerking, S.D., 1957. A method of sampling the littoral macrofauna and its application. *Ecology*, Vol. 38, pp. 219–255.
- Gilliam, J.F. and D.F. Fraser, 1987. Habitat selection under predation hazard: test of a model with foraging minnows. *Ecology*, Vol. 68, pp. 1856–1862.
- Glass, N.R., 1971. Computer analysis of predation energetics in the largemouth bass. In, *Systems analysis and simulation ecology*, edited by B.C. Patten, Academic Press, New York, pp. 325–363.
- Gotceitas, V. and J.A. Brown, 1993. Substrate selection by juvenile Atlantic cod (*Gadus morhua*): effects of predation risk. *Oecologia*, Vol. 93, pp. 31–37.
- Gotceitas, V. and P. Colgan, 1989. Predator foraging success and habitat complexity: quantitative test of the threshold hypothesis. *Oecologia*, Vol. 80, pp. 158–166.
- Hall, D.J. and E.E. Werner, 1977. Seasonal distribution and abundance of fishes in the littoral zone of a Michigan lake. *Trans. Am. Fish. Soc.*, Vol. 106, pp. 545–555.
- Harvey, B.C., 1991. Interactions among stream fishes: predator-induced habitat shifts and larval survival. *Oecologia*, Vol. 73, pp. 501–512.
- Harvey, B.C. and A.J. Stewart, 1991. Fish size and habitat depth relationships in headwater streams. *Oecologia*, Vol. 87, pp. 336–342.
- Heck Jr., K.J. and T. Thoman, 1981. Experiments on predator–prey interactions in vegetated aquatic habitats. *J. Exp. Mar. Biol. Ecol.*, Vol. 53, pp. 125–134.
- Heck Jr., K.J., K.W. Able, M.P. Fahay and C.T. Roman, 1989. Fishes and decapod crustaceans of Cape Cod eelgrass meadows: species composition, seasonal abundance patterns and comparison with unvegetated substrates. *Estuaries*, Vol. 12, pp. 59–65.
- Heck, K.L. and L.B. Crowder, 1991. Habitat structure and predator–prey interactions in vegetated aquatic systems. In, *Habitat structure: the physical arrangement of objects in space*, edited by S.S. Bell, E.D. McCoy and J. Mushinsky, Chapman Hall, New York, pp. 281–299.
- Hoese, H.D. and R.H. Moore, 1977. *Fishes of the Gulf of Mexico, Texas, Louisiana, and adjacent waters*. Texas A and M Press, College Station, Texas, 327 pp.
- Holt, R.D., 1987. Population dynamics and evolutionary processes: the manifold roles of habitat selection. *Evol. Ecol.*, Vol. 1, pp. 331–347.
- Huffaker, C.B., 1958. Experimental studies on predation: dispersion factors and predator–prey oscillations. *Hilgardia*, Vol. 27, pp. 343–383.
- Kerfoot, W.C. and A. Sih, 1987. *Predation: direct and indirect effects on aquatic communities*. University Press of New England, Hanover, New Hampshire, 386 pp.
- Kilby, J.D., 1955. The fishes of two Gulf coastal marsh areas of Florida. *Tulane Stud. Zool.*, Vol. 2, pp. 173–247.
- Lima, S.L. and L.M. Dill, 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.*, Vol. 68, pp. 619–640.
- Livingston, R.J., 1975. Impact of kraft pulp-mill effluents on estuarine and coastal fishes in Apalachee Bay, Florida, USA. *Mar. Biol.*, Vol. 32, pp. 19–48.
- Luczkovich, J.J., 1987. The patterns and mechanisms of selective feeding on seagrass-meadow epifauna by juvenile pinfish, *Lagodon rhomboides* (Linnaeus). Ph.D. dissertation, Florida State University, Tallahassee, Florida, 157 pp.
- Luczkovich, J.J., 1988. The role of prey detection in the selection of prey by pinfish *Lagodon rhomboides* (Linnaeus). *J. Exp. Mar. Biol. Ecol.*, Vol. 123, pp. 15–30.
- Main, K.L., 1987. Predator avoidance in seagrass meadows: prey behavior, microhabitat selection and cryptic coloration. *Ecology*, Vol. 68, pp. 170–180.

- McIvor, C.C. and W.E. Odum, 1988. Food, predation risk and microhabitat selection in a marsh fish assemblage. *Ecology*, Vol. 69, pp. 1341–1351.
- Minello, T.J., 1993. Chronographic tethering: a technique for measuring prey survival time and testing predation pressure in aquatic habitats. *Mar. Ecol. Prog. Ser.*, Vol. 101, pp. 99–104.
- Minello, T.J. and R.J. Zimmerman, 1983. Fish predation on juvenile brown shrimp, *Penaeus aztecus* Ives: the effect of simulated *Spartina* structure on predation rates. *J. Exp. Mar. Biol. Ecol.*, Vol. 72, pp. 211–231.
- Nelson, W.G., 1979. Experimental studies of selective predation on amphipods: consequences for amphipod distribution and abundance. *J. Exp. Mar. Biol. Ecol.*, Vol. 38, pp. 225–245.
- Orth, R.J. and K.L. Heck Jr., 1980. Structural components of eelgrass (*Zostera marina*) meadows in the Lower Chesapeake Bay: fishes. *Estuaries*, Vol. 3, pp. 278–288.
- Orth, R.J., K.L. Heck Jr. and J.V. Montfrans, 1984. Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator–prey relationships. *Estuaries*, Vol. 7, pp. 339–350.
- Power, M.E., 1987. Predator avoidance by grazing fishes in temperate and tropical streams: importance of stream depth and prey size. In: *Predation: direct and indirect effects on aquatic communities*, edited by W.C. Kerfoot and A. Sih, University Press of New England, Hanover, New Hampshire, pp. 333–352.
- Pulliam, H.R., 1988. Sources, sinks, and population regulation. *Am. Nat.*, Vol. 132, pp. 652–661.
- Pulliam, H.R. and B.J. Danielson, 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. *Am. Nat.*, Vol. 137, pp. S50–S66.
- Robins, C.R., R.M. Bailey, C.E. Bond, J.R. Brooker, E.A. Lachner, R.N. Lea and W.B. Scott, 1991. *A list of common and scientific names of fishes from the United States and Canada*. American Fisheries Society, Bethesda, Maryland, 183 pp.
- Rozas, L.P. and W.E. Odum, 1988. Occupation of submerged aquatic vegetation by fishes: testing the roles of food and refuge. *Oecologia*, Vol. 77, pp. 101–106.
- Ryan, J.D., 1981. Nocturnal predator–prey relationships of some fishes in a temperate seagrass meadow. M.Sc. thesis, Florida State University, Tallahassee, Florida, 109 pp.
- Ryer, C.H., 1988. Pipefish foraging: effects of fish size, prey size and altered habitat complexity. *Mar. Ecol. Prog. Ser.*, Vol. 48, pp. 37–45.
- Savino, J.F. and R.A. Stein, 1982. Predator–prey interaction between largemouth bass and bluegills as influenced by simulated, submersed vegetation. *Trans. Am. Fish. Soc.*, Vol. 111, pp. 255–266.
- Savino, J.F. and R.A. Stein, 1989. Behavior of fish predators and their prey: habitat choice between open water and dense vegetation. *Env. Biol. Fish.*, Vol. 24, pp. 287–293.
- Sogard, S.M. and K.W. Able, 1991. A comparison of eelgrass, sea lettuce macroalgae, and marsh creeks as habitats for epibenthic fishes and decapods. *Estuar. Coast. Shelf Sci.*, Vol. 33, pp. 501–519.
- Sogard, S.M. and B.L. Olla, 1993. The influence of predator presence on utilization of artificial seagrass habitats by juvenile walleye pollock, *Theragra chalcogramma*. *Env. Biol. Fish.*, Vol. 37, pp. 57–65.
- Stoner, A.W., 1980. Feeding ecology of *Lagodon rhomboides* (Pisces: Sparidae): variation and functional responses. *Fish. Bull.*, Vol. 78, pp. 337–352.
- Stoner, A.W., 1982. The influence of benthic macrophytes on the foraging behavior of pinfish, *Lagodon rhomboides* (Linnaeus). *J. Exp. Mar. Biol. Ecol.*, Vol. 58, pp. 271–284.
- Stoner, A.W., 1983. Distribution of fishes in seagrass meadows: role of macrophyte biomass and species composition. *Fish. Bull.*, Vol. 81, pp. 837–846.
- Stoner, A.W. and R.J. Livingston, 1984. Ontogenetic patterns in diet and feeding morphology in sympatric sparid fishes from seagrass meadows. *Copeia*, Vol. 1984, pp. 174–187.
- Underwood, A.J., 1981. Techniques of analysis of variance in experimental marine biology and ecology. *Ocean. Mar. Biol. Ann. Rev.*, Vol. 19, pp. 513–605.
- Vince, S., I. Valiela, N. Backus and J.M. Teal, 1976. Predation by the salt marsh killifish *Fundulus heteroclitus* L. in relation to prey size and habitat structure: consequences for prey distribution and abundance. *J. Exp. Mar. Biol. Ecol.*, Vol. 23, pp. 255–266.
- Werner, E.E., J.F. Gilliam, D.J. Hall and G.G. Mittlebach, 1983. An experimental test of the effects of predation risk on habitat use in fish. *Ecology*, Vol. 64, pp. 1540–1548.
- Zimmerman, M.S. and R.J. Livingston, 1979. Dominance and distribution of benthic macrophyte assemblages in a north Florida estuary (Apalachee Bay, Florida). *Bull. Mar. Sci.*, Vol. 29, pp. 27–40.