Water Depth Modifies Relative Predation Risk for a Motile Fish Taxon in Bahamian Tidal Creeks

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ABSTRACT: We evaluated the influence of water depth on relative predation risk for mojarra (*Eucinostomus* spp.) in six tidal creeks on Andros Island, Bahamas. Relative predation risk was determined using a tethering protocol combined with underwater visual census. In one experiment, we found that relative predation risk increased predictably with water depth ($r^2 = 0.83$), and survival of tethered mojarra decreased with water depth ($r^2 = 0.71$). We identified three depth zones containing differing levels of predation threat: refugia (0–19 cm), transition (20–69 cm), and predation (> 70 cm). Predation on mojarra rarely occurred within the refugia zone (2% eaten) and always in the predation zone (100% eaten). Additional factors not examined in this study (e.g., mangrove complexity, predator density) likely drive variability of relative predation risk within the transition zone. In a second experiment, we directly examined influence of water depth on relative predation risk at fixed locations from high tide to low tide in a single creek. Mean relative predation risk was significantly higher during higher tides at deeper water depths. Results provide experimental evidence that exploitation of shallow water refugia by motile prey can significantly reduce predation risk. We expect the distribution of motile fishes is at least partially influenced by spatially-dynamic shallow water refugia.

Introduction

One of the long-standing questions in coastal ecology is why organisms disperse into newly flooded shallow water areas with rising tides (Kneib 1987; Gibson et al. 1998; Layman 2000; Hindell and Jenkins 2004; Harter and Heck 2006). The spatial location of shallow water areas, a function of bathymetry and hydrology, generally moves shoreward during the flood tide, and many estuarine organisms move in conjunction with this dynamic (Vance et al. 1996; Finelli et al. 2000; Lewis and Eby 2002; Gibson 2003; Osgood et al. 2003). For many species, it is assumed either food availability or predator avoidance, or some combination thereof, are the most likely reasons that species movements are linked to tidal variation (Heck and Thoman 1981; McIvor and Odum 1988; Clark et al. 2003; Ryer et al. 2004; Lehtiniemi and Linden 2006).

Numerous studies have demonstrated an apparent link between tidally-driven fish movements and food availability based on tagging and telemetry studies (Szedlmayer and Able 1993; Hartill et al. 2003; Krumme 2004; Bretsch and Allen 2006), diet analyses (Laffaille et al. 2002; Holsman et al. 2003; Hollingsworth and Connolly 2006), and habitat inference (Hindell et al. 2000; Layman 2000;

Nagelkerken et al. 2000). For most species though, direct empirical evidence as to how predation risk specifically influences or drives these movement patterns remains lacking. Water depth has been implicated as a potentially critical variable in determining predation risk for fishes in a number of estuaries, although debate exists over exactly where, when, and for what species depth may be critical (Sheaves 2001; Ellis and Bell 2004; Baker and Sheaves 2005). Such observations are essential for demonstrating the relative importance of predation. Clarification in this regard could be especially enlightening for ecosystems where environmental factors, such as water depth, are relatively predictable at various temporal and spatial scales.

We explored the relationship between water depth and relative predation risk on mojarra (*Eucinostomus* spp.), an abundant, motile fish taxon typical of shallow water in tidal creeks on Andros Island, Bahamas. We used a tethering method to assess differences in relative predation risk across a wide range of water depths at which these fishes are found. These data are used to discuss implications that water depth has for understanding species distribution in tidal ecosystems. We also provide a context for evaluating the importance of water depth relative to other factors (e.g., mangrove structural complexity) in determining the value of habitats as predation refugia.

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Materials and Methods

STUDY LOCATION

Field experiments took place in six tidal creeks on Andros Island, Bahamas, during May 2005. Tidal creeks on Andros Island range in size from several hectares with maximum depths of 2 m to thousands of hectares with maximum depths > 10 m. Our experiments were conducted in systems that fall at the lower end of this range. These systems are generally characterized by a relatively narrow tidal mouth (lined by red mangrove, *Rhizophora mangle*) that opens to a broad, shallow wetland area (Valentine et al. In press). Substrate is variable, including fine silt, coarse sand, rocky outcroppings, and seagrass (Layman et al. 2004). Tidal creeks on Andros have a semi-diurnal tidal regime, with average daily tidal range of 0.8 m. Small fishes are numerous and diverse in tidal creeks, with mojarra as one of the most abundant taxa (Layman et al. 2004). Mojarra are frequently used as live baitfish in commercial snapper fisheries and, based on their high abundance, may represent a critical linkage in energy transfer to upper trophic levels in estuarine food webs (Cain and Dean 1976; Ley et al. 1994; Ayala-Pérez et al. 2001; Serafy et al. 2003). Abundant creek predators include gray snapper (*Lutjanus griseus*), schoolmaster snapper (*Lutjanus apodus*), cubera snapper (*Lutjanus cyanopterus*), and barracuda (*Sphyraena barracuda*).

TETHERING METHOD

Two separate experiments were conducted, each following a general tethering protocol. Experiments were initiated by collecting mojarra using a cast net along creek shorelines. Immediately upon capture, fish were transferred to a live well. The mojarra species used in experiments were members of an abundant yet challenging taxa to identify in the field that included the following species: *Eucinostomus jonesi* (slender mojarra), *Eucinostomus lefroyi* (mottled mojarra), and *Eucinostomus gula* (silver jenny). We did not distinguish among *Eucinostomus* spp., following the lead of other studies in similar systems (Nagelkerken et al. 2000; Layman et al. 2004). We attached individual mojarra to a 1-m long tether made of 2-lb test monofilament (0.18 mm diameter) by threading the line through a small hole that we cut in the side of the snout (protrusible mouth) and tying an improved cinch knot. The other end of the tether was tied to a 3-mm diameter metal rod (25 cm in length) that was inserted into the substrate (near the mangrove fringe along creek shorelines) to anchor the fish. Each fish was allowed time to recover (5–30 min) prior to initiation of the experiment. Although mojarra obviously were restricted compared to their natural swimming behav-

ior, all were able to swim in an area 1 m around the tethering pool. Fish that did not maintain equilibrium or exhibited other erratic swimming behavior were not included in the trials.

There are limitations and artifacts to all tethering experiments (e.g., Kneib and Scheele 2000; Aronson 2001). The main assumption of all tethering experiments is that a relationship exists at a particular site between loss of tethered prey (relative predation risk) and natural mortality of free prey due to predation (Kneib and Scheele 2000). Even though the loss of tethered prey is not an exact proxy for natural mortality, tethering remains one of few means by which to gather direct empirical information related to relative predation risk in marine communities (Aronson and Heck 1995). The utility of tethering data is supported by a number of recently published studies that used tethering to assess relative predation risks (Belanger and Corkum 2003; Ellis and Bell 2004; Manderson et al. 2004; Díaz et al. 2005; Smith and Hindell 2005). In the present study, we examine the effect of a single variable (water depth) on predation risk using a tethering method, and assume that this provides insight into relative rates of natural mortality across this gradient. Based on field observations during the course of this study, we do not believe that tethering artifacts (e.g., entanglement) differed among treatments or among creeks (Peterson and Black 1994).

EXPERIMENT 1

Tethering rods with tethered mojarra were staked to the substrate adjacent to mangrove prop roots at haphazard locations and water depths (3–120 cm) in six study tidal creeks (total n = 180 trials). Mojarra are commonly found throughout this entire depth range (Layman et al. 2004). We attempted to make sure that depth coverage in experiments was similar across sites by distributing site selection across the entire depth gradient under consideration. Substrate type and density of mangrove prop roots varied within and among tidal creeks; mojarra were always tethered such that they had access to mangrove root structure for potential cover. Water depth, start time, and standard length (SL; mm) of mojarra were measured prior to deployment. Water depth was measured using a meter stick placed into the substrate at a 90 degree angle. When depths exceeded 1 m, a wooden rod (5 m) with affixed measuring tape was used. Each mojarra was observed throughout the trial by an observer using mask and snorkel. Observers remained 5 m from tethered fish and attempted to minimize movement during trials. Extensive visual surveys in these tidal creek systems suggest that this observer distance has minimal effects on predator

TABLE 1. Identity of predators that were observed to have consumed tethered mojarra during experimental trials in six Bahamian tidal creeks, May 2005. Number observed does not reflect the total number of trials but rather the number of predators identified during underwater visual census.

Common Name	Species	Number Observed	% of Total Number
Schoolmaster snapper	*Lutjanus apodus*	80	48.5
Grey snapper	*Lutjanus griseus*	63	38.2
Barracuda	*Sphyraena barracuda*	6	3.6
Cubera snapper	*Lutjanus cyanopterus*	3	1.8
Black-fingered mud crab	*Panopeus herbstii*	3	1.8
Needlefish	*Strongylura marina*	2	1.2
Checkered pufferfish	*Sphoeroides testudineus*	2	1.2
Nassau grouper	*Epinephelus striatus*	2	1.2
Bar jack	*Caranx rubber*	1	0.6
Batfish	*Ogcocephalus cubifrons*	1	0.6
Nurse shark	*Ginglymostoma cirratum*	1	0.6
Bonefish	*Albula vulpes*	1	0.6
Total		165	100

(see complete species list in Table 1) behaviors (Valentine et al. In press). For each predation event, the observer noted exact time of predation, water depth, and, if possible, predator species. Predation was defined as an attack on a tethered mojarra in which the mojarra was consumed or killed. Each observation trial ended at the moment of predation, or after 30 min (longer trials may have covered time periods with significant water depth variation due to tides) if predation did not occur.

Two separate regression analyses (exponential decay and logistic) were performed on data from all tidal creeks to evaluate the relationship between water depth and time to predation. An exponential decay regression was chosen (based on inspection of regression residuals from a number of different models) to model the relationship between water depth and the exact time required for each mojarra to be eaten. A logistic regression modeled the relationship between water depth and whether a mojarra survived the experiment or was consumed. The logistic regression required creation of a new variable, experimental outcome (1 = survival, 0 = mortality due to predation), which provided insightful information on overall survival (rather than time to predation). Variability within the goodness of fit (r^2) of these relationships subsequently was explored by examining the standard deviation (SD) of the mean predation risk within 10-cm water depth blocks. By evaluating the SD within these depth blocks, we identified three water depth zones of differing predation risk variability, i.e., high variability (> 5 SD) or low variability (< 5 SD) in time to predation.

EXPERIMENT 2

In Bahamian tidal creeks, water depth is regulated predominantly by semi-diurnal tides. To provide additional insight as to how tides modify the water depth-relative predation risk relationship (through variation in water depth), we assessed relative predation risk using our tethering protocol at eight fixed locations throughout a high-to-low tide cycle (ca. 6 h) in Staniard Creek on May 27, 2005. This experiment was carried out such that four fish were tethered at the same spot at different times in the tidal cycle. We assumed that other variables were relatively constant over the tidal cycle (e.g., turbidity, benthic substrate cover) at each of the eight sites, so any differences in predation risk could be attributed to water depth. This design was employed to provide additional evidence that patterns demonstrated in Experiment 1 were indeed due to water depth variation and not particular site characteristics within a creek. While controlling for among site variability, we hypothesized that relative predation risk would decrease with lower water depths at each location. Eight observers (one at each of eight fixed locations) performed separate tethering trials during high tide (HT), early ebb tide (EE, 1.5 h post HT), late ebb tide (LE, 3 h post HT), and low tide (LT, 4.5 h post HT; total n = 32 trials). All trials were conducted for 30-min periods unless preempted by a predation event, and water depth was measured at the end of each trial to examine how each tidal period changed water depths along with relative predation risk.

To compare relative predation risk among tidal periods we used repeated measures analysis of covariance (ANCOVA). In this model, data from each of the eight observers were grouped by tidal period, mean time to predation in each tidal period was the dependent variable, tidal period (HT, EE, LE, LT) was the repeated factor, and prey size (SL) was a covariate. Since prey size was nonsignificant in this model (df = 3; Wald test = 1.65; p = 0.20), we reran the model as a repeated measures analysis of variance (ANOVA) and reported the significance of this more simplified model. All analyses were performed using Statistica software (version 6.0; Statsoft, Inc; Tulsa, Oklahoma) and considered significant if $\alpha < 0.05$.

Results

EXPERIMENT 1

We observed 12 different species (11 fish taxa, 1 crab species) consume tethered mojarra during experiments, the majority of which were schoolmas-
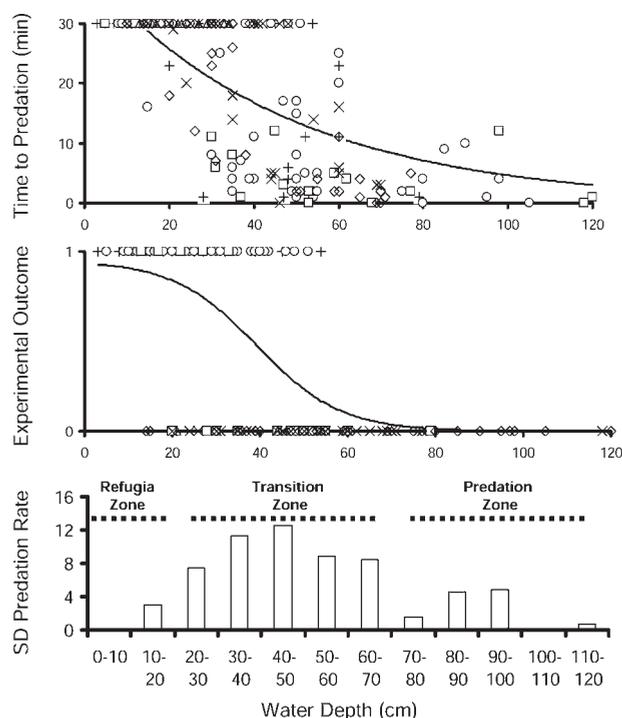
Fig. 1.   Time until predation as a decay function ($r^2 = 0.83$) of water depth at which mojarra were tethered. (+ = Sommerset Creek, ○ = Staniard Creek, □ = White Bight, ◇ = Lovehill Creek, x = Middle Creek, △ = Conch Sound). Experimental outcome (1 = survival, 0 = predated) as a logistic function of water depth ($r^2 = 0.71$). Trials ended if predation did not occur within 30 minutes. Standard deviation of mean predation rate in all tidal creeks by 10-cm water depth increments. The refugia and predation zones were demarcated by either a low (refugia) or high (predation) probability of predation and a low standard deviation (standard deviation < 5) in mean time to predation. The transition zone was marked by more uncertain experimental outcomes and a high standard deviation (> 5) in mean time to predation.

ter (49%) or grey (38%) snapper, but also included larger piscivores such as barracuda, sharks, and batfish (*Ogcocephalus cubifrons*; Table 1). Across sites in six different tidal creeks, time to predation decreased significantly with increasing water depth (Fig. 1; exponential decay regression; $r^2 = 0.83$, n = 180, p < 0.0001). When each creek was considered separately, the effect of depth on relative predation risk was stronger (e.g., higher r^2 values; Table 2). Survival of tethered fish also was strongly influenced by water depth (Fig. 1; logistic regression; $r^2 = 0.71$, n = 180, p < 0.0001). When broken down by individual creek, the logistic regression r^2 generally increased, although the magnitude of these increases was not as great as those observed for the exponential regressions.

We estimated three water depth zones for mojarra based on variability (e.g., SD) of relative predation risk throughout 10-cm water depth blocks (Fig. 1):

TABLE 2.   Exponential decay and logistic predation risk-depth relationships for six tidal creeks on Andros Island, Bahamas.

Site	n	Exponential		Logistic	
		R^2	p	R^2	p
All Sites	180	0.83	< 0.0001	0.71	< 0.0001
White's Bight	21	0.92	< 0.0001	0.79	< 0.0001
Staniard Creek	53	0.85	< 0.0001	0.82	< 0.0001
Sommerset Creek	28	0.89	< 0.0001	0.70	< 0.0001
Middle Creek	34	0.93	< 0.0001	0.72	< 0.0001
Lovehill Creek	34	0.90	< 0.0001	0.63	< 0.0001
Conch Sound	10	1.00	< 0.0001	1.00	< 0.0001

refugia zone (0–19 cm), transitional zone (20–69 cm), and predation zone (> 70 cm). These zones are not intended to be universal zones that apply to all species and all ecosystems (as we do not present data for greater water depths or other ecosystem types), but rather a generalization of the relative predation risk associated with different water depths for motile prey in the Bahamian tidal creeks. Mojarra tethered in water < 20 cm deep survived until the end of the 30 min trial 98% of the time, while mojarra tethered in water 20–70 cm survived until the end of the 30 min trial 42.1% of the time. Mojarra in water > 70 cm never survived until the end of trial; the longest time to predation in water > 70 cm was 12 min. The transition zone was marked by highly variable time to predation, including 53 fish that were not eaten and 32 that were eaten within 5 min.

EXPERIMENT 2

We found significant differences in relative predation risk at different water depths throughout a low-to-high tide cycle when replicating tethering trials at eight specific locations. Relative predation risk differed significantly among tethering periods (repeated measures ANOVA; df = 3, F =4.66, p = 0.009). Tukey's honest difference post-hoc comparisons of means during each tidal period revealed that relative predation risk was significantly lower during LT and LE compared to HT and EE (Fig. 2). Within the range of prey sizes employed (30–90 mm SL), prey size did not significantly influence relative predation risk (ANCOVA; df = 3, Wald test = 1.65, p = 0.20).

Discussion

We present direct experimental evidence that mojarra, an abundant, motile fish taxon, experienced higher relative predation risk in deeper water. This supports the notion that there are specific fitness benefits (reduction of predation risk) when mojarra move into shallow water refugia. Even though food availability also may be important, this study directly supports hypotheses that
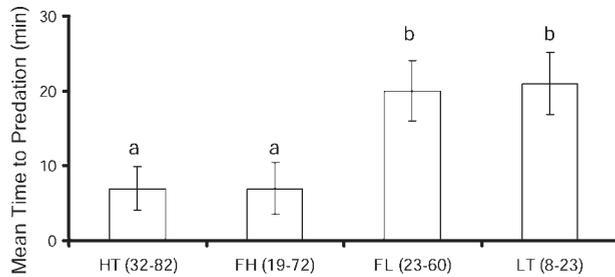
Fig. 2. Mean relative predation risk at eight fixed sites adjacent to mangrove habitat in Staniard Creek, Andros, through four tidal periods, May 27, 2005. Error bars represent ± 1 standard error. Letters denote significant differences in mean relative predation risk (Tukey's p < 0.05). HT = high tide, EE = early ebb tide, LE = late ebb tide, LT = low tide. Water depth ranges for each period are found in parentheses along the x-axis.

distribution of small fishes in nearshore coastal ecosystems is determined, to some degree, by variable predation risk associated with changes in water depth (Blaber and Blaber 1980; Sogard et al. 1989; Kennedy and Gray 1993; Rozas and Zimmerman 2000; Vance et al. 2002).

We have also presented evidence that predation risk is linked to semi-diurnal tides in Bahamian tidal creeks (Experiment 2) since tides are essentially modulating water depth. An alternative interpretation of this experiment's results might be that predator feeding rhythms are enhanced during high tide and this contributes just as much as water depth to higher predation risk for mojarra at high tide (Bollens and Stearnes 1992; Reebs 2002; Rypel and Mitchell 2007). When the repeated measures analysis for Experiment 2 was rerun as an ANCOVA model with predation risk as the dependent variable, tidal period as a grouping variable, and prey size and water depth as covariates, an insignificant model was generated (df = 3, F = 2.34, p = 0.33) with water depth as a highly significant covariate (p = 0.002). This suggests that water depth is a key factor regulating predation in tidal creeks.

Using mojarra in tidal creeks, we defined three zones of predation based on the likelihood of predation. Predation rarely occurred in the refugia zone (water depth: 0–19 cm), always occurred in the predation zone (water depth > 70 cm), and was less predictable in the transition zone (water depth: 20–69 cm). Larger body sizes of predators (mainly snapper, but also barracuda and sharks) likely constrain their access to shallow waters, so relative predation risk was very low, and survival very high, at these shallow depths. This finding is consistent with other studies describing the physical constraints on the distribution of larger fishes in coastal areas (Boesch and Turner 1984; Ruiz et al. 1993; Paterson and Whitfield 2000; Linehan et al. 2001; Gibson et al. 2002), as well as how the threat of avian

predation from birds, such as osprey *Pandion haliaetus* (Stevens et al. 2006), may affect predatory fish distributions. At deeper depths, mojarra experience a relatively high risk of predation (0% survival), because of the increased likelihood of encountering a predator in areas when predators are able to move in a relatively unconstrained manner (Gause 1934; Sih 1984; Temple 1987; Hugie and Dill 1994; Sih and Christensen 2001).

The depth range we label as the transition zone was marked by high variability in mortality and time to predation. We suggest a mixture of ecological factors, in addition to depth, likely contribute to variability in relative predation risk within the transition zone of tidal creeks.

Predator density: At higher predator densities, the probability of prey encountering and being attacked by a predator increases (Gause 1934; Werner and Hall 1979; Sih et al. 1985; Sih 1992). Predator densities vary among Bahamian tidal creeks (Valentine et al. In press) due to both natural factors (e.g., availability of mangrove habitat) and anthropogenic effects (e.g., alteration of tidal flow). Tidal creeks with higher predator densities should result in higher predator-prey encounter frequencies, and faster times to predation, compared to tidal creeks with low predator densities.

Distance to predator source locations: In many shallow Bahamian tidal creeks, much of the intertidal zone drains completely at low tide, and large, piscivorous fishes (e.g., snapper) retreat to localized deep refuges (Valentine et al. In press). Predators emigrate from these pools, which may be restricted to a few discrete locations in the main channel, as the incoming tide increases water depths and inundates intertidal areas. During flood tides, as predators move out of the source pools, encounter frequency of tethered mojarra by predators will be higher closer to these predator source locations.

Habitat complexity: Structurally complex habitats, such as mangrove roots, seagrasses, and rocky outcrops, may reduce prey encounter rates, attack rates, capture efficiency, and consumption rates by predators (Crowder and Cooper 1982; Gotceitas and Colgan 1989; Spitzer et al. 2000; Sih and Christensen 2001; Hindell and Jenkins 2004). Mangrove complexity in particular has been implicated as a factor that can lower predation risk (Primavera 1997; Rönnbäck et al. 1999; Clynick and Chapman 2002; Sheridan and Hays 2003; de la Moriniere et al. 2004). Dense mangrove root complexes may offer mojarra ample cover from which to evade and escape predators with larger body sizes that are able to access attractive transition zone-mangrove habitats during the high tide.

Other factors: Other site specific factors, such as shade and water turbidity, can affect a predator's ability to detect and capture prey, and can modify predation rates (Helfman 1981; Aksnes and Giske 1993; McCartt et al. 1997; Ellis and Bell 2004). In extremely turbid environments where visibility is limited, efficiency of predators could be reduced, perhaps resulting in a lower predation risk.

Relative importance of the above factors largely will depend on characteristics of the prey species of interest. Mojarra are highly motile prey (Rueda and Santos-Martínez 1999) that can exploit the temporally and spatially-dynamic shallow water predation refugia. Depth seems to be one of the most important physical variables in defining predation refugia for this species. Other tropical and sub-tropical estuarine fishes, e.g., pomacentrid damselfish (*Pomacentrus* spp.), are more sedentary and structure oriented. For such species, other factors, like localized habitat complexity, may be more important in determining relative predation risk since these individuals typically do not move across the landscape with each tidal cycle (Crowder and Cooper 1982; DeVries 1990; Rönnbäck et al. 1999; Hindell and Jenkins 2004).

Currently, the literature is replete with conflicting claims on factors that determine predation risk in estuarine habitats (and conflicting claims on the value of different habitat types as nurseries; e.g., Dahlgren et al. 2006; Sheaves et al. 2006; Layman et al. 2006). We propose that some of this ambiguity stems from a lack of evaluating relative predation threats throughout the estuarine water depth gradient. Water depth characteristics defined by local bathymetry and hydrology likely shapes the location and composition of predators in the estuarine landscape. Though we only examined predation risk in this paper, the balance between food availability and predation risk likely drives the distribution of motile prey in estuaries. Moving beyond our current understanding of these factors will ultimately require simultaneous quantification of both these factors. Here we present strong experimental evidence that predation risk is indeed, at least partially, responsible for the distribution of motile prey taxa in Bahamian tidal creeks and estuaries.

ACKNOWLEDGMENTS

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