

Conditional Use of Mangrove Habitats by Fishes: Depth as a Cue to Avoid Predators

WILLIAM L. ELLIS* and SUSAN S. BELL

Biology Department, SCA(110), University of South Florida, 4202 East Fowler Avenue, Tampa, Florida 33620

ABSTRACT: The flooded intertidal zone in coastal estuarine systems (e.g., mangroves and salt marshes) is thought to provide nekton with both food and refuge from predators. The primary aim of this study was to identify the relative contribution of root structure, shading, and leaf litter, all characteristic features of mangrove forests, in shaping the intertidal distribution of tidally migrating fishes. We manipulated the structure and shade in 9-m² sample plots in a shallow, mangrove-fringed, intertidal embayment in Tampa Bay, Florida. In a separate field experiment, we compared fish association with standing mangrove leaf litter and bare sand substrate. Shade and leaf litter had a water depth-dependent effect on the distribution of the fish; no effect was associated with the presence of mangrove roots. In shallow water (< 45 cm), fish were captured primarily in plots without shade, but this distribution shifted progressively with increasing water depth, so that when water was greater than 55 cm most fish were captured in shaded plots. Fish were more frequently associated with, and feeding in, plots covered in leaf litter than bare sand plots. This relationship did not persist at depths greater than 15 cm because fish abundance declined greatly. Tethering experiments using *Cyprinodon variegatus* demonstrated that predation pressure was quadratically correlated with water depth (inflection point approximately 60 cm). Our results suggest that small fishes will abandon well-lighted foraging grounds in favor of the potential refuge of shaded waters as water depth increases. We suggest that studies of intertidal nekton should be carefully interpreted in the context of water depth.

Introduction

The flooded intertidal zone of coastal habitats is used extensively by nektonic fauna (Thayer et al. 1987; Irlandi and Crawford 1997; Layman 2000; Clynick and Chapman 2002; Hindell and Jenkins 2004). Although the drainage of the intertidal zone can displace nektonic organisms by great distances into the subtidal zone (Gibson 1973; Lotrich 1975; Sweeney et al. 1998), they commonly return to the intertidal zone during subsequent high tides (Gibson 2003). Attempts to explain the association between nekton and the intertidal zone include suggestions that intertidal areas contain abundant resources and possess characteristics that could reduce threats from predators (Boesch and Turner 1984; Kneib 1984, 1987; but see Sheridan and Hays 2003). The intertidal distribution of nekton is seldom spatially or temporally homogenous (Rozas and Zimmerman 2000; Rönnbäck et al. 2002; Vance et al. 2002) suggesting that opportunities for feeding and sheltering from predators are themselves unevenly distributed even within the intertidal zone (Brown 1988; Kennedy and Gray 1993; Miltner et al. 1995).

The distribution of nekton is influenced by the arrangement of structurally complex microhabitats

within larger landscapes. Fish and crustaceans are frequently associated with structurally complex habitats that provide a refuge from predators (relative to structurally depauperate areas; Jenkins and Wheatley 1998; Moksnes et al. 1998). Submerged structure serves as a refuge from predators (Crowder and Cooper 1982; Rozas and Odum 1988; Everett and Ruiz 1993) as it impairs predator movement (Minello and Zimmerman 1983; Bartholomew et al. 2000) and interrupts the predator's visual contact with prey items (Savino and Stein 1982). Within the intertidal zone of salt marshes, the distribution of nekton has been linked to that of emergent vegetation (Hettler 1989; Ellis 1995; Rozas and Zimmerman 2000). Rönnbäck et al. (1999) found that structural complexity within the mangrove intertidal zone influenced the distribution of shrimp and fish. Others have not found this relationship in mangroves (Sheridan 1992; Mullin 1995; Meager et al. 2003) despite evidence that mangrove structures offer increased survivorship in the presence of predators (Acosta and Butler 1997; Primavera 1997).

Water depth, generally uneven over the surface of the flooded intertidal zone, also shapes the distribution of nekton in a variety of habitats (Blaber and Blaber 1980; Sogard et al. 1989; McDonald et al. 1992; Ruiz et al. 1993; Laffaille et al. 2001). This effect is commonly exhibited in the intertidal zone

* Corresponding author; tele: 813/974-5420; e-mail: wellis@chuma1.cas.usf.edu

as a segregation of nekton by body size along the water depth gradient (Kneib 1987; Sogard et al. 1989; Paterson and Whitfield 2000; Gibson et al. 2002), which may reduce predator-prey encounter rates (McIvor and Odum 1988; Ruiz et al. 1993; Gibson et al. 1998; Linehan et al. 2001). Water depth has been identified by some as an important determinant of the distribution of nekton within the mangrove intertidal zone (Vance et al. 1996; Ley et al. 1999) while others have reported a lack of such an influence (Sheridan 1992; Halliday and Young 1996; Meager et al. 2003).

The mangrove canopy, a distinctive attribute of the mangrove intertidal zone, may also play a significant role in shaping the faunal community of mangrove-dominated habitats. Shade provides a source of protection from predators (Wesche et al. 1987), although the influence of canopy shading by mangroves on nekton distribution has been the subject of limited investigation (Laegdsgaard and Johnson 2001). Shaded areas are actively selected by some fish species (Casterlin and Reynolds 1978; Hair et al. 1994; Kogane et al. 1996) even when conditions within the shaded areas are otherwise unfavorable (Scherer and McNicol 1998). In fact, some species select structurally simple habitats with low ambient light preferentially over structurally complex, but well-lighted habitats (Goddard and Mathis 1997). Shade reduces the visibility of nekton, making them less susceptible to some predators (Helfman 1981; McCartt et al. 1997). In conjunction with shading, the mangrove canopy sheds leaves that are a food source of debatable quality and importance to nekton (see review by Sheridan and Hays 2003), but have been demonstrated to attract fish and crustaceans as they decompose on the mangrove forest floor (Rajendran and Kathiresan 1999).

The primary aim of this study was to examine the association of mangrove fishes with mangrove root structure, shading, and leaf litter. A set of experimental field studies was conducted to identify the relative contribution of each of these features in shaping the intertidal distribution of mangrove-associated fishes. To aid in the interpretation of findings, an examination of the influence of water depth on the potential predation risk faced by these fishes was also conducted.

Methods

Studies were carried out between 1996 and 2002 in a sandy, mangrove-rimmed (*Rhizophora mangle*, *Avicennia germinans*, and *Laguncularia racemosa*), intertidal embayment of Tampa Bay, Florida (Fig. 1). Tampa Bay (27°53'N, 82°39'W), at the northern latitudinal boundary for mangroves in the United States, is subject to a mixed tidal pattern (mean

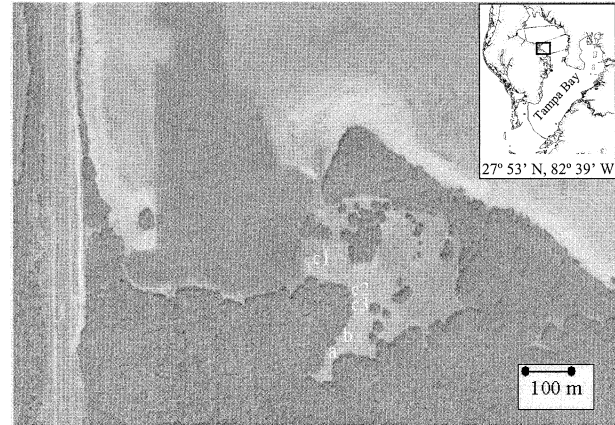


Fig. 1. Study site location in Tampa Bay, Florida (USA). All experiments and observations were conducted in this unnamed mangrove-fringed embayment. These included a shade-structure study (Point a), a visual examination of fish attraction to leaf litter (Point b), and fish tethering trials over depth (Points c1, c2, and c3).

tidal range = 0.7 m). Salinity varies seasonally in this estuarine system (range 15–38‰).

In 1996, six 9.0-m² (4-mm mesh) bottomless lift nets (Rozas 1992) with polyvinyl chloride-lined trenches were permanently positioned in the western portion of the embayment (Fig. 1, Point a). When sampling, nekton were collected from each lift net by 3 repeated sweeps of a purse seine net. In each sweep, the purse seine net was fixed at one end to the interior of the lift net wall via clamps while the free end was walked completely around the interior perimeter of the lift net. When the two ends (one free, the other fixed to the lift net wall) of the purse seine net met, a draw string affixed to the bottom of the purse seine net was pulled, collapsing the netting and trapping the fish. Little disturbance of the featureless sand bottom was noticeable after sampling. Recapture efficiency trials ($n = 2$) using fifty *Cyprinodon variegatus* per net indicated that an average of $92 \pm 9\%$ (mean \pm SE) of the fish in the lift net was recovered.

INITIAL SHADE STUDY

Back plastic tarps (9.0-m²) were suspended 0.25 m over the high tide water surface from the support posts of four of the six lift nets. These tarps were either left intact, simulating a complete mangrove canopy (total shading) or punctured with holes (approximately 6 cm diam) removing 30% of the tarp area and simulating an open mangrove canopy (partial shading). Tarp treatment (total shade, partial shade, or no shade) for the lift nets was randomly assigned (2 replicates each) at least 18 h prior to sampling. Sampling was conducted at high tide on seven separate dates and on the

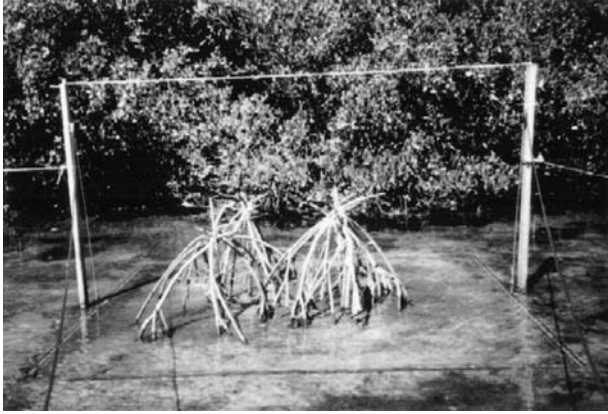


Fig. 2. Prop root bundles in lift net plot. Four prop root bundles were placed in the interior of each structure-containing plot.

ebbing tide on a single occasion. The nets were lifted, two at a time, until all nets were raised (total time 5 min). All fish collected from the nets were immediately stored on ice and later identified to species. Fish abundance data were analyzed using a two-way analysis of variance (ANOVA) with shade level and date as treatment factors. Student-Newman-Keuls (SNK) tests were used to perform multiple comparisons of treatment factor means while controlling for family-wise experimental error ($\alpha = 0.05$).

SHADE-STRUCTURE STUDY

In 1998, the partial shade treatment was eliminated and mangrove root structures were added as an additional treatment element. In order to create a balanced design with which to test the fish attractant qualities of shade, structure, and their interaction, two additional lift nets were installed in the embayment. Mangrove root bundles were made from *R. mangle* prop roots pruned from nearby mangroves. Each bundle included four highly branched prop roots that were devoid of epibionts (i.e., barnacles, oyster, or bryozoans). These four prop roots were attached to a central wooden rod using cable ties and configured to resemble natural mangrove structure with prop roots radiating out and down from the central dowel. Four of these root bundles were placed in each of four lift net plots designated as structure plots (Fig. 2). These structure plots had a resulting root density of approximately 16 roots m^{-2} . At least 18 h prior to a sampling event, the shade tarps and root bundles were randomly assigned to a net so that each of 5 sampling dates included two replicates of each treatment type: shade-structure, shade-no structure, no shade-structure, and no shade-no structure. The root bundles were removed from

each net after the walls were lifted but prior to collecting nekton with the purse seine net. Fish abundance data were analyzed by means of a three-way ANOVA (shade, structure, and date). SNK tests were used to perform multiple comparisons of treatment factor means while controlling for family-wise experimental error ($\alpha = 0.05$).

ANALYSIS OF COMBINED DATA SETS

The two data sets (i.e., from Initial Shade Study and Shade-structure Study) were combined so that the influence of shade could be detected. Given a lack of statistically significant difference between them, the partial and total shading treatments were pooled into a single category, shaded. Since this pooling and the dissimilarity in the number of sampling plots for each date resulted in a lack of balance between shaded and unshaded replicate plots, the average nekton density per plot per treatment level (shaded or unshaded) per date was used in the analysis as the response variable. These data were then analyzed using a G-test with replication ($\alpha \leq 0.05$) under the null hypothesis that 50% of the total mean density of fish would be found in each plot type (Sokal and Rohlf 1981). Deviations from this prediction ($\alpha \leq 0.05$) were interpreted as an indication of a shading effect. The statistical significance of the deviation from this 50% prediction for each sampling date also was calculated.

MANGROVE LITTER AS A FISH ATTRACTANT

In the investigation of fish association with various mangrove features, leaf litter was not included in the shade-structure lift net trials due to logistical constraints. Litter, if present in appreciable quantities in the lift net-bounded plots would degrade the efficiency of purse seine net fish collections. Aged litter also contains fine organic particles that could not be effectively removed and randomly re-assigned to another plot for each trial without leaving potentially confounding remnants behind. A separate experimental layout was used to determine the degree of association between fishes and mangrove litter.

A series of eight 1.0-m² plots, each delineated at their corners by plastic tent stakes, was created in the sandy intertidal of the shallow embayment in which the shade-structure lift net study was conducted (Fig. 1, Point b). These plots were arranged in two rows and placed 1.25 m apart. Mangrove litter, mostly decaying *Rhizophora* leaves, was hand collected from the ground in the subcanopy intertidal zone of nearby mangrove stands and placed in four of the plots so that the entire area within each plot was covered by at least a 1 cm depth of litter. Two plots in each row were covered in litter

so that an alternating pattern of litter-covered and bare plots was created.

The litter plots were observed by a researcher at the onset of tidal flooding of the intertidal zone on October 6, 2001, using binoculars from an elevated position 5 m away (Lorenz et al. 1997). The inundation depth, number of fish, species composition, and the presence or absence of feeding behavior was noted for each plot at 5-min intervals and continued until the water depth made it too difficult to enumerate and identify fish (approximately 25 cm deep). The data set was examined by means of two-way repeated measures ANOVA with depth and litter as treatment factors. The treatment means were compared using SNK tests. The association of feeding behavior with plot type (litter or no litter) was determined with a Chi-square test of the observed frequencies of feeding.

FISH TETHERING

Fish tethering experiments were conducted to support the ecological interpretation of the shade/structure fish distribution study results. In all trials ($n = 11$), four fish (*C. variegatus*) were tethered in each of the eight study plots bounded by the undeployed lift nets (Fig. 1, Point a). The treatment factors of shade, structure, their combination, and a control were randomly assigned to each plot as was described previously. These fish, placed no closer than 1 m from one another in order to eliminate tether entanglement, remained tethered for 1.0–1.3 h before retrieval. Differences in the treatment-specific loss rates (fish lost min^{-1}) were determined by one-way ANOVA.

The tethering apparatus consisted of several parts. A 0.75-m (12 lb test) monofilament center line with a 45-g lead weight attached at one end and a 2.5-cm float attached to the other was positioned in the desired location in each study plot. Then 8 cm of fine (4 lb test) monofilament was threaded through the fish's mouth, between the gill arches, and out the opercular aperture so that the two ends could be tied together to form a complete loop. This loop was then affixed to a 25 cm length of 4 lb test monofilament via a simple swivel snap. The 25 cm length of monofilament was connected to the monofilament center line using another swivel snap so that the snap could move freely along the centerline's extent from the lead weight up to the float. A single fish was connected to each tethering apparatus.

Tethering in this fashion was advantageous over other previously employed methods (Danilowicz and Sale 1999) in several respects. Traditional fish tethering techniques necessitated injury to the fish (threading the tether through the body wall), but the fish that were tethered for trials in the present

study were not noticeably injured. As a result, the potential for the expression of predator-attractant odor plume was reduced. The tethered fish did not exhibit behavior that indicated injury and could have likewise increased the likelihood of predator-prey encounters (Ellis and Sass unpublished data). The present tethering method permitted movement by the *C. variegatus* throughout a cylindrical space with a diameter of approximately 50 cm and a length equivalent to the depth of inundation, rather than restricting the tethered fishes to a single position in the water column.

TETHERING BY DEPTH

Tethering trials designed to test how depth and position within the intertidal zone affected predation pressure were conducted in March and April 2002. Fish were tethered on four dates at three intertidal stations within the intertidal of the embayment (Fig. 1, Points c1: Station 1, c2: Station 2, and c3: Station 3). These stations were 10, 150, and 200 m from the subtidal margin of the intertidal zone (Station 1, Station 2, and Station 3, respectively). Station 2 was 20 cm and Station 3 was 30 cm higher in elevation than Station 1. The substrate at each of the three stations was firm sand, and patches of drift algae were present at Stations 2 and 3. Drift algae completely covered the bottom of the embayment in the area of the lift nets during March and April 2002, precluding the creation of a tethering station there.

Tethering trials began early in the flood tide on each day and continued for at least 5 h. At each station, ten *C. variegatus* were tethered 1.5 m apart in a line perpendicular to the shore, beginning approximately 10 m from the mangrove shoreline and extending into the open water. The number of tethered fish remaining at each station was noted visually at approximately 1 h intervals. Missing fish were replaced so that the number tethered at the beginning of each interval at each station was maintained at ten individuals. Water depth (cm) was measured hourly at each station. Fish loss rates (arcsine square root transformed) at each station were compared by means of a two-way repeated measures ANOVA with stations and date as factors and hourly observations nested within date as the repeated measure. Loss rates of the stations were compared by means of SNK multiple comparison tests. The influence of water depth on loss rates of tethered fish was explored for each station via polynomial regression analysis. Because loss rates varied by date, they were standardized for each date prior to regression analysis as a percentage of the day's maximum hourly loss rate.

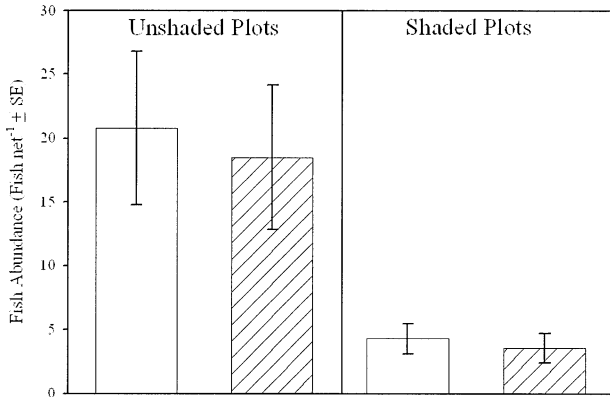


Fig. 3. Mean (± SE) fish abundance in lift net (9.0 m²) samples from different treatments in the shade-structure study (ANOVA: shade × structure, F_{1,20} = 0.100, p = 0.755). Hashed bars represent plots containing structure.

Results

ASSOCIATION OF FISHES WITH SIMULATED MANGROVE FEATURES

The initial 1996 study indicated that fish abundance varied by date but not under different levels of shading (F_{5,18} = 1.046, p = 0.422 and F_{2,18} = 0.534, p = 0.595, respectively). In subsequent trials that included just two levels of shading (i.e., shade or no shade), the effect of shade varied with date (F_{4,20} = 6.548, p = 0.002). Also the abundance of fish was not influenced by the presence of mangrove root structure (F_{1,20} = 0.292, p = 0.595) irrespective of shade treatment (F_{1,20} = 0.100, p = 0.755; Fig. 3). When the data from these two experiments were combined, a depth-dependent association with shade was evident (G = 106.1; Table 1); fish were more abundant in unshaded plots at shallow depths while they were more numerous in shaded plots at deeper depths. The percentage of

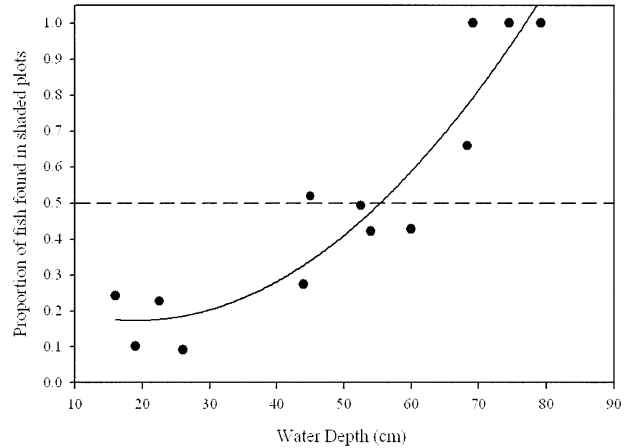


Fig. 4. Fish use of shaded plots as a function of depth (all species and dates included); $y = 0.262 - (0.00937 \times \text{depth}) + (0.000247 \times \text{depth}^2)$, ($r^2 = 0.885$, $p < 0.001$). Reference line (gray dashed) at 0.5 represents the expectation when no preference or avoidance of shading exists.

fish using shaded plots was positively correlated with water depth ($y = 0.262 - 0.00937x + 0.000247x^2$, $r^2 = 0.89$, $p < 0.001$; Fig. 4).

Species composition (*C. variegatus*, *Diapterus plumieri*, *Eucinostomus gula*, *Floridichthys carpio*, *Fundulus grandis*, *Fundulus similis*, *Gobionellus smaragdus*, *Harengula jaguana*, *Lucania parva*, *Menidia peninsulae*, *Oligoplites saurus*, and *Pogonias cromis*) also varied with depth. A dominant species (56.7% of the 945 total captured fish), sheepshead minnow *C. variegatus*, was abundant in depths less than 55 cm but was represented by fewer than 5 individuals at greater depths (Fig. 5). When the distribution of the *C. variegatus* diverged from the null prediction (50% of total in shaded plots), this species consistently occurred in nonshaded, as opposed to shaded, plots (Table 1). The co-dominant species

TABLE 1. The association of fishes with shaded and unshaded plots over several water depths as determined by G-tests for all captured fish, *Cyprinodon variegatus*, and *Eucinostomus gula*. H₀: Observed proportion of fish using shaded plots is not distinguishable from 0.5. df = 1 for all tests. When the result was significant (* = p < 0.05), the direction of the association was noted.

Water Depth (cm)	All Fish		<i>Cyprinodon variegatus</i>		<i>Eucinostomus gula</i>	
	G	Association	G	Association	G	Association
16.0	2.3	None	2.35	None	—	—
19.0	8.91*	No Shade	4.82*	No Shade	—	—
22.5	5.1*	No Shade	3.94*	No Shade	—	—
26.0	40.3*	No Shade	36.81*	No Shade	—	—
44.0	6.23*	No Shade	6.99*	No Shade	—	—
45.0	0.04	None	0.53	None	—	—
52.5	0.003	None	0.74	None	0.37	None
54.0	0.82	None	1.29	None	1.93	None
60.0	0.29	None	0.75	None	0.02	None
68.3	4.7*	Shade	0.07	None	15.84*	Shade
69.2	14.06*	Shade	—	—	4.51*	Shade
74.5	0.28	None	—	—	0.03	None
79.2	23.07*	Shade	—	—	2.91*	Shade

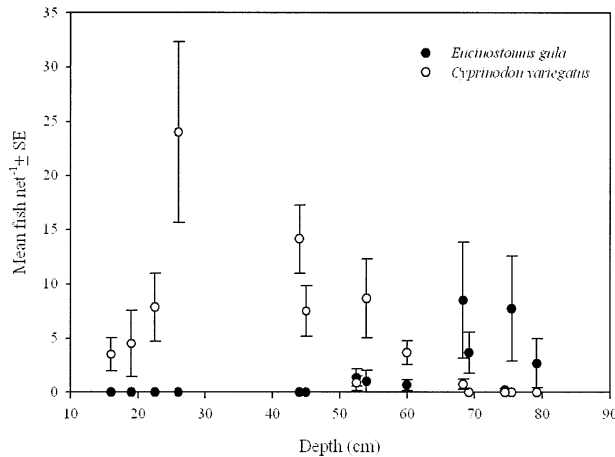


Fig. 5. Mean (\pm SE) *Cyprinodon variegatus* and *Eucinostomus gula* abundance in lift net (9.0 m²) samples across depths in Tampa Bay, Florida (1996–1998).

(12.9% of the total fish abundance), the gerreid *E. gula*, was absent from depths less than 52 cm, but increased in both abundance (Fig. 5) and proportional shade usage with increasing water depth. When both of these dominant species are excluded from the analysis, a significant and positive correlation between depth and fish association with shade persists ($y = -0.167 + 0.0132x$, $r^2 = 0.53$, $p = 0.042$). The abundance of these nondominant species was too low, or their representation across depth was too limited, to test their association with shade individually.

FISH AND LITTER

Fish (*C. variegatus*, *F. carpio*, *F. grandis*, and *F. similis*) were more abundant in plots that contained litter than litter-free plots at some, but not all depths ($F_{13,78} = 4.45$, $p < 0.001$; Fig. 6). Fish feeding behavior was observed to occur more frequently in the plots containing litter than in litter-free plots ($\chi^2 = 25.12$, $p < 0.001$).

TETHERING STUDIES

Out of eleven replicated tethering trials, each employing 32 tethered fish, a total of four tethered individuals (< 1%) were lost from the shade-structure study plots. Only three of these were lost to predators, with the fourth found dead without any outward sign of physical damage. On one occasion, a single fish was lost in a control plot (no shade-no structure). In another trial, two fish were lost, each in a different treatment combination (1 in no shade-structure, 1 in shade-structure). A Kruskal-Wallis one way ANOVA was unable to detect any treatment effect ($p = 0.80$).

Greater predator-prey encounter rates were found in tethering trials conducted at the three

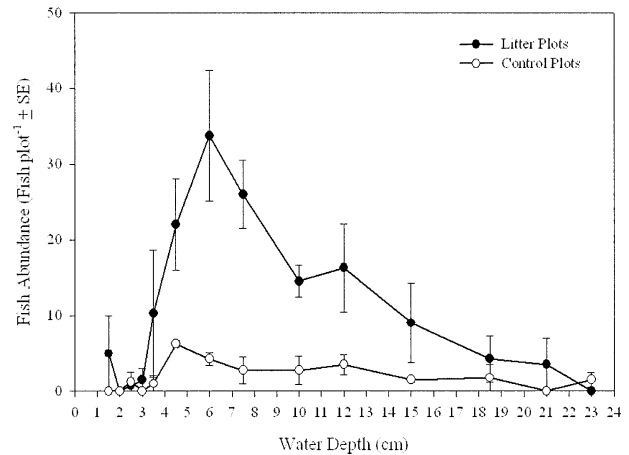


Fig. 6. Mean (\pm SE) fish abundance in litter and control plots with changing tidal height at Point b (Fig. 1), Tampa Bay, Florida.

intertidal stations (Fig. 1, Points c1–c3) within the embayment. Out of a total of 600 tethered fish (20 trials with 10 fish tethered at each of three intertidal stations), 131 (22%) disappeared and were presumed lost to predators. The needle fish (*Strongylura notata*) and blue crab (*Callinectes sapidus*) were positively identified as predators responsible for many tethered fish losses. *S. notata* were found on 22 tether lines after they swallowed *C. variegatus* whole. *C. sapidus* were observed capturing tethered fish, removing them from the tethers, and consuming them.

Loss rates differed among stations (Fig. 7) and marginally by date ($F_{2,32} = 19.696$, $p < 0.001$ and $F_{3,32} = 2.551$, $p = 0.092$, respectively). Station 1, the deepest station, experienced a greater average loss rate than either Stations 2 or 3, which did not

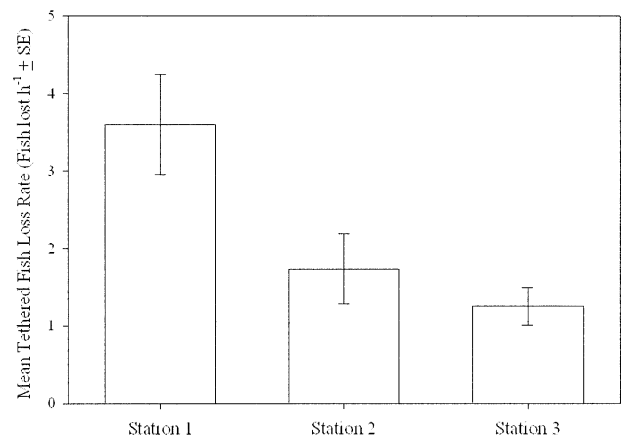


Fig. 7. Comparison of loss rates of tethered fish [mean (\pm SE) fish lost h⁻¹] by station (ANOVA: station, $F_{2,32} = 19.696$, $p < 0.001$). Stations 1, 2, and 3 were located in the sandy embayment (Fig. 1) at c1, c2, and c3, respectively.

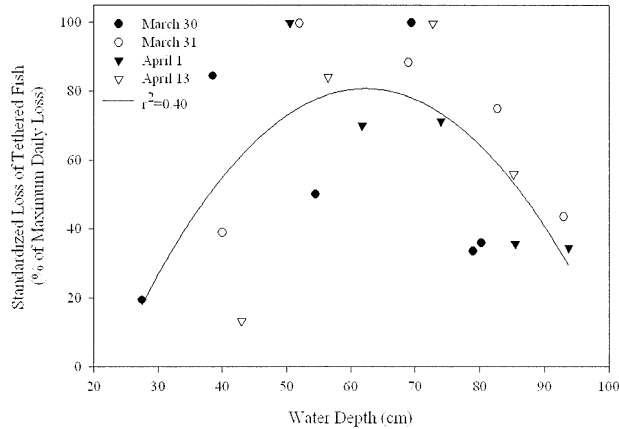


Fig. 8. Standardized loss of tethered fish as a function of water depth at Station 1 (c1, Fig. 1) over four sampling dates ($r^2 = 0.40$, $p = 0.03$). Loss rates were standardized by date as a percentage of the day's maximum hourly loss rate.

differ ($p = 0.248$). Examination of the standardized loss rates by water depth within each station revealed no significant relationship at Stations 2 and 3 ($r^2 = 0.03$, $p = 0.49$ and $r^2 = 0.06$, $p = 0.295$, respectively). Standardized loss rates with depth at the deepest station, Station 1, were best explained with a quadratic function ($y = -1.207 + 0.0647x - 0.000520x^2$, $r^2 = 0.40$, $p = 0.031$; Fig. 8), which indicated that maximum daily losses occurred at approximately 60 cm depth.

Discussion

Identifying the particular attributes of a habitat that are essential for the support of fauna is often difficult (Rose 2000). This task is complicated by the fact that habitat association and usage by animals often varies over time (Chapman 2000; Beck et al. 2001). The results of this study suggest that whereas fish respond to shade and mangrove litter, the degree of fish association with these attributes is conditionally dependent on the water depth. Fish association with shaded plots shifted from apparent avoidance to attraction with increasing water depth. Mangrove litter-covered areas were abandoned with increasing tidal inundation. Although no single fish species was present at all inundation depths, the depth-related increase in association with shade cannot be explained by static shade preferences of depth-segregated species; both *C. variegatus* and *E. gula* showed an increased association with shade with increased water depth over their respective depth ranges. Several, but not all, of the less abundant species also displayed this trend but their numbers were insufficient across depth to conduct valid statistical analyses of individual habitat preferences.

The conditional nature of fish association with

shade may be an adaptive response to a rise in predation pressure with increasing water depth. Water depth has been shown consistently to be positively correlated with the abundance of large predators in a variety of aquatic habitats (Dittel et al. 1995; Gibson et al. 2002). Although higher abundances of predators do not necessarily result in higher attrition rates of prey (Abrams 1993), one might predict a direct relationship between predation pressure and water depth as predators gain access to the intertidal zone during tidal inundation. Whereas fish tethering trials provided rudimentary support for this prediction (loss rates were lower in shallow water), they did not unambiguously support the notion that predation risk is directly proportional to water depth. Tethered fish losses at two of three stations (Stations 2 and 3) did not show a clear relationship with depth. Although a statistically significant correlation between tethered fish loss and depth was identified at Station 1, this relationship was not a simple linear increase of losses coincident with increases in water depth.

The lack of statistical association between water depth and predator-prey encounter rates at Stations 2 and 3 was potentially an artifact. Drift algae were cleared from tethering Stations 2 and 3 (algae were not found at Station 1) 1 h prior to tethering, but currents returned algal clumps back within the reach of the tethered fish. Drift algae, found in clumps of 10–100 cm in diameter and 1–10 cm in height from the substrate surface, provided *C. variegatus*, with a means of avoiding visual detection by predators. Any water depth-related increase in predation pressure may have been mitigated in these experiments by the refuge afforded by drift algae (Heck and Thoman 1981; Gilliam and Frasier 1987).

The unimodal quadratic response of the tethered fish loss rates to changes in water depth at Station 1 has two possible explanations. The tethered fish were observed to hover directly beneath, and in contact with, the float when the water depth was approximately 75 cm or more. Nektonic prey association with flotsam has been shown to reduce their detection by predators (Kogane et al. 1996), and the float may have provided a refuge in deep water (≥ 75 cm). Maximum prey mortality at intermediate water depths may also be predicted from the natural history of the two primary predators of the tethered fish: *S. notata* and *C. sapidus*. *S. notata* uses shallow portions of the intertidal during the early portion of the flood tidal stage (Sogard et al. 1989). In our study, *S. notata*, trapped at the end of the tethers as they swallowed the tethered fish whole, were found only between 25 and 57 cm water depth, suggesting a reduction in *Strongylura* feeding activity at depths greater than 60 cm.

C. sapidus, although present in the study area over the full range of water depths sampled, typically occurred in higher densities at depths greater than 30–40 cm (Fitz and Wiegert 1991), and so may have added to this pattern of maximum loss at intermediate depths. Whereas the intention of this tethering study was to discern the influence of water depth on predator-prey encounter rates, the tidally driven changes in water depth also bring about changes in water flow rates. Tidal current velocities, which vary over the course of a tidal cycle, may have played a role in the effectiveness of *C. sapidus* in detecting the tethered *C. variegatus*. *C. sapidus* are most capable of efficient chemosensory location of prey under conditions of rapid water movement (Finelli et al. 2000). Tidal current velocities in this portion of Tampa Bay are generally greatest at mid flood (which was approximately 60 cm deep on each of the four tethering dates), as the tides are generated by a stationary wave (Lewis 1997). Regardless of the causes of the pattern of losses with depth, it is clear that predator-prey encounter rates were lowest at shallow water depths.

Shifts in the distribution of mobile organisms as a response to the presence of predators are well documented (Schlosser 1987; Persson and Eklov 1995; Jordan et al. 1996; Bartolini et al. 1997). Individuals will typically increase their use of habitats that reduce predator induced mortality even if these refuges are less than optimal in other respects (Werner et al. 1983). For example, young-of-year lake trout (*Salvelinus namaycush*) shift their distribution from open, food-rich waters to shallow refuges in an apparent trade between an increase in survivorship and a reduction in growth (McDonald et al. 1992). In our study, when the water was shallow, fish (primarily *C. variegatus*) were found actively foraging in litter-covered plots and apparently avoiding shaded areas. This association of fishes with mangrove litter has been demonstrated previously by Rajendran and Kathiresan (1999), who suggested that invertebrate prey items were particularly abundant within the litter. As water depth increased within the intertidal, these fish abandon the microhabitats that seemingly favor their foraging success and move into the refuge of the shade. Shaded areas may reduce the efficiency of feeding by reducing the effectiveness of visual foraging (Duffy-Anderson and Able 2001), and remaining in shade over all depths would be energetically inefficient (McCartt et al. 1997).

These shifts in habitat association by fish occurred in spite of the fact that predator densities in the upper reaches of the intertidal zone are generally thought to be low (Kneib 1984; Yozzo and Smith 1998; Lewis and Eby 2002). Several lines of

evidence indicate that predator densities were low in our study site's upper intertidal zone. Large predators were absent in lift net collections, regardless of the depth. Their absence may simply be an illustration of a gear bias of lift nets, but the fact that none of the 352 fish tethered in these shade-structure plots at water depths below 53 cm were lost to predators suggests that it is, instead, a reflection of low predator densities or activity. No large predators were observed in the vicinity of the litter plots during the course of the visual observations, even when small fish began to abandon the area for higher elevations.

Habitat shifts by prey in response to conditions that potentially favor predator activity, rather than in response to the predators themselves, have previously been identified (Muotka et al. 1999). *Littorina irrorata* (marsh snail) begins its migration up cord grass culms immediately prior to tidal inundation in what has been interpreted as a preemptive effort to avoid predators, which arrive with the incoming tide (Rochette and Dill 2000). Sih (1992) argued that such preemptory action is advantageous to species that have a high probability of mortality in an encounter with a predator. Fixed behavioral responses to habitat cues, which may signal increased risk of mortality, can enhance survivorship (Pierce 1988). This sort of fixed preemptory response may be the reason that shade, a potential source of refuge for fishes, is not abandoned at greater depths if a reduction in predator-prey encounter rates occurs after the period of peak losses at intermediate water depths. Once the shade refuge is utilized, the risk of venturing into adjacent habitats of uncertain predation pressure is not easily outweighed by the potential foraging gains (Sih 1992).

The results of our study differ from those of Laegdsgaard and Johnson (2001) who also constructed artificial mangrove habitat plots by adding simulated pneumatophore structure and shading in an area adjacent to one devoid of these features. They found that, of those fish species that showed a preference, structure was a weak attractant and shading was avoided. Although our results may differ because of the disparate fish assemblages of Tampa and Deception Bays, differences in both the experimental methods and setting of the studies may also be responsible. The lack of influence of structure in our study may reflect the low structural density of the root clusters or the shallow water depths over which we examined fish association with structure. The value of structured habitats as refuge and foraging sites is dependent on structural density (Crowder and Cooper 1982; Gotceitas and Colgan 1989; Mantatunge et al. 2000; Spitzer et al. 2000; Hovel and Lipcius 2001). The reliance

of nekton on structure as a refuge from predators is reduced in shallow habitats (Copp 1990; DeVries 1990; Rozas and Zimmerman 2000). The structural density employed by Laegdsgaard and Johnson (2001) was clearly higher (200 pneumatophores m^{-2}) than used in our study (16 prop roots m^{-2}), and whereas the actual sampling depths were not specified, they indicated a maximum 1 m water depth at their study site, versus 44 cm in our shade-structure study.

If we had not considered the effect of variation in water depth across our replicate samples, we would have, like Laegdsgaard and Johnson (2001), concluded that fish either show no plot preference or avoid shade. This is not to suggest that depth-mediated association between fish and shade is a universal phenomenon. Because Deception Bay is fairly turbid (Laegdsgaard and Johnson 1995), fish may be less responsive to shade because turbidity tends to reduce the refuge value of shaded waters (Gregory 1993; Benfield and Minello 1996). It is possible that the fish in Deception Bay show a similar shift in shade use that would be detectable only with sampling over a range of depths.

We identified a depth-dependent association of fish with shade and mangrove leaf litter. Our results suggest that small fishes, such as described here and elsewhere in Tampa Bay mangroves (Price and Schlueter 1985; Mullin 1995), will abandon well-lighted foraging grounds in favor of the potential refuge of shaded waters as water depth increases. Adaptive responses to variable physical conditions in dynamic settings, such as the intertidal zone, are likely characteristic of the fauna that inhabit them (Chapman 2000). We suggest that studies of intertidal nekton should be carefully interpreted in the context of water depth.

ACKNOWLEDGMENTS

We would like to thank Greg Sass and Nona Butler for their assistance in the field. A special thank you is owed to Thomas Farrand for aid in the construction of the modified lift nets. Dr. Pete Sheridan, Carole McIvor, and two anonymous reviewers helped greatly in the preparation of this manuscript.

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Received, December 1, 2003

Revised, July 1, 2004

Accepted, August 12, 2004