

Habitat selection by three littoral zone fishes: effects of predation pressure, plant density and macrophyte type

Chick JH, McIvor CC. Habitat selection by three littoral zone fishes: effects of predation pressure, plant density and macrophyte type. Ecology of Freshwater Fish 1997: 6: 27–35. © Munksgaard, 1997

Abstract – We conducted laboratory experiments which demonstrated that three littoral zone fishes differentially selected among three macrophytes when seeking refuge from predation. In the presence of a predator (a juvenile *Micropterus salmoides*), mosquitofish (*Gambusia holbrooki*), sailfin mollies (*Poecilia latipinna*), and dollar sunfish (*Lepomis marginatus*) displayed differential use of four tank areas containing patches of either *Hydrilla verticillata*, *Potamogeton illinoensis*, *Panicum hemitomon*, or no plants. Patterns of habitat selection, and the consistency of these patterns among replicates, differed among the three fishes and among three plant-density treatments - natural (each macrophyte presented at its mean field density), equal (all three macrophytes at the same density), and control (no plants). Selection for *H. verticillata* by mosquitofish was significant for both the equal and natural treatments, and thus was not caused by differences in plant density alone. Sailfin mollies displayed significant selection for *H. verticillata* only in the natural plant-density treatments. Dollar sunfish showed less consistent habitat selection than either mosquitofish or sailfin mollies. Significant habitat selection was not found in the absence of a predator, and there was no evidence for selection among the tank areas in control treatments. Patterns of habitat selection by the three fishes in our laboratory study corresponded to observed habitat use in Lake Okeechobee.

J. H. Chick, C. C. McIvor*

National Biological Service, Florida Cooperative Fish and Wildlife Research Unit, University of Florida, Gainesville, USA

*Present address: National Biological Service, Arizona Cooperative Fish and Wildlife Research Unit, University of Arizona, Tucson, USA

Key words: habitat selection; predation pressure; plant density; macrophyte type

John H. Chick, Institute of Ecology, University of Georgia, Athens, GA 30602-2202, USA

Accepted for publication March 5, 1996

Un resumen en español se incluye detrás del texto principal de este artículo.

Introduction

Field studies in lentic environments have revealed that certain fishes, or life stages of fishes, are more abundant in vegetated than unvegetated habitats (Hall & Werner 1977, Werner, Hall & Werner 1978, Conrow, Zale & Gregory 1990, Gelwick & Matthews 1990, Meals & Miranda 1991). This pattern is thought to be influenced by differences in food resources and predation risk between vegetated and unvegetated habitats (McIvor & Odum 1988, Rozas & Odum 1988, Heck & Crowder 1991). Dense aquatic vegetation can reduce predator foraging rates, which may lower the mortality rates of fishes in vegetated habitats (Savino & Stein 1982, 1989a, b, Winfield 1986, Ryer 1988). Additionally, fishes

vulnerable to predators are able to recognize and select between habitats differing in refuge value such as areas with and without simulated vegetation (Savino & Stein 1989b), areas with differing densities of simulated vegetation (Gotceitas & Colgan 1987, 1990), and areas differing in water depth (Devries 1990, Fraser & Gilliam 1992). Fishes can also select habitats based on food availability or type, and can alter foraging activities in response to predators (Holbrook & Schmitt 1988, Gotceitas & Colgan 1990, Wildhaber & Crowder 1991).

Whereas the patterns of fish distribution between vegetated habitats and unvegetated habitats and the mechanisms influencing these patterns are well documented, less is known about the distribution of fish among different macrophyte types. We have previ-

ously reported significant differences in the abundance of juvenile and forage fishes among different macrophyte types in Lake Okeechobee, Florida (Chick & McIvor 1994). Habitat selection may be an important mechanism behind these patterns because macrophytes can differ in characteristics that may be detectable by fishes, such as plant density and architecture (Bell & Westoby 1986b, Dionne & Folt 1991, Lillie & Budd 1992), water chemistry (Frodge, Thomas & Pauley 1990), and availability of invertebrate prey (Krecker 1939, Chilton 1990, Kornijow & Gulati 1992, Lalonde & Downing 1992, Paterson 1993).

We conducted experiments to determine whether mosquitofish (*Gambusia holbrooki*), sailfin mollies (*Poecilia latipinna*), and dollar sunfish (*Lepomis marginatus*) would select among different macrophyte species in a manner that reflected the patterns of habitat use that we observed for these species in Lake Okeechobee (Fig. 1). Mosquitofish and sailfin mollies were used because they were very abundant during our field study (Chick & McIvor 1994) and

lend themselves well to laboratory experimentation (Meffe & Snelson 1989, Winkelman & Aho 1993). We used dollar sunfish because their distribution patterns differed from those we observed for mosquitofish and sailfin mollies (Fig. 1).

We examined habitat selection in the absence and presence of a predator. Comparing these patterns allowed us to determine whether predators significantly affected the habitat selection behavior of the three fishes. We also examined whether habitat selection patterns could be attributed solely to plant density, and whether the patterns varied among the three fishes as was observed in Lake Okeechobee.

Material and methods

Experimental animals

We collected fish by seining on and around boat ramps in Lake Okeechobee, Florida, where little aquatic vegetation occurred. The sizes of the prey fish used were: mosquitofish, 15–34 mm standard length (SL); sailfin mollies, 22–46 mm SL; and dollar sunfish, 34–58 mm SL. We used juvenile large-mouth bass (*Micropterus salmoides*, 80–120 mm SL) for predators. Fish were held in circular 61-cm diameter (D) tanks and fed commercial fish food. We acclimated fish to laboratory conditions for a minimum of 72 h prior to use in experiments. Large-mouth bass were starved for 24 h prior to being used in an experiment. Water temperature and oxygen concentration ranged from 19 to 22°C and 7.4 to 8.6 mg O₂ · l⁻¹ respectively.

Macrophytes

Macrophytes used in these experiments (*Hydrilla verticillata*, *Potamogeton illinoensis*, and *Panicum hemitomon*) corresponded to the habitats we sampled in the field (Chick & McIvor 1994). *H. verticillata* is a submersed plant with small leaves in whorls. *P. illinoensis* is submersed, with medium-sized lance-shaped leaves; and *P. hemitomon* is an emergent grass with round straight stems. To establish the plant densities to be used in these experiments, we sampled macrophytes in Lake Okeechobee in June 1991 (Table 1). We took 10 samples of each species from three areas along the western shore of the lake using a 25.4-cm D cylinder. Experimental plants used were collected from Lake Okeechobee and ponds in Gainesville, FL. We visually inspected and rinsed vegetation to remove any potential prey items before use in an experiment.

We placed plants in the experimental tanks in a manner approximating their typical appearance in Lake Okeechobee. Both *P. illinoensis* and *H. verti-*

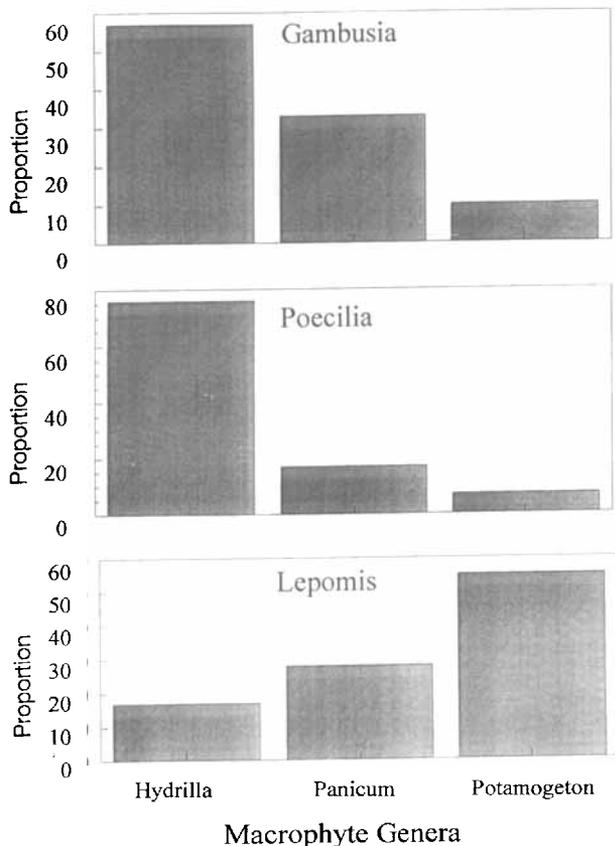


Fig. 1. The percentage of the total catch of *Gambusia holbrooki*, *Poecilia latipinna* and *Lepomis marginatus* in *H. verticillata* (Hydrilla), *P. hemitomon* (Panicum) and *P. illinoensis* (Potamogeton) in the littoral zone of Lake Okeechobee, Florida, December 1989 to December 1990. See Chick & McIvor (1994) for sampling details.

Habitat selection by three littoral zone fishes

Table 1. Average plant densities determined in the field, and the corresponding number of plants/disk used in experiments. SD=standard deviation.

Vegetation type	Field survey means (plants · m ⁻²)	Field survey SD	Corresponding plants per disc
<i>H. verticillata</i>	759	369	33
<i>P. hemitomom</i>	533	393	23
<i>P. illinoensis</i>	553	313	24
Overall mean	615	370	27

cillata plants extended from tank bottom to the surface of the water, and whole *P. hemitomom* plants (i.e., both submersed and emergent portions) were used. As *P. illinoensis* rarely grew in the absence of *Vallisneria americana* (a submersed macrophyte with long ribbon-like leaves), we included three to five *V. americana* plants in the *P. illinoensis* patches used in these experiments. *H. verticillata* often grows at the surface without rooting in the sediments, so the *H. verticillata* patches included three to five floating plants above the rooted plants.

Experimental tanks

Experiments were conducted in 1.22-m D by 0.91-m deep cylindrical tanks filled to a depth of 61 cm. To reduce outside disturbance, the area surrounding the tanks was enclosed in black plastic sheeting from floor to ceiling. Lighting was provided by a single fluorescent shop-light (two 40-w bulbs/fixture) centered 1.5 m above each tank. Black plastic sheeting was hung above the light and attached to the outside of the tanks just below the tank tops. We observed fish through three equally spaced windows (61 cm wide × 31 cm tall) fitted into the sides of each tank and covered with autoglass tint-film. The combination of the tint-film and the lack of lighting outside the tanks allowed us to observe fish without disturbing them. We divided the bottom of each tank into four equal areas (i.e., each comprising 25% of the total tank area), including a circular area in the center and three areas along the edge. Boundaries for the four areas were marked on the bottom of the tanks.

Plants were anchored by wooden clothespins glued to circular 29-cm D clay discs. We randomly assigned discs containing one of the three plant species to each of the three outer tank sections (a separate species in each area). A blank disc was placed in the center area. Plants were only placed in the outer three areas because fish are known to orient to the sides of tanks (Savino & Stein 1982, Gotceitas & Colgan 1987, Devries 1990). Because the outer three sections had equal amounts of tank side and window, we avoided possible confounding of plant type effects with possible artifacts from tank configuration.

Experimental design

We examined the habitat selection of the three prey fishes under two levels of predation risk (absence/presence of a largemouth bass) in three plant-density treatments. The plant-density treatments were natural (mean field densities of each species), equal (all at the same overall mean density), and a control treatment in which the anchoring disks without

plants were used (Table 1). Control treatments were used to assess effects of experimental artifacts (selection for tank areas, anchoring disks, or acclimation effects) on the behavior of the prey fishes. We used the equal density treatment to determine whether habitat selection that might be expressed in the natural plant-density treatments could be attributed to plant density alone. Each of the plant-density treatments was replicated three to four times per plant-density treatment for each of the prey fishes.

At the start of each experiment, we released 10 individuals of a single prey species into the center of the experimental tank. This density falls within the range of densities observed for these three species in Lake Okeechobee (Chick & McIvor 1994). After a 10-min acclimation period, the number of fish in each of the four sections was recorded. Additional counts were made every 10 min for one hour (six counts in all). After the first hour, we released a bass into the center of the tank (no predator was added in control treatments). After another 10-min acclimation period, the counting procedure for prey fish was repeated for a second hour. General behavioral observations were recorded throughout the experiments. Prey fish and the predator were transferred from holding tanks to the experimental tank via a small plastic container filled with water.

The second hour of data collection was not started until the predator was actively searching for prey (i.e. the acclimation period was extended until the predator was active). Experiments were terminated if the predator was not actively searching for prey after 20 min. In general, predators usually began to actively search for prey in 10 min or less, and the 10 min acclimation periods appeared to be adequate for the three prey species (i.e. after approximately 5 min, the general behavior of the fish remained relatively consistent over time).

Prey fish were never used in more than one replicate, whereas predators were used in multiple replicates because of the difficulty of collecting adequate numbers of juvenile largemouth bass. We randomly determined the order in which replicates were run (regarding fish species and plant density). After each replicate we removed the vegetation and

drained the tanks. We conducted this study from August through November 1991.

Data analysis

Because we counted the number of fish in a tank section, the four tank sections were the experimental units for this study, and the patches of vegetation placed within the tank sections were treatments applied to these experimental units. For each replicate, raw counts at each 10-min interval were converted to proportions, and the mean proportion of prey fish in the absence and presence of a predator was calculated for each section. To comply with assumptions of normality and homoscedasticity, we transformed all data to the arcsine of the square root of the proportion.

We used multivariate analysis of variance (MANOVA) to test for habitat selection differences among the prey species and plant-density treatments (prey, density, interaction) in the absence and presence of a predator. For this experimental design, knowing the proportion of organisms in three of the four areas mathematically determines the proportion of organisms in the fourth section. Therefore, it would be inappropriate to conduct the MANOVA using all four sections. Because we were interested in the responses fishes to the different macrophyte types, we formed response vectors from the proportion of fish in the three sections containing macrophytes (*H. verticillata*, *P. illinoensis*, *P. hemitomom*), dropping the center section (plant free).

Three specific MANOVAs were conducted to examine habitat selection: 1) in the absence of a predator, 2) in the presence of a predator, and 3) to test for differences between these two conditions. Wilk's lambda *P*-values were used to determine significance ($P \leq 0.05$). When main effects or interactions were significant, Hotelling's T^2 was used to further test for significance among the levels of the main effects.

To test for habitat selection in the absence of a predator we formed a response vector=(hyd-pan, hyd-pot, pot-pan); where hyd-pan refers to the difference in the proportion of fish in areas containing *H. verticillata* and the proportion of fish in areas containing *P. hemitomom*; hyd-pot refers to the difference in the proportion of fish in areas containing *H. verticillata* and the proportion of fish in areas containing *P. illinoensis*; etc. We only utilized observations made in the absence of a predator for this analysis (i.e. data from the first hour). To test for habitat selection in the presence of a predator we ran the same MANOVA, but only utilized observations made in the presence of a predator (i.e. data from the second hour).

To test for shifts in the patterns of habitat selection after the introduction of a predator, we formed a response vector (hyd-phyd, pan-ppan, pot-ppot); where hyd-phyd is the difference in the proportion of fish in areas containing *H. verticillata* in the absence and presence of a predator; pan-ppan is the difference in the proportion of fish in areas containing *P. hemitomom* in the absence and presence of a predator; etc. This analysis is similar to, but more restricted than, a repeated measures MANOVA.

Results

Habitat selection in the absence of a predator

Neither the prey nor density main effects were significant, nor was there a significant interaction (Table 2). Thus, we have little evidence from this analysis that prey fish selected among the macrophytes when a predator was not present in the tank (Fig. 2-4, clear bars).

Habitat selection in the presence of a predator

In the presence of a predator, the distribution of fish among tank areas containing macrophytes differed significantly among the prey species (Table 2). Specific contrasts (using Hotelling's T^2) revealed that the habitat selection of mosquitofish and sailfin mollies did not differ significantly ($P=0.1334$), whereas the habitat selection of dollar sunfish was significantly different from both mosquitofish ($P=0.0449$) and sailfin mollies ($P=0.0299$). The prey×density interaction was also significant, suggesting that patterns among the plant- density treatments differed among of the three prey fishes (Fig. 2-4). The patterns of habitat selection in each of the plant-density treatments are described for each of the prey species below.

Differences in habitat selection patterns in the presence and absence of a predator

In this analysis, both the prey and density main effects were significant, as was their interaction. Spe-

Table 2. Results from the MANOVAs examining habitat selection in the absence and presence of a predator, and testing for differences between these two conditions.

Source	df	MANOVA		
		<i>P</i> No predator	<i>P</i> With predator	<i>P</i> Differences
Prey	4	0.7067	0.0231	0.0341
Density	4	0.2928	0.2497	0.0237
Prey × density	8	0.6860	0.0489	0.0028

Gambusia

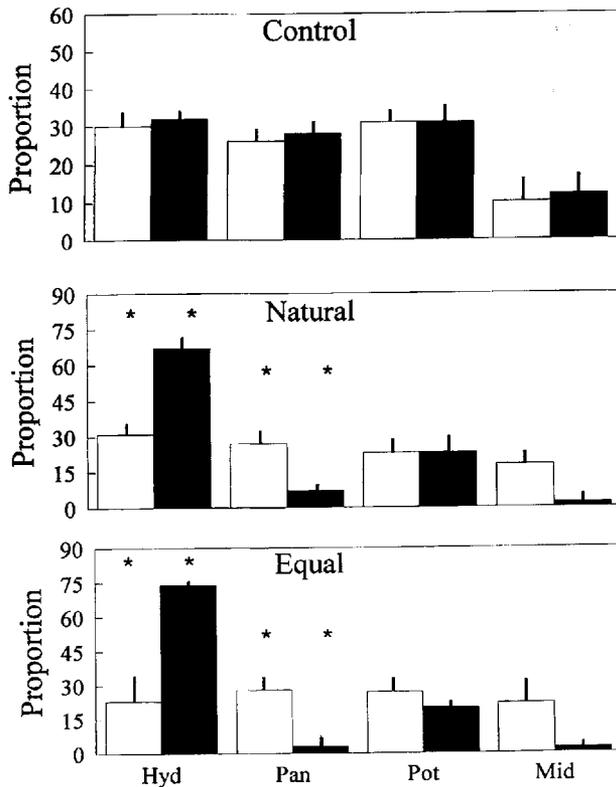


Fig. 2. Mean proportion of *Gambusia holbrooki* in the four tank areas, both without a predator (clear bars) and with a predator (dark bars), in the three plant-density treatments. Error bars are 1 Standard error above the mean. Hyd = tank areas with *H. verticillata*, Pan=tank areas with *P. hemitomon*, Pot=tank areas with *P. illinoensis*. Asterisks denote shifts (predator absent vs. predator present) that were significant at the $\alpha=0.05$ level.

cific contrasts revealed that behavior of the prey species in control treatments differed significantly from the natural plant-density treatments ($P=0.0103$), but was not significantly different from equal plant-density treatments ($P=0.2076$). The equal and natural plant-density treatments also did not significantly differ ($P=0.1116$). These contrasts, however, were somewhat obscured because the differences among the plant-density treatments were not consistent across all three prey species.

Mosquitofish. When a predator was present in the natural and equal plant-density treatments, the proportion of mosquitofish increased significantly ($P=0.0499, 0.0047$) in areas that contained *H. verticillata*, and decreased significantly ($P=0.0204, 0.0042$) in areas that contained *P. hemitomon* (Fig. 2). Mosquitofish displayed no selection for any of the tank areas in control experiments. In the equal and natural plant-density treatments the mean number of mosquitofish consumed by largemouth bass were

Lepomis

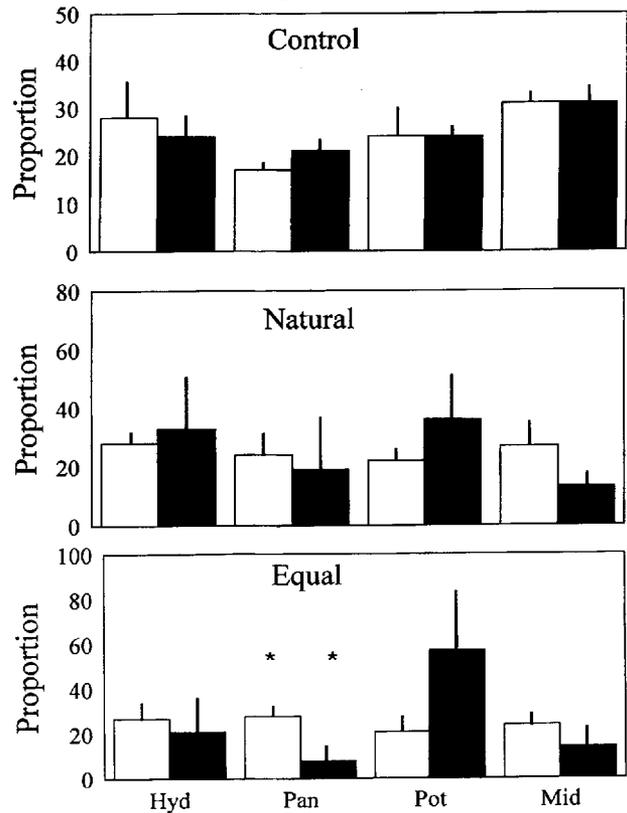


Fig. 3. Mean proportion of *Poecilia latipinna* in the four tank areas, both without a predator (clear bars) and with a predator (dark bars), in the three plant-density treatments. Error bars are 1 Standard error above the mean. Hyd=tank areas with *H. verticillata*, Pan=tank areas with *P. hemitomon*, Pot=tank areas with *P. illinoensis*. Asterisks denote shifts (predator absent vs. predator present) that were significant at the $\alpha=0.05$ level.

2.57. This amount of mortality could theoretically account for a significant decrease in the proportion of mosquitofish in areas containing *P. hemitomon*, but could not account for a concurrent increase in the proportion of mosquitofish in areas containing *H. verticillata*. Because the patterns of habitat selection were similar in both the equal and natural plant-density treatments, mosquitofish habitat selection cannot be attributed solely to plant density.

Dollar sunfish. Dollar sunfish displayed no selection for any of the tank areas in control treatments, and displayed no significant habitat selection in natural plant-density treatments. In equal plant-density treatments, the presence of a predator led to significant ($P=0.0477$) decreases in the proportions of dollar sunfish in areas containing *P. hemitomon*, and increased proportions in areas containing *P. illinoensis* that approached significance ($P=0.0583$, Fig. 3). These shifts cannot be attributed to plant density because they occurred in the equal plant-density treat-

Poecilia

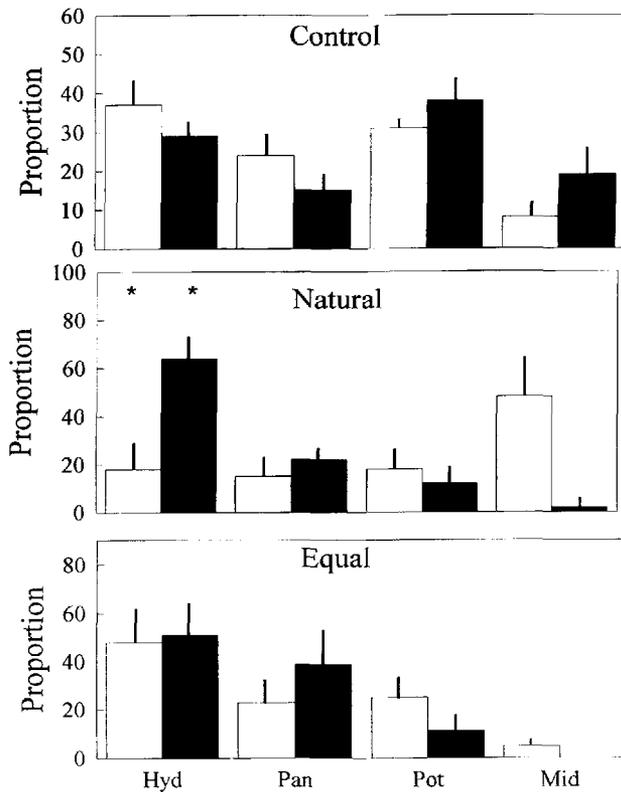


Fig. 4. Mean proportion of *Lepomis marginatus* in the four tank areas, both without (clear bars) and with (dark bars) a predator, in the three density treatments. Error bars are 1 standard error above the mean. Hyd=tank areas with *H. verticillata*, Pan=tank areas with *P. hemitomon*, Pot=tank areas with *P. illinoensis*. Asterisks denote shifts (predator absent vs. predator present) that were significant at the $\alpha=0.05$ level.

ment. Differential mortality cannot account for these shifts, as only one dollar sunfish was consumed in all of the equal plant-density treatment replicates.

Sailfin mollies. Sailfin mollies displayed no selection for any of the tank areas in control experiments, and displayed no significant response to predator presence in equal plant-density treatments. In natural plant-density treatments, the presence of a predator led to significantly ($P=0.0075$) increased proportions of sailfin mollies in areas containing *H. verticillata* (Fig. 4). An average of 1.75 sailfin mollies were consumed in the natural plant-density treatments, which cannot account for the significant increases in areas containing *H. verticillata*. Because habitat selection was not significant in the equal plant-density treatments, we cannot reject the hypothesis that the patterns of habitat selection observed in the natural plant-density treatments were based solely on plant density.

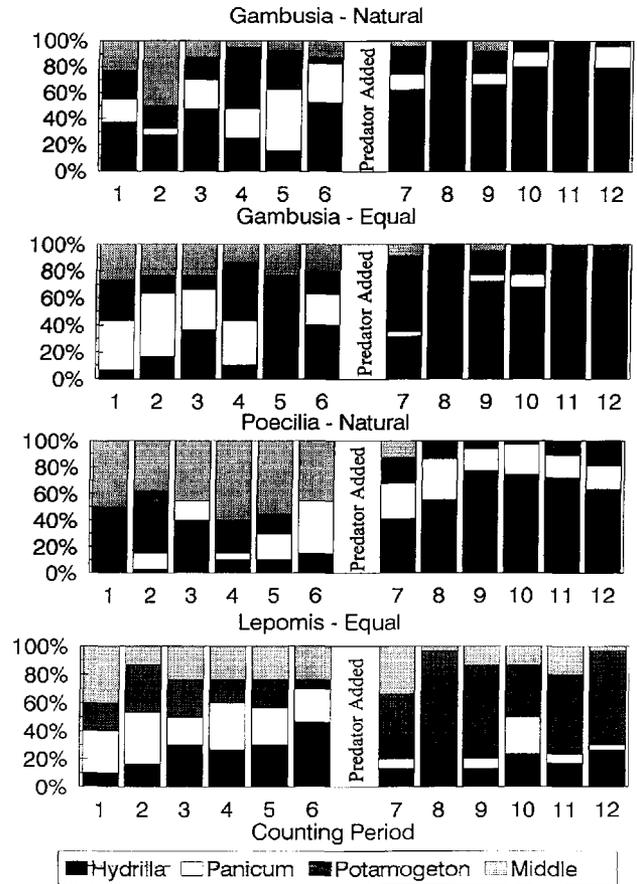


Fig. 5. Mean proportion of prey fish in the four tank areas for treatments in which significant habitat selection occurred. Counting periods 1-6 occurred in the absence of a predator, whereas counting periods 7-12 occurred in the presence of a predator.

The significance of the interaction terms in the MANOVA's discussed above was influenced by the fact that none of the three prey fishes selected habitats (i.e., selected among tank areas) in the control treatments. The three prey fishes also responded differently to the natural and equal plant-density treatments. In response to predator presence, mosquitofish displayed significant shifts in habitat selection in both the natural and equal plant-density treatments, whereas sailfin mollies only displayed habitat shifts in the natural plant-density treatments and dollar sunfish only displayed habitat shifts in the equal plant-density treatments.

Discussion

In general, when the three prey species displayed significant macrophyte-specific selection in response to predator presence, the patterns of habitat selection were similar to the patterns of habitat use

observed in Lake Okeechobee (Fig. 1). In Lake Okeechobee, mosquito fish and sailfin mollies were captured most frequently in *H. verticillata*, whereas dollar sunfish were most frequently captured in *P. illinoensis*. This corresponds to the patterns of habitat selection that we observed in the presence of a predator (Fig. 2–4, dark bars). Our results suggest that patterns in the abundance and composition of fishes among the different macrophytes, such as those observed in Lake Okeechobee, may be influenced by habitat selection in response to predation risk (Chick & McIvor 1994).

The lack of selection in the control treatments indicates that there were minimal experimental artifacts (i.e., inherent differences among the outer tank areas) affecting the distribution of fish in the tank, and negligible behavior towards the clay discs used to anchor plants. We concluded, therefore, that the habitat selection in the equal and natural plant-density treatments can be attributed to the presence of the macrophytes rather than experimental artifacts.

Control treatments were designed primarily to assess any effects due to experimental artifacts. Because macrophytes were not present in control treatments we cannot state unequivocally that the habitat selection observed during the second hour would not have occurred in the absence of a predator. Nevertheless, the presence of an active predator had obvious effects on the behavior of the prey fishes. When no predator was present, fish freely explored all areas of the tank (Fig. 5, counting periods 1–6). The presence of an active predator changed this behavior as fish quickly sought cover within the patches of vegetation (Fig. 5, counting periods 7–12). Fish generally avoided spending time away from cover and remained relatively motionless in the patches so long as the predator was actively searching for prey. Given these behavioral changes, it is unlikely that the macrophyte-specific selection of the three prey fishes was unrelated to the presence of a predator. It is possible, however, that fish may have eventually displayed significant habitat selection in the absence of a predator if they had been observed over a longer time period.

Differences in the behavior of fish between the natural and equal plant-density treatments were not consistent among the three prey species. Mosquito fish differentially selected among the macrophytes in both the natural and equal plant-density treatments, whereas sailfin mollies only displayed selection in the natural, and dollar sunfish only in the equal plant-density treatment. Other studies have found plant density to be an important factor affecting the habitat selection of fish (Bell & Westoby 1986b, Gotceitas & Colgan 1987, 1990). The lack of consistent behavioral differences between the

equal and natural plant-density treatments may reflect the relatively small range of plant densities examined in this study and insufficient time for fish to acclimate and respond to these differences. Nevertheless, the fact that mosquitofish and dollar sunfish showed selection in the equal plant-density treatment suggests that vegetation characteristics other than plant density may also be important to the habitat selection of fish avoiding predators.

For example, recent studies have shown or hypothesized that plant growth form or architecture can significantly affect the foraging ability of fish and may be a useful index of habitat quality (Ryer 1988, Dionne & Folt 1991, Lillie & Budd 1992). Growth forms of the three vegetation types used in this study exhibited obvious differences. In addition to differences in the size and distribution of leaves, canopy branching of *H. verticillata* offers more cover near the surface than either *P. illinoensis* or *P. hemitomon*. In our study, mosquitofish and sailfin mollies generally hid in *H. verticillata* patches near the surface when in the presence of a predator, apparently taking advantage of the surface cover that *H. verticillata* provides.

In the equal plant-density treatments, dollar sunfish generally stayed in *P. illinoensis* patches at mid-depth or near the bottom. The habitat preferences of dollar sunfish, however, were not as consistent as those of sailfin mollies and mosquitofish. One possible explanation is that the larger size of these fish made them less vulnerable to the predators used in these experiments. Indeed, fewer dollar sunfish were consumed during these experiments (0–1 per replicate) than either mosquitofish or sailfin mollies (1–4 per replicate).

All three prey species demonstrated some level of macrophyte-specific habitat selection in response to the presence of a predator. Our results are consistent with the premise that fish have the ability to select among a variety of different habitat types (Bell & Westoby 1986a, Gotceitas & Colgan 1987, 1990, Holbrook & Schmitt 1988, Savino & Stein 1989b, Devries 1990, Wildhaber & Crowder 1991), and that predation can have important effects on fish behavior (Stein 1979, Helfman 1986, Kerfoot & Sih 1987, Heck & Crowder 1991). Conversely, in the absence of a predator, little habitat selection was apparent.

In nature, several factors other than predation risk might lead to differential use of, and selection for, different macrophyte types by fishes. Aquatic macrophyte species may differ in the abundance of important prey items of fish such as macroinvertebrates (Krecker 1939, Chilton 1990, Kornijow & Gulati 1992, Lalonde & Downing 1992, Paterson 1993), and may affect several water quality param-

ters (Barko et al. 1988, Frodge et al. 1990). In this study, we attempted to exclude potential prey items from the patches of macrophytes used, and no measurable differences in either temperature or dissolved oxygen (measured in a subsample of the experiments) were apparent among the patches of different macrophytes. Thus, the lack of habitat selection in the absence of a predator might simply reflect the absence of any factors, other than predation risk, that could have provided the impetus for habitat selection.

Non-lethal effects of predators on fish populations and communities have become an important research topic (Fraser & Gilliam 1992, Winkelman & Aho 1993). Our study suggests that small forage fishes may be able to select among different macrophytes when confronted with predation risk. This behavior could have important consequences for several other processes, including changes in the rate of cannibalism (Winkelman & Aho 1993), growth and reproduction (Fraser & Gilliam 1992), and interspecific and intraspecific competition (Mittelbach 1986, 1988).

Resumen

1. Realizamos experimentos de laboratorio que demostraron que tres especies típicas de litoral seleccionaron entre tres macrófitas distintas en la búsqueda de refugio ante la presencia de un predador. En presencia del predador, juvenil de *Micropterus salmoides*, *Gambusia holbrooki*, *Poecilia latipinna* y *Lepomis marginatus*, utilizaron de forma distinta cuatro zonas de tanques que o bien no contenían vegetación o bien contenían *Hydrilla verticillata*, *Potamogeton illinoensis* ó *Panicum hemitomon*.
2. Los patrones de selección de hábitat, y la consistencia de estos patrones entre las repeticiones experimentales, fué distinto tanto entre las especies como entre los tres tratamientos realizados en condiciones de distintas densidades de vegetación. Estas condiciones de densidad de vegetación fueron las siguientes: natural (cada especie macrófita con la misma densidad que en condiciones naturales), en equilibrio (las tres especies con la misma densidad), y control (sin vegetación).
3. *Gambusia holbrooki* seleccionó a *H. verticillata* de forma significativa, tanto en condiciones de equilibrio como naturales, mientras que *P. latipinna* sólo mostró selección significativa hacia *H. verticillata* en condiciones naturales. Por último, *L. marginatus* mostró una selección menos consistente que *G. holbrooki* y *P. latipinna*. No se encontró selección de hábitat ni en ausencia de predador ni en los tratamientos control.
4. Los patrones de selección de hábitat en nuestro estudio se corresponden con el uso de hábitat observado en las poblaciones naturales del Lago Okeechobee (Florida, USA).

Acknowledgments

We thank Kristina Jackson and Eric Flickenger for their assistance in the laboratory and field. Gary Grossman, Frank Jordan, Thomas Reinert, Julie Wallin and Dana Winkelman provided helpful reviews of this manuscript. This research was com-

pleted in partial fulfillment of the requirements of the M.S. degree in the Department of Fisheries and Aquatic Sciences at the University of Florida. We thank Dan Canfield, Chuck Cichra and Wiley Kitchens for their contributions toward this work as part of Mr. Chick's graduate committee. We thank the National Biological Survey, Southeastern Biological Science Center, Gainesville, FL; the Florida Cooperative Fish and Wildlife Research Unit; and the Department of Fisheries and Aquaculture at the University of Florida for providing laboratory space and equipment used in these experiments. Funding for this research was provided by the South Florida Water Management District. This is Journal series number 00000 of the Florida Agricultural Experiment Station.

References

- Barko, J. W., Godshalk, G. L., Carter, V. & Rybicki, N. B. 1988. Effects of submersed aquatic macrophytes on physical and chemical properties of surrounding water. Aquatic Plant Control Research Program Technical Report A-88-11, Department Army, U.S. Army Corps of Engineers, Washington, D.C. 28 pp.
- Bell, J. D. & Westoby, M. 1986a. Abundance of macrofauna in dense seagrass is due to habitat preference, not predation. *Oecologia* 68: 205-209.
- Bell, J. D. & Westoby, M. 1986b. Variation in seagrass height and density over a wide spatial scale: effects on common fish and decapods. *Journal of Experimental Marine Ecology* 104: 275-295.
- Chick, J. H. & McIvor, C. C. 1994. Patterns in the abundance and composition of fishes among beds of different macrophytes: viewing a littoral zone as a landscape. *Canadian Journal of Fisheries and Aquatic Sciences* 51: 2873-2882.
- Chilton, E. W. 1990. Macroinvertebrate communities associated with three aquatic macrophytes (*Ceratophyllum demersum*, *Myriophyllum spicatum*, and *Vallisneria americana*) in Lake Onalaska, Wisconsin. *Journal of Freshwater Ecology* 5: 455-466.
- Conrow, R., Zale, A. V. & Gregory, R. W. 1990. Distributions and abundances of early life stages of fishes in a Florida lake dominated by aquatic macrophytes. *Transactions of the American Fisheries Society* 119: 521-528.
- Devries, D. R. 1990. Habitat use by bluegill in laboratory pools: Where is the refuge when macrophytes are sparse and alternative prey are present? *Environmental Biology of Fishes* 29: 27-34.
- Dionne, M. & Folt, C. L. 1991. An experimental analysis of macrophyte growth forms as fish foraging habitat. *Canadian Journal of Fisheries and Aquatic Sciences* 48: 123-131.
- Fraser, D. F. & Gilliam, J. F. 1992. Nonlethal impacts of predator invasion: facultative suppression of growth and reproduction. *Ecology* 73: 959-970.
- Frodge, J. D., Thomas, A. L. & Pauley, G.B. 1990. Effects of canopy formation by floating and submerged aquatic macrophytes on the water quality of two shallow Pacific Northwest lakes. *Aquatic Botany* 38: 231-248.
- Gelwick, F. P. & Matthews, W. J. 1990. Temporal and spatial patterns in littoral zone fish assemblages of a reservoir (Lake Texoma, Oklahoma-Texas, U.S.A.). *Environmental Biology of Fishes* 27: 107-120.
- Gotceitas, V. & Colgan, P. 1987. Selection between densities of artificial vegetation by young bluegill sunfish avoiding predation. *Transactions of the American Fisheries Society* 116: 40-49.
- Gotceitas, V. & Colgan, P. 1990. The effects of prey availability

Habitat selection by three littoral zone fishes

- and predation risk on habitat selection by juvenile bluegill sunfish. *Copeia* 2: 409–417.
- Hall, D. J. & Werner, E. E. 1977. Seasonal distribution and abundance of fishes in the littoral zone of a Michigan lake. *Transactions of the American Fisheries Society* 106: 545–555.
- Heck, K. L. & Crowder, L. B. 1991. Habitat structure and predator-prey interactions in vegetated aquatic systems. In: Bell, S. S., McCoy, E. D. & Muchinsky, H., ed. *Habitat structure: the physical arrangement of objects in space*. New York: Chapman Hall, pp. 281–299.
- Helfman, G. F. 1986. Behavioral responses of prey fishes during predator-prey interactions. In: Feder, M.E. & Lauder G.V., ed. *Predator-prey relations: perspectives and approaches from the study of lower vertebrates*. Chicago: University of Chicago Press, pp. 135–157.
- Holbrook, S. J. & Schmitt, R. J. 1988. Effects of predation risk on foraging behavior: mechanisms altering patch choice. *Journal of Experimental Marine Ecology* 121: 151–163.
- Kerfoot, W. C. & Sih, A. 1987. *Predation: direct and indirect impacts on aquatic communities*. Hanover, NH: University Press of New England, 386 pp.
- Krecker, F. 1939. A comparative study of the animal population of certain submersed aquatic plants. *Ecology* 20: 553–562.
- Kornijow, R. & Gulati, R. D. 1992. Macrofauna and its ecology in Lake Zwemlust, after biomanipulation. II. Fauna inhabiting hydrophytes. *Archives of Hydrobiologia* 123: 349–359.
- Lillie, R. A. & Budd, J. 1992. Habitat architecture of *Meriophyllum spicatum* L. as an index to habitat quality for fish and macroinvertebrates. *Journal of Freshwater Ecology* 7: 113–125.
- Lalonde, S. & Downing, J. A. 1992. Phytofauna of eleven macrophyte beds of differing trophic status, depth, and composition. *Canadian Journal of Fisheries and Aquatic Sciences* 49: 992–1000.
- McIvor, C. C. & Odum, W. E. 1988. Food, predation risk, and microhabitat selection in a marsh fish assemblage. *Ecology* 69: 1341–1351.
- Meals, K. O. & Miranda, L. E. 1991. Variability in abundance of age-0 centrarchids among littoral habitats of flood control reservoirs in Mississippi. *North American Journal of Fish Management* 11: 298–304.
- Meffe, G. K. & Snelson, F. F. 1989. *Ecology and evolution of livebearing fishes (Poeciliidae)*. New Jersey: Prentice Hall, 453 pp.
- Mittelbach, G. G. 1986. Predator-mediated habitat use: some consequences for species interactions. *Environmental Biology of Fishes* 16: 159–169.
- Mittelbach, G. G. 1988. Competition among refuging sunfishes and effects of fish density on littoral invertebrates. *Ecology* 69: 614–623.
- Paterson, M. 1993. The distribution of microcrustacea in the littoral zone of a freshwater lake. *Hydrobiologia* 263: 173–183.
- Rozas, L. P. & Odum, W. E. 1988. Occupation of submerged aquatic vegetation by fishes: testing the roles of food and refuge. *Oecologia* 77: 101–106.
- Ryer, C. H. 1988. Pipefish foraging: effects of fish size, prey size and altered habitat complexity. *Marine Ecology Progress Series* 48: 37–45.
- Savino, J. F. & Stein, R. A. 1982. Predator-prey interaction between largemouth bass and bluegills as influenced by simulated, submersed vegetation. *Transactions of the American Fisheries Society* 111: 255–266.
- Savino, J. F. & Stein, R. A. 1989a. Behavior of fish predators and their prey: habitat choice between open water and dense vegetation. *Environmental Biology of Fishes* 24: 287–293.
- Savino, J. F. & Stein, R. A. 1989b. Behavioral interactions between fish predators and their prey: effects of plant density. *Animal Behavior* 37: 311–321.
- Stein, R. A. 1979. Behavioral response of prey to fish predators. In: Stroud, R. H. & Clepper H., ed. *Predator-prey systems in fisheries management*. Washington DC: Sport Fishing Institute, pp. 343–353.
- Werner, E. E., Hall, D. J. & Werner, M. D. 1978. Littoral zone fish communities of two Florida lakes and a comparison with Michigan lakes. *Environmental Biology of Fishes* 3: 163–172.
- Wildhaber, M. L. & Crowder, L. B. 1991. Mechanisms of patch choice by bluegills (*Lepomis macrochirus*) foraging in a variable environment. *Copeia* 2: 445–460.
- Winfield, I. J. 1986. The influence of simulated aquatic macrophytes on the zooplankton consumption rate of juvenile roach, *Rutilus rutilus*, rudd, *Scardinius erythrophthalmus*, and perch, *Perca fluviatilis*. *Journal of Fish Biology* 29(supplement A): 37–48.
- Winkelman, D. L. & Aho, J. M. 1993. Direct and indirect effects of predation on mosquitofish behavior and survival. *Oecologia* 96: 300–303.