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Neil Hammerschlag
University of Miami, nhammerschlag@rsmas.miami.edu

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NOCTURNAL FISH DISTRIBUTION, FEEDING AND PREDATION RISK IN RELATION TO A MANGROVE-SEAGRASS ECOTONE

By

Neil Hammerschlag

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NOCTURNAL FISH DISTRIBUTION, FEEDING AND PREDATION RISK IN RELATION TO A MANGROVE-SEAGRASS ECOTONE

Neil Hammerschlag

Approved:

_________________ Joseph E. Serafy, Ph.D. Research Associate Professor of Marine Biology and Fisheries	_________________ Terri A. Scandura, Ph.D. Dean of the Graduate School
_________________ Larry E. Brand, Ph.D. Professor of Marine Biology and Fisheries	_________________ Michael R. Heithaus, Ph.D. Professor of Biology Florida International University
_________________ Diego Lirman, Ph.D. Research Assistant Professor of Marine Biology and Fisheries	_________________ Todd Kellison, Ph.D. Chief, Fisheries Ecosystem NOAA Fisheries – Beaufort Lab
_________________ Gary Thomas, Ph.D. Professor of Marine Biology and Fisheries	

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Nocturnal Fish Distribution, Feeding and Predation Risk in Relation to a Mangrove-Seagrass Ecotone (Fall 2009)

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The combined effects of food availability and predation risk on fish foraging behavior have been investigated via both laboratory and field experiments, primarily in temperate, freshwater systems and during daylight hours. In contrast, relatively little attention has been directed towards fish foraging decisions along subtropical shorelines, which serve as nursery grounds for a variety of economically important fishes, as well as at night, when many species emerge from refuges to feed. The mangrove-seagrass ecotone and adjacent seagrass beds constitute nocturnal feeding grounds for fish secondary-tertiary consumers. In subtropical Biscayne Bay, Florida (USA), I investigated the influences of food and risk on nocturnal seagrass use by gray snapper (*Lutjanus griseus*), bluestriped grunt (*Haemulon sciurus*), great barracuda (*Sphyraena barracuda*), and seabream (*Archosargus rhomboidalis*) along a distance gradient, spanning from the mangrove fringe to 120 m from shore. This was accomplished by conducting a series of integrated field and laboratory studies, including: (1) nocturnal seine sampling to determine fish abundance patterns in relation to the mangrove-seagrass interface; (2) fish stomach content analysis to reveal feeding habits and trophic relationships; and (3) diel field tethering experiments to explore nearshore gradients in predation pressure. With these data I tested *a priori* predictions of fish distributions relative to food and predation risk that were generated from foraging theory: (1) fishes will be distributed across the distance gradient in proportion to their food supply (i.e., ideal free distribution, IFD); or (2) fishes will avoid high risk areas such that their abundances will be lower than predicted by food resources in high-risk habitats (i.e., food-risk trade-off). Results revealed that fish assemblage composition differed by season and distance from shore, with the zone nearest the mangroves generally harboring the lowest densities of late-stage juvenile fishes. Stomach content analysis demonstrated that gray snapper fed on a variety of small fishes and crustaceans, while bluestriped grunt fed primarily on caridean shrimp. Seabream fed almost exclusively on vegetation and great barracuda was almost entirely piscivorous; however, seasonal shifts in diet and feeding habits were evident. Seasonal shifts in major food resource use generally did not correspond with changes in relative abundance of food supply. Seasonal trophic niche breadth differences were evident for gray snapper, great barracuda and bluestriped grunt, while niche breadth was equivalent between seasons for seabream. Based on seasonal food supply in the environment, niche breadth values did not match basic foraging theory predictions, which state niche breadth should expand as preferred food resources become scarce. Tethering experiments indicated that predation rates were highest nearest the mangrove edge and decreased with increasing distance from shore. Moreover, predation pressure at night was nearly twice as high compared to the day. Testing these data against my predictions from foraging theory, I found that none of the fishes examined (gray snapper, seabream and bluestriped grunt) were distributed according to IFD. Seabream and gray snapper avoided foraging close to the mangrove-edge, where their food was most abundant, but risk was highest.

Bluestriped grunt appeared to forage randomly across the distance gradient despite spatial variation in food and predation risk. Overall, results suggest that: (1) spatial patterns of utilization of seagrass habitat adjacent to the mangrove-seagrass ecotone differs by species, life-stage and season; (2) Seasonal shifts in diet were not correlated with changes in relative abundance of food supply; (3) trophic niche breadth of late juveniles did not expand with declines in their food resources; (4) the mangrove-seagrass ecotone appears to serve as a hunting corridor for predators targeting juvenile fishes moving about the mangroves; and (5) two of the three species examined appeared to give up food in return for safety by avoiding foraging near the mangroves, despite high food availability.

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Predators can affect the distribution and abundance of their prey directly through mortality (i.e., killing and consumption) as well as behaviorally through risk effects (i.e., frightening their prey) (Brown et al. 1999; Heithaus et al. 2008; Creel and Christianson 2008). Risk effects arise when prey alter their behavior in response to predators (i.e., anti-predator behavior). This includes changes in time allocation to foraging or by using vigilance, which carry costs such as sacrificing feeding or reproduction opportunities for safety (Brown 1999; Brown and Kotler 2004). These predation risk effects can cascade through communities, resulting in alterations in community composition and dynamics that may equal or exceed those from direct mortality (Peacor and Werner 2001; Werner and Peacor 2003). Growing evidence suggests that risk-effects are context dependent (Schmitz 2007) and are strongly influenced by landscape features (e.g., habitat edges, Heithaus et al. 2009).

The effects of predation risk on fish foraging behavior has been relatively well studied in both the laboratory and field. I conducted a review of 57 studies, published over the past 26 years, which explored predation pressure to fishes in aquatic environments (Table 1.1). Of these studies, 56 % were conducted in the field, where tethering experiments were the most common method employed to empirically quantify patterns of predation pressure (~ 70 %). Nearly 80 % of all studies reviewed were conducted solely during daylight hours, although at night, many fishes emerge from refuges to feed. Relatively little attention (~ 20 % of studies) has been directed towards examining predation pressure to fishes along tropical or subtropical shorelines, which serve as nursery habitats for a variety of economically important fishes. In addition, of the reviewed studies, less than 10 % considered the responses of multiple fish species to predation pressure, even though most systems contain a variety of fishes and responses may be species-specific (e.g., Heithaus et al. 2009). The reviewed studies which investigated the effects of predation pressure on fish habitat use, typically examined foraging behavior in discrete habitat patches, for example, structurally complex "safe" habitats versus open "risky" habitats (Lima and Dill 1990; Lima 1998) and few studies (< 20 %) examined the effects of predation pressure to fishes along a habitat gradient that varies in relative safety. Moreover, few of the reviewed studies (~ 5 %) considered edges or transition zones between habitat patches. However, fishes are often at high risk from predation when crossing transition zones between sheltered and feeding patches. Such transition zones, or ecotones, can serve as hunting corridors for predators (reviewed by Decamps and Naiman, 1988; Ries and Sisk 2004). It has been recently suggested that progress toward identifying general trends in habitat selection might be achieved by focusing survey efforts on ecotones at a time when movement relating to feeding occurs (Ley and Halliday 2007).

Subtropical Biscayne Bay, Florida (USA) provides an opportunity to investigate the combined effects of food availability and predation risk on the nocturnal distributions of multiple fish species across their foraging landscape, spanning from the mangrove-seagrass ecotone into adjacent seagrass beds. During daylight hours, a diverse group of juvenile fishes utilize the Bay's mangrove-fringed shorelines as shelter from predators (Serafy et al. 2003; Serafy et al. 2007). However, a combination of gut content (e.g. Randall 1967), stable isotope (Kieckbusch et al. 2004; Nagelkerken and Van der Velde 2004a,b), direct visual observation (Rooker and Dennis 1991) and tracking studies (Luo et al. 2009) suggest that fishes disperse from the mangrove prop roots at night to forage in adjacent seagrass beds. While foraging at night, these fishes are likely vulnerable to predation; however, it remains unclear how predation risk drives spatial variation in fish habitat use.

Behavioral optimization theory and associated foraging models provide frameworks for studying the influence of predation risk on fish foraging habitat use (Brown 1999; discussed by Wirsing et al. 2008). The ideal free distribution model (IFD; Fretwell and Lucas 1970) can be used as a null model for assessing factors influencing habitat use during foraging, including predation risk (e.g. van Baalen and Sablelis 1993; Heithaus et al. 2007b; Wirsing et al. 2008). The basic IFD model predicts that foragers will be distributed across habitat patches in proportion to their food supply. This can be expressed algebraically as:

$$p_i = s_i / (s_i + s_j) \text{ [Equation 1]}$$

Where: p = proportion of fish in a patch; s = food supply; i, j, k etc. denote habitat patches. Therefore, if consumers follow an IFD, the densities of foragers relative to their food availability (i.e., the ratio of relative foragers to their food densities) should be equal across habitat patches. Numerous studies have indeed found support for IFD (reviewed by Tregenza 1995). However, if predation risk varies across habitats, most foragers will sacrifice foraging opportunities for safety (see Lima and Dill 1990; Lima 1998 for reviews). This should lead to relative densities of foragers in safer habitats being greater than they would be in the absence of predation risk. Applying this framework in Shark Bay, Australia, Wirsing et al. (2007b) found that Dugongs (*Dugon dugon*) used shallow and deep habitats in proportion to their food supply during periods when their predators (tiger sharks, *Galeocerdo cuvier*) were scarce; but Dugongs "overused" deep (food-poor) habitats when sharks were common. Numerous foraging models have been proposed for optimizing the trade-off between predation risk and food availability (see Fraser and Gilliam 1987; Brown 1992; Brown and Kotler 2004). However, Gilliam and Fraser (1987) proposed a model whereby foragers employ a habitat use strategy that minimizes total mortality risk while allowing some net energy gain. This model is algebraically expressed as:

Select H_i, if $\mu_i/f_i < \mu_j/f_j$ (i.e., minimize μ/f) [Equation 2]

Where: H = habitat patch; μ = predation risk; f = foraging rate; *i, j, k* etc. denote habitat patches. Gilliam and Fraser (1987) found that data on juvenile creek chub (*Semotilus atromaculatus)* foraging under predation risk agreed well with the model's theoretical predictions.

Using this theoretical framework, I examined the combined effects of predation risk and food supply on fish distributions along the subtropical ecotone in Biscayne Bay, Florida. This was accomplished by testing the following predictions (based on foraging theory): (1) fishes will be distributed across their foraging landscape in proportion to their food supply (i.e., ideal free distribution theory, Fretwell and Lucas 1970); or (2) fishes will avoid high-risk habitats so that relative abundances are lowest in habitats with relatively high-risk and *vice versa* (i.e., food risk tradeoffs, Gilliam and Fraser 1987).

To apply this framework, I needed to quantify the necessary IFD and food-risk tradeoff model parameters (p, s, f, μ; see Equation 1 and 2) across the mangrove edge and along the adjacent seagrass habitat of Biscayne Bay. This was accomplished in this dissertation by conducting a series of integrated field and laboratory studies which are presented in the four data chapters that follow. These studies include: (Chapter 2) seine surveys to determine the nocturnal distribution and abundance patterns of the focal fishes in relation to distance from the mangrove-seagrass interface; (Chapter 3) stomach content analysis of the focal fishes to reveal feeding habits and trophic relationships; (Chapter 4) field manipulation experiments to explore nearshore gradients in predation pressure; and (Chapter. 5) applying foraging models with empirical field data collected to evaluate the influence of food availability and risk on nocturnal fish distribution patterns in relation to distance from the mangrove-seagrass interface. Research focused on the foraging habitat use of gray snapper (*Lutjanus griseus*), bluestriped grunt (*Haemulon sciurus*), seabream (*Archosargus rhomboidalis*) and great barracuda (*Sphyraena barracuda*). These fishes were selected because they are among the most abundant species in the bay (Serafy et al. 1997; Serafy et al. 2003) and two have economic importance in the region's recreational fishery and dive tourism industry (i.e., great barracuda and gray snapper).

This dissertation contributes to a growing understanding of the nursery function of nearshore, back-reef systems (Adams et al. 2006a). Recently, there has been a focus on determining the nursery function of different habitats in these systems (i.e., the contribution of different habitat types to the growth and survival of juveniles) in order to prioritize areas for management and conservation purposes, such as marine reserves or identify essential fish habitats (Beck et al. 2001; Adams et al. 2006a; Dahlgren et al. 2006). Factors that have been identified as priorities for determining nursery function include quantifying predation effects and production rates (Beck et al. 2001; Adams et al. 2006a). However, direct, field-based studies examining predation risk in mangroves and/or seagrass beds are few and little is known about how predation influences fish abundance patterns. This dissertation directly evaluates how predation risk influences fish distribution and abundance patterns during foraging. Several recent studies have attempted to generate production rates for juvenile fishes occupying mangroves based on diurnal surveys (Valentine-Rose et al. 2007; Faunce and Serafy 2008a). However, for realistic production estimates, knowledge of the total area utilized by the fishes is crucial. Since many fishes use mangroves as refuges during the day, but forage in adjacent habitats at night, estimating fish production based solely on diurnal observation may be misleading. By examining nocturnal foraging distributions of juvenile fishes, this study provides new insights for understanding predator-prey interactions as well as evaluating nocturnal habitat use of fishes, which have management implications such as estimating secondary production of fishes.

In summary, there is a growing demand for predictive models in these back-reef nursery habitats for development of effective management strategies that optimize ecosystem production and diversity (e.g. Beck et al. 2001; Adams et al. 2006a; Dahlgren et al. 2006). However, these models have largely overlooked the role of predation risk in structuring marine communities due to a lack of understanding of species interactions. My work directly investigates the influences of food availability and predation risk on nocturnal fish habitat use patterns along a continuous mangrove-seagrass distance gradient. The chapters that comprise my dissertation are:

1. General introduction and scope of work
2. Nocturnal fish utilization of a subtropical mangrove-seagrass ecotone: stage-specific patterns of abundance in four species

3. Seasonal diet and feeding habits of juvenile fishes foraging along a subtropical marine ecotone
4. Relative predation risk for juvenile fishes along a subtropical mangrove-seagrass ecotone
5. The influence of food supply and predation risk on nocturnal fish distributions along a subtropical mangrove-seagrass ecotone
6. Summary and conclusions.

Table 1.1. Review of 57 studies published between 1983 and 2009 investigating predation pressure on fishes. Studies were included in the review if predation pressure to fishes was quantified by some means (e.g. tethering experiments or predator abundance surveys) or simulated (e.g. odor stimulus in lab experiment). “Study location” refers to the site of field studies or location where fish were collected from for laboratory (Lab) studies. Fresh = freshwater; Mes = Mesocosm field study or experiment; Crep = crepuscular; Table heading “Land. or Grad. (Y/N)” refers to whether the study was conducted across the fish’s foraging landscape or along a habitat gradient of more than two patches that varied in relative safety. NR=Not reported.

Table 1.1

Reference	Study Location	Focal Fish Species	Env.	Study Type	Time of Day	Land. or Grad.
Werner et al. (1983)	Michigan, USA	*Micropterus salmoides*	Fresh	Mes	Day	N
Schmitt & Holbrook. (1985)	California, USA	*Embioroca jacksoni*	Marine	Lab & Mes	Day	N
Shulman (1985)	St. Croix, USVI	*Haemulidae spp.*	Marine	Field	Day	N
Gilliam & Fraser (1987)	New York, USA	*Semotilus atromaculatus*	Fresh	Mes	Day	N
Harvey et al. (1988)	Oklahoma, USA	*Curnposrorna unomulwn*	Fresh	Mes	Day	N
Holbrook & Schmitt (1988)	California, USA	*Embioroca jacksoni*	Marine	Lab & Mes	Day	N
McIvor & Odum (1988)	Virginia, USA	*Fundulus Heteroclitus*	Fresh	Field	Day	N
Rozas & Odum (1988)	Virginia, USA	*F. Heteroclitus*	Fresh	Field	Day	N
Schlosser (1988)	Minnesota, USA	*Nocomis bigutattus*	Fresh	Lab	Day; Night	N
Croy & Hughes. (1991)	NR	*Gasterosteus aculeatus*	Fresh	Lab	Day	N
Labeelund et al. (1993)	Norway	*Salvelinus alpinus*	Fresh	Field	Day	N
Pettersson & Bronmark. (1993)	Sweden	*Carassius carassius*	Fresh	Lab	Day	N
Ruiz et al. (1993)	Chesapeake Bay, USA	*F. Heteroclitus*	Fresh	Field	Day	Y
Utne et al. (1993)	Norway	*Gobiusculus flavescens*	Marine	Lab	Day	N
Limburg (1996)	New York, USA	*Alosa sapidissima*	Fresh	Field	Day	Y
Ryer & Olla (1996)	Oregon, USA	*Oncorhynchus keta*	NR	Lab	Day	N
Grand & Dill (1997)	British Columbia, CA	*O. kisutch*	Fresh	Lab	Day	N
Damsgard & Dill. (1998)	British Columbia, CA	*O. kisutch*	Fresh	Lab	Day	N
Abrahams & Sutterlin (1999)	New Brunswick, CA	*Salmo salar*	NR	Lab	Day	N
Danilowicz & Sale (1999)	Teague Bay, US Virgin Islands	*H. flavolineatum*	Marine	Field	Day; Night; Crep.	N
Landry et al. (1999)	British Columbia, CA	*O. mykiss*	Fresh	Field	Day; Crep.	N
Brown and Cowan (2000)	New York, USA	*Chrosomus neogaeus*	Fresh	Lab	Day	N
Dahlgren & Eggleston (2000)	Great Exuma Island, Bahamas	*Epinephelus striatus*	Marine	Field	Day; Night	N
Halpin (2000)	Rhode Island, USA	*F. Heteroclitus*	Marine	Field	Day; Night	N
Linehan et al. (2001)	Newfoundland, CA	*Gadus morhua, G. ogac*	Marine	Field	Day; Night; Crep.	Y
Skalski & Gilliam (2002)	North Carolina, USA	*Nocomis leptocephalus*	Fresh	Lab	Night	N
Biro et al. (2003a)	British Columbia, CA	*O. mykiss*	Fresh	Field	Day	N
Biro et al. (2003b)	British Columbia, CA	*O. mykiss*	Fresh	Field	Day	N

Table 1.1 (Cont.)

Reference	Study Location	Focal Fish Species	Env.	Study Type	Time of Day	Land. or Grad.
Johnsson (2003)	Sweden	*O. mykiss*	Fresh	Lab	Day	N
Laurel et al. (2003)	Newfoundland, CA	*Gadus spp.*	Marine	Field	Day	Y
Shoup (2003)	Ohio, USA	*Lepomis macrochirus*	Fresh	Lab	Day; Night	N
Scheuerell & Schindler (2003)	Alaska, USA	*O. nerka*	Fresh	Field	Day; Night	Y
Adams et al. (2004)	Florida, USA	*Lagodon rhomboides*	Marine	Field	Day	N
Alofs & Polvika (2004)	Washington, USA	*Clinocottus acuticeps*	Marine	Lab	Day	N
Biro et al. (2004)	British Columbia, CA	*O. mykiss*	Fresh	Field	Day; Crep.	N
Ellis & Bell (2004)	Florida, USA	*Cyprinodon variegatus*	Marine	Field	Day	N
Ellis & Bell (2004)	Florida, USA	*C. variegatus*	Marine	Field	Day	Y
Hoare et al. (2004)	New Brunswick, CA	*F. diaphanus*	Marine	Lab	Day	N
Manderson et al. (2004)	New Jersey, USA	*Pseudopleuronectes americanus*	Marine	Field	Crep.	Y
Nakamura & Sano (2004)	Ryukyu Islands, Japan	*Stethojulis & Apogon spp.*	Marine	Field	Day	N
Biro et al. (2005)	British Columbia, CA	*O. mykiss*	Fresh	Field	Day	N
Chittaro et al. (2005)	Turneffe Atoll, Belize	*H. chrysargyreum*	Marine	Field	Day	N
Foam et al. (2005a)	NR	*Archocentrus nigrofasciatus*	Fresh	Lab	Day	N
Foam et al. (2005b)	NR	*A. nigrofasciatus*	Fresh	Lab	Day	N
Borcherding et al. (2006)	Germany	*Perca fluviatilis*	Fresh	Lab	Day	N
Lister & Neff (2006)	Ontario, CA	*L. macrochirus*	Fresh	Lab	Day	N
Baker & Sheaves (2007)	Northern Australia	*Various*	Marine	Field	Day; Night	Y
Chiba et al. (2007)	Nova Scotia, CA; S. Carolina, USA	*Menidia menidia*	Marine	Lab	Day	N
Holker et al. (2007)	Germany	*Rus rutilus, P. fluviatilis, Scardinius erythrophthalmus*	Fresh	Field	Day; Night	N
Horinouchi (2007)	Miura Peninsula, Japan	*Acentrogobius spp.*	Marine	Field	Day; Night	N
Rypel et al. (2007)	Andros Island, Bahamas	*Eucinostomus spp.*	Marine	Field	Day	Y
Rypel et al. (2007)	Andros Island, Bahamas	*Eucinostomus spp.*	Marine	Field	Day	Y
Vilhunen et al. (2008)	Finland	*A. trutta*	Fresh	Lab	Day	N
Oswald & Robison (2008)	India	*Danio rerio*	Fresh	Lab	Day	N
Dorenbosch et al. (2009)	Curacao, Netherlands Antilles	*H. flavolineatum*	Marine	Field	Day	N
Gorman et al. (2009)	Newfoundland, CA	*Gadus spp.*	Marine	Field	Day	N
Gorman et al. (2009)	Newfoundland, CA	*Gadus spp.*	Marine	Field	Day	Y

Chapter 2. Nocturnal fish utilization of a subtropical mangrove-seagrass ecotone: stage-specific patterns of abundance in four species

Summary

While diel fish migration between mangrove and seagrass habitats has been recognized for decades, quantitative studies have focused mainly on *diurnal* patterns of fish distribution and abundance. In general, previous studies have shown that fish abundances decline with increasing distance from mangroves; however, evidence for such a pattern at night, when many fishes are actively feeding, is scarce. The present study is the first to report *nocturnal* fish abundances along a continuous distance gradient from mangroves across adjacent seagrass habitat (0-120m). Here, I used nocturnal seine sampling to test the null hypothesis (based on diurnal studies and limited nocturnal work) that fish abundance would decrease with increasing distance from shoreline. I focused on species and life-stage-specific abundance patterns of *Lutjanus griseus, Sphyraena barracuda*, *Archosargus rhomboidalis*, and *Haemulon sciurus*. Results indicated that assemblage composition and structure differed significantly by season, likely influenced by temperature. However, within each season, fish habitat use pattern at both the assemblage and species-specific level generally failed to support my working null hypothesis. Species-specific analyses revealed that, for most species and life-stages examined, nocturnal abundance either increased or did not change with increasing distance from the mangrove-seagrass ecotone. My results suggest that analyses where taxa are grouped to report overall patterns may have the potential to overlook significant species- and stage-specific variation. For fishes known to make nocturnal migrations, I recommend nocturnal sampling to determine habitat utilization patterns, especially when inferring nursery value of multiple habitats or when estimating fish production.

Background

Several studies indicate that, during daylight hours, mangrove-lined shorelines can harbor high fish densities with individuals presumably benefitting from reduced predation risk among the prop-roots (e.g., Parrish 1989; Robertson and Blaber 1992; Laegdsgaard and Johnson 1995). Within mangrove shorelines, fish densities tend to be lower at night, as components of the assemblage disperse into adjacent habitats to forage, returning back to the prop roots before, or soon after, daybreak (Rooker and Dennis 1991; Nagelkerken et al. 2001; Ley and Halliday 2007). Based on evidence from gut content (Randall 1967), stable isotope (Kieckbusch et al. 2004; Nagelkerken and van der Velde 2004a, b) and tagging investigations (Verweij and Nagelkerken 2007; Luo et al. 2009), seagrass beds are the prime nocturnal feeding destinations, especially for immature stages of snappers (*Lutjanidae*), grunts (*Haemuliae*) and other species that ultimately occupy coral reefs as adults.

While diel fish migration between mangrove and seagrass habitats has been recognized for decades (Hobson 1965; Starck and Schroeder 1970; Rooker and Dennis 1991; Nagelkerken et al. 2001), quantitative studies have focused mainly on *diurnal* patterns of fish distribution and abundance at different distances from the mangrove-seagrass ecotone. Using a various sampling techniques, these diurnal studies have consistently reported fish densities to be higher near to, as opposed to far from, the mangrove fringe (Thayer et al. 1987; Laegdsgaard and Johnson 1995; Nagelkerken et al. 2001; Newman and Gruber 2002; Christian 2003; de la Moriniere et al. 2004; Jelbart et al. 2007; Newman et al. 2007; Unsworth et al. 2008; Unsworth et al. 2009). However, interpreting fish utilization patterns in nearshore seagrass beds based on diurnal observations alone may be misleading, especially when inferring the nursery “value” (Beck et al. 2001) of single or multiple habitat types, or for estimating secondary production of fishes (e.g., Valentine-Rose et al. 2007; Faunce and Serafy 2008a).

To date, only a few studies have reported nocturnal fish density patterns in seagrass beds at various distances from mangrove shoreline. Off the southwestern coast of Florida (USA), Christian (2003) compared nocturnal fish densities via visual surveys in seagrass beds 10 m versus 30 m from the mangrove fringe. Finding fish densities to be uniformly low and that density differences between sampling locations were insignificant, Christian (2003) concluded that nocturnal foraging migrations, if present, extended beyond the range of her sampling effort. Off southwestern Australia, Jelbart et al. (2007) conducted diurnal and nocturnal seine sampling in seagrass beds < 200 m versus > 500 m from mangroves and found that fish densities decreased with increasing distance from shore by day as well as by night. Finally, off Hoga Island, Indonesia, Unsworth et al. (2008) compared diel fish densities using seine sampling in seagrass beds < 50 m versus 3.5 to 6.5 km from shore and reported that by both day and night, fish abundance in close proximity to mangroves was at least twice that found in seagrass beds that were more distant from shore. However, resolving nocturnal fish abundance-mangrove proximity relationships in seagrass beds from the above studies is difficult given that: (1) each study only compared two distances; (2) distance differences may have been either too small (Christian 2003) or large (Jelbart et al. 2007; Unsworth et al. 2008) to reveal the nature of abundance-proximity relationships (e.g., linear or parabolic), if they existed; and (3) results were not broken down, for the most part, at the species- and stage-specific level.

Because no studies have reported nocturnal fish abundances along a continuous distance gradient from mangrove edge across adjacent seagrass habitat, I conducted a study in subtropical Biscayne Bay, Florida, USA - a marine system rimmed by mangroves (mostly *Rhizophora mangle*) that transition into dense seagrass (mostly *Thalassia testudinum*). While several recent studies have examined seasonal and spatial patterns of fish use of Biscayne Bay's mangrove habitats, all have been focused on diurnal observations along the mangrove fringe (Serafy et al. 2003; Serafy et al. 2007; Faunce and Serafy 2008b). In the present study, I used nocturnal seine net sampling to investigate nocturnal fish habitat use patterns at 20 m intervals along a 120 m- transect extending from the mangrove edge across adjacent seagrass habitat. I tested the null hypothesis (based on diurnal studies and the nocturnal results of Jalbert et al. 2007 and Unsworth et al. 2008) that fish abundance would decrease with increasing distance from shoreline. Prior to this study I conducted some diurnal seine sampling within Biscayne Bay and also found that fish abundance patterns decreased with distance from shore (see Appendix A). My focus is on abundance and size information pertaining to four fishes: great barracuda (*Sphyraena barracuda*), seabream (*Archosargus rhomboidalis*), bluestriped grunt (*Haemulon sciurus*) and gray snapper (*Lutjanus griseus*). These fishes were selected because: (1) they are among the most abundant and easily identified to species level; (2) each is representative of a different trophic guild (great barracuda - piscivore, seabream - herbivore, bluestriped grunt - crustacean zoobenthivore, gray snapper - generalist omnivore); and (3) two have economic importance (great barracuda and gray snapper), especially in the recreational fishery of the region.

Materials and methods

Study site

This study was conducted over two seasons (wet season: July – October, 2007; dry season: January-April, 2008) along the eastern boundary of southern Biscayne Bay, Florida, USA along the leeward side of Elliott Key between latitudes N 25.427164 and N 25.406472 (Fig. 2.1). Sampling was conducted along three, 120 m-long transects that extended perpendicularly from shore and shared the following characteristics: (1) consistently high seagrass and macroalgae bottom cover (mean: 91 % ± 8.0 SD); (2) consistently shallow depths (mean: 88 cm ± 14 SD) out to 120 m from shore; and (3) stable annual salinity due to its close proximity to oceanic waters (mean: 37 ± 1.0 SD). Collectively, the above characteristics were chosen to reduce within- and between-transect variation in factors that might cloud relationships between fish abundance and distance from the mangrove shoreline. At these sites, water temperature varies somewhat between seasons (mean wet season: 32 ºC ± 1.0 SD; dry season: 24 ºC ± 2.0 SD); but within a season, water temperature is virtually identical within and between transects.

Fish Sampling

Center-bag seine nets (21.3 m long, 1.8 m high, 3 mm mesh) were used to sample fishes every 20 m along the three, 120 m-long transects (Fig. 2.1D). Although no gear is without bias, seine nets were selected because this gear has been found as an effective tool for examining the abundance patterns of the fishes under investigation in the current study (e.g. Newman et al. 2007). Moreover, previous diurnal studies using seine nets at this and other sites have found fish abundances patterns that decline with increasing distance from shore (e.g. Jelbart et al. 2007; Newman and Gruber 2002; Appendix A). A

120-m transect was selected, because 120 m was the maximum distance from shore where depths were consistently shallow enough to permit sampling with seine nets. My seining technique followed Purtlebaugh and Rogers (2007), whereby nets are hauled parallel to shore, against the current (or wind if stronger) and pursed such that a standardized area of 142 m^2 was sampled with each haul. At least two seine samples were collected simultaneously and the sequence at which each distance was sampled was chosen randomly. At each sampling event, seining began in complete darkness, a half an hour after sunset, occurred within 2.5 hrs of low tide and all sampling took less than 2 hrs to complete. Each transect was visited on different days within each season to enable the collection of three to four seine samples for each transect-distance-season combination.

Life History Stage (LHS) Designation

All collected fishes were identified to species and measured to the nearest mm total length (TL). Fish length information and published size-age relationships (de Sylva 1963; Billings and Munro 1974; Manooch III and Matheson III 1981; Stoner and Livingston 1984; Domeier et al. 1996) were used to assign all individuals to one of two life-history stages (LHS). Individuals measuring less than reported size at age 1 were designated as early juveniles and those larger than age-one size, but smaller than reported size at maturity were designated as late juveniles.

Data Analyses

Assemblage Level

Multivariate analysis was used to investigate potential differences in focal fish assemblage composition and structure among seasons, transects and distances from shore. Following the approach used by Ley and Halliday (2007), stepwise one-way analysis of similarity (ANOSIM) was employed to assess the influence of each factor (season, transect, distance) separately. Bray-Curtis similarity coefficients were generated based on fourth-root-transformed fish densities to create the similarity matrix (Clarke and Warwick 1994). Nonmetric multidimensional scaling (MDS) in conjunction with hierarchical agglomerative cluster analysis, incorporating group-average linking, was used to search for transect and distance groupings based on the similarity matrix generated (Clarke and Warwick, 1994). All multivariate analyses were performed using Plymouth Routines in Marine Environmental Research (PRIMER) (copyright M.R. Carr and K.R. Clarke, Marine Biological Laboratory, Plymouth, UK; Clarke and Warwick, 1994). Statistical significance was declared at the $P < 0.05$ level.

Species- and Stage-Specific Level

Spatial patterns of fish density were examined by comparing seine catches of juvenile gray snapper, bluestriped grunt, seabream and great barracuda along the distance gradient. At the species- and LHS-specific level, density data were positively skewed and zero values predominated and thus were inappropriate for use in conventional parametric statistical analyses. Therefore, species- and stage- specific mean densities (per 142 m^2) for each season-transect-distance combination were determined using a delta-distribution mean estimator (Fletcher et al. 2005): a measure of fish density that separately considers the proportion of samples positive for a given assemblage component (i.e., frequency of occurrence) and its mean density when present (i.e., concentration). This approach was previously used to examine mangrove fish density patterns in Biscayne Bay (Faunce and Serafy 2007; Serafy et al. 2007; Faunce and Serafy 2008a,b). Among-transect differences in absolute abundances have the potential to obscure overall relative abundance-proximity patterns. Therefore, to reveal overall density patterns with distance, I expressed transect-specific fish densities as residuals about their transect-specific means (Winer 1971). Using SAS (1990) statistical software, these standardized, zero-centered values were then regressed against distance from shore by applying linear and quadratic models. Statistical significance was declared at the $P < 0.05$ level.

Results

General

A total of 134 nocturnal seine samples (62 wet season; 72 dry season) yielded 1,706 specimens of the four focal species, which ranged in size from 3.5 to 30.0 cm TL (Table 2.1). For all four species, early-juveniles were composed of individuals less than 10 cm TL; late-juvenile stages included fishes up to 20 cm TL for seabream, 25 cm TL for gray snapper and bluestriped grunt, and 30 cm TL for great barracuda. Of the 134 samples, the percentage of samples positive for the early stages of the focal species ranged from 22.4 % to 91 %; those positive for the late stages ranged from 32.8 % to 65.7 %. Other fishes captured included: redfin needlefish (*Strongylura notata*), pipefish (*Syngnathidae sp.*), bandtail puffer (*Sphoeroides spengleri*), checkered puffer (*Sphoeroides testudineus*), Gulf toadfish (*Opsanus beta*), yellow stingray (*Urolophus jamaicensis*) and striped mullet (*Mugil cephalus*). However, catches of these species were too sparse for statistical treatment.

Assemblage Level

Overall, multivariate analyses (cluster, MDS, ANOSIM) indicated that season exerted the strongest effects on the focal species assemblage composition and structure

(ANOSIM, $P<0.001$, Table 2.2); thus, subsequent analyses were conducted by season. Within the wet season, there was a significant difference between distances from shore ($P<0.003$), but not among transects. Similarly, during the dry season, the assemblage differed significantly between distances from shore ($P<0.016$), but not among transects. Both cluster and MDS analysis within each season (grouped by transect) revealed that assemblage composition and structure closest to the mangroves differed from the rest (Fig. 2.2A,B). Within both seasons, samples closest to the mangroves separated at about 80 % similarity level, while the remaining 5 distances were similar at ≥ 90 % similarity.

Species- and LHS- Specific Level

With two exceptions, my data failed to support my working hypothesis that nocturnal fish abundance would decline with increasing distance from shore (Fig. 2.3, 2.4). The exceptions were dry season patterns of early juvenile seabream and great barracuda. Otherwise, each component's abundance trend was either uniform across the distance gradient, increased linearly or was parabolic. Among the early juveniles, the following density-distance patterns emerged: (1) *uniform* – gray snapper (dry and wet season), bluestriped grunt, seabream and barracuda (wet); (2) *negative linear (i.e., decrease with distance)* – seabream and great barracuda (dry); and (3) *parabolic* – bluestriped grunt (dry). The following density-distance patterns emerged for the late juveniles: (1) *uniform*- bluestriped grunt (wet), gray snapper and barracuda (dry); (2) *positive linear (i.e., increase with distance)* – bluestriped grunt (dry), gray snapper and seabream (wet); and (3) *parabolic* – seabream (dry) and great barracuda (wet).

Discussion

Nocturnal sampling along a distance gradient from mangrove edge across adjacent seagrass habitat (0-120 m) revealed fish habitat use patterns at the assemblage and the species- LHS- specific level that diverge from the reported pattern of decreasing density with increasing distance from shore observed diurnally (and in two cases nocturnally: Jalbert et al. 2007 and Unsworth et al. 2008) in a wide range of tropical and subtropical systems. Within each season, the assemblage differed according to distance from shore, with the zone closest to the mangrove edge being significantly distinct. Species-specific analyses revealed mostly uniform patterns of abundance with distance from shore for early juveniles. Except for the piscivorous *S. barracuda*, the zone nearest the mangrove edge tended to harbor the lowest fish densities for late juveniles. I suspect fewer patterns of fish decline with distance from the mangrove edge will emerge as more nocturnal, as opposed to diurnal, fish density data are collected.

My ability to contrast these results with other studies is limited because comparable investigations are lacking. Several authors also have found lower densities of gray snapper, bluestriped grunt, seabream and great barracuda within or near the mangroves at night versus the day (Rooker and Dennis 1991; Nagelkerken et al. 2001; Christian 2003; Yeager and Ariaz-Gonzalez 2008). Recent acoustic tracking studies of juvenile gray snapper have demonstrated that at sunset, these fishes migrate rapidly out of the mangroves in a synchronized fashion and do not forage in seagrass nearest the mangroves, but rather offshore (Luo et al. 2009; S. Whitcraft, Pers. Comm.). However, these studies could not determine where or how far the snappers moved offshore due to the ~500 m detection range of the acoustic receivers (a limitation of the technology).

Without presenting data, Starck and Davis (1966) commented that gray snapper feed up to 1.6 km from diurnal resting areas on the reef. Working in Spanish Water Bay, Curacao, Verweij and Nagelkerken (2007) reported that French grunt (*Haemulon flavolineatum*) and bluestriped grunt moved a mean distance of 23 m from mangroves to adjacent seagrass beds in the afternoon, presumably to begin foraging at night. On a coral reef, Ogden and Ehrlich (1977) reported grunts migrating up to 300 m at night to feed, while Stark and Davis (1966) claimed that bluestriped grunt fed as much as 400 m from their nearest point of diurnal concentration.

From the present study, I can only speculate as to the mechanisms driving fish habitat use decisions; however, because fish are feeding at night, it seems likely that their abundance patterns are related to prey availability. For example, gray snapper and bluestriped grunt feed on a wide variety of benthic invertebrates, with late-stages consuming larger invertebrates and, in the case of gray snapper, also small fishes (Randall 1967; Starck and Schroeder 1970; de la Moriniere et al. 2003; Nagelkerken et al. 2006). Perhaps some of these species tended to avoid foraging near the mangrove-seagrass ecotone, due to low prey supply there. This may result from fishes occupying mangrove shorelines during the day and overgrazing prey under or within meters of the prop-roots (i.e., creating a halo affect) as has been found in reef systems (Hay 1984). But, working in different systems, Rodriguez and Villamizar (2000), Skilleter et al. (2005), Kopp et al. (2007) all found that abundance of invertebrate prey was highest (not lowest) nearest the mangroves and decreased with increasing distance from shore. Moreover, late-stage seabream are herbivorous feeding primarily on aquatic vegetation (Randall 1967; Vaughan 1976; Stoner and Livingston 1984). However, their densities were also lowest nearest the mangroves where vegetation cover and seagrass canopy height were highest. With a few exceptions, early-juvenile fishes in both seasons generally followed a uniform distribution pattern with distance from shore. Vegetation cover and canopy height was relatively high across the distance gradient. Seagrass and macroalgae cover averaged 90 % (minimum 66 %, maximum 99%) in both seasons. Thus, the observed uniform abundance pattern of early juveniles may reflect sufficiently high vegetation cover and seagrass canopy height (above some threshold level) along the distance gradient providing early juveniles with ample prey supply and shelter to forage. However, to adequately explore relationships between nocturnal fish utilization and prey supply in my study domain, gut content analysis and prey distribution studies are needed.

Nocturnal fish habitat use at this site may also be influenced by predation risk. For example, several fishes may be avoiding the mangrove-seagrass edge due to increased risk of predation there at night. Transition zones between refuges and feeding areas are potentially predictable “hot spots” in space and time where animals are vulnerable to predation (Decamps and Naiman 1998; Sheaves 2005). At night, when secondary consumers leave the safety of the mangroves to feed on emerging benthic or epibenthic prey, tertiary predators may patrol the mangrove shoreline to ambush them. For example, great barracuda are piscivorous (de Sylva 1963; Schmidt 1989) and they may be positioning themselves to ambush small fishes migrating about the mangroves and feeding offshore. Thus, the mangrove-seagrass interface and its surroundings may act as a gauntlet to fishes migrating to forage, especially between dawn and dusk when predators have a visual advantage (Munz and McFarland 1973). Organisms may be at highest risk from predation when crossing ecotones between sheltered and feeding patches. For example, Shulman (1985) and Sweatman and Robertson (1994) provided experimental evidence that juvenile fishes avoided seagrass bordering the coral reef edge, along a reef-seagrass gradient, due to increased predator encounters. Exploring gradients of predation pressure to fishes along the distance gradient (e.g., via tethering experiments) would provide a means to quantify relative predation pressure with mangrove proximity (Aronson and Heck 1995; Baker and Sheaves 2007).

Conclusions and implications

Although it is well recognized that a large portion of fish feeding activity primarily occurs at night, studies examining nocturnal fish utilization of mangroves and seagrass beds are extremely limited. For example, Faunce and Serafy (2006) reviewed 111 studies published between 1955 and 2005 examining fish habitat use in mangrove systems; of these, only 6 (5%) were conducted at night. In a recent international symposium on mangroves as fish habitat (Serafy and Araujo, eds. 2007), only one of the 25 (4%) published studies reported on fish abundance at night (Ley and Halliday 2007). My investigation of nocturnal fish habitat use across a mangrove-seagrass distance gradient revealed abundance-distance trends that varied according to season, species and life-stage. Further nocturnal investigations of fish habitat use in mangrove-seagrass systems would provide valuable insight into the ecology of nearshore fishes. In my study, the mangrove-seagrass ecotone generally harbored low densities of late-juvenile gray snapper, seabream and bluestriped grunt. My results support the notion imparted by Ley and Halliday (2007) that progress toward identifying general trends in habitat selection of fishes might be achieved by focusing survey efforts on ecotones at a time (i.e., night) when feeding occurs.

It is worth considering that my results are based on sampling that took place relatively early in the night. Thus, it is possible that fish distributions during this period may not be the same as much later in the night or just before dawn the next morning. It is possible that as the night progresses, fishes may become satiated and return to the mangroves and exhibit declines in distribution with distance from shore. However, Luo et al. (2009) tracked gray snapper in Biscayne Bay and found that snapper left the mangroves at sunset to forage offshore and did not return until the following morning. I recommend that future work at this site investigate if and how fish distributions may change throughout the course of the night.

Previous diurnal studies investigating fish abundance in relation to mangroves have generally analyzed data where taxa were either grouped by species, trophic level, and/or life-history stage. Here, density patterns clearly varied by species and life-history stage. This suggests that analyses where taxa are grouped to report overall patterns may have the potential to overlook significant species- and stage-specific variation. This has implications for fisheries management of economically important species, which typically operates at the species- and stage- specific level.

Recent research has focused on determining habitat-specific secondary production rates of nearshore fishes for conservation and management purposes, such as prioritizing areas for marine reserve planning (Mumby et al. 2004; Valentine-Rose et al. 2007), identifying nursery habitats (Beck et al. 2001) or effective juvenile habitats (Dahlgren et al. 2006) and characterizing essential fish habitats (Faunce and Serafy, 2008a). As a result, several recent studies have generated secondary production rates for juvenile fishes occupying mangroves based on diurnal surveys. For example, Faunce and Serafy

(2008a) reported production estimates for gray snapper in Florida Keys mangroves between 6-11 g m^{-2} y^{-1}. Similarly, Valentine-Rose et al. 2007 reported production rates for gray snapper ranging between 50-150 g m^{-2} y^{-1} in mangroves within Bahamian tidal creeks. However, for realistic secondary production estimates, knowledge of the area utilized by the fishes is crucial. The present study reveals patterns of fish utilization of seagrasses at odds with those derived from daytime studies, with some species abundances steadily increasing out to 120 m from the mangrove-seagrass ecotone. Thus, secondary production rates calculated for mangrove-dwelling fishes based solely on diurnal studies may be overestimates as the full areal extent of seagrass use has not been taken into account. Moreover, attributing production to a single habitat (e.g. mangroves or seagrass) may be inappropriate since many fishes use multiple habitats over the diel cycle to survive and grow.

My study system is likely to share features in common with other aquatic systems. For example, Dorenbosch et al. (2005) investigated diurnal reef fish abundance along a distant gradient from coral reef across adjacent seagrass. Adult densities of reef fish species were highest on the coral reef and decreased in adjacent seagrass with increasing distance from reef edge. At night, reef species like *Lutjanidae* and *Haemulidae* leave the reef to forage in habitats up to 1.6 km from diurnal resting areas (Starck and Davis 1966; Ogden and Ehrlich 1977; Burke 1995). This scenario is comparable to the fish habitat use patterns found in the present study. Thus, my approach and conclusions may be applicable to the study of other marine environments.

Table 2.1. Numbers and size composition of early and late juvenile sampled during the wet (n= 62 seines) and dry (n = 72 seines) season. At each sampling event, seining began a half an hour after sunset in complete darkness and all sampling was completed within 2 hrs. In the wet season, sampling occurred on average between 2030 and 2230 hrs and in the dry season between 1930 and 2130 hrs. See text for more details.

	Numbers Fishes Collected			**Total Length (cm)**		
Species	**Wet**	**Dry**	**Total (Early-Juv; Late-Juv)**	**Min**	**Max**	**Average**
Gray snapper	78	129	207 (155; 89)	5.20	17.20	10.16
Bluestriped grunt	619	474	1093 (841; 238)	3.50	21.80	8.00
Great barracuda	110	57	167 (88; 150)	5.40	18.70	10.83
Seabream	128	111	239 (91; 70)	3.80	30.00	10.56

Table 2.2. Results of stepwise one-way analysis of similarity (ANOSIM). Overall analysis indicated that season was the strongest grouping factor, thus, subsequent analyses were conducted by season. Within each season, there was a significant difference between distances from shore; but not among transects. The R statistic can range from -1 to 1 with a value of 1 indicating that all replicates within a sample are more similar to each other than to any replicates from the other samples and with a value of 0 indicating that the similarities between and within samples are on average equal. P values indicate if R is significantly different from zero.

Step	Grouping Factor	Factor Analyzed	R %	P Value
1	None	Season	38	0.001
1	None	Transect	4.7	0.095
1	None	Proximity	14.6	0.005
2	Season (Wet)	Transect	10	0.100
2	Season (Wet)	Proximity	33	0.003
3	Season (Dry)	Transect	2.1	0.340
3	Season (Dry)	Proximity	28	0.015

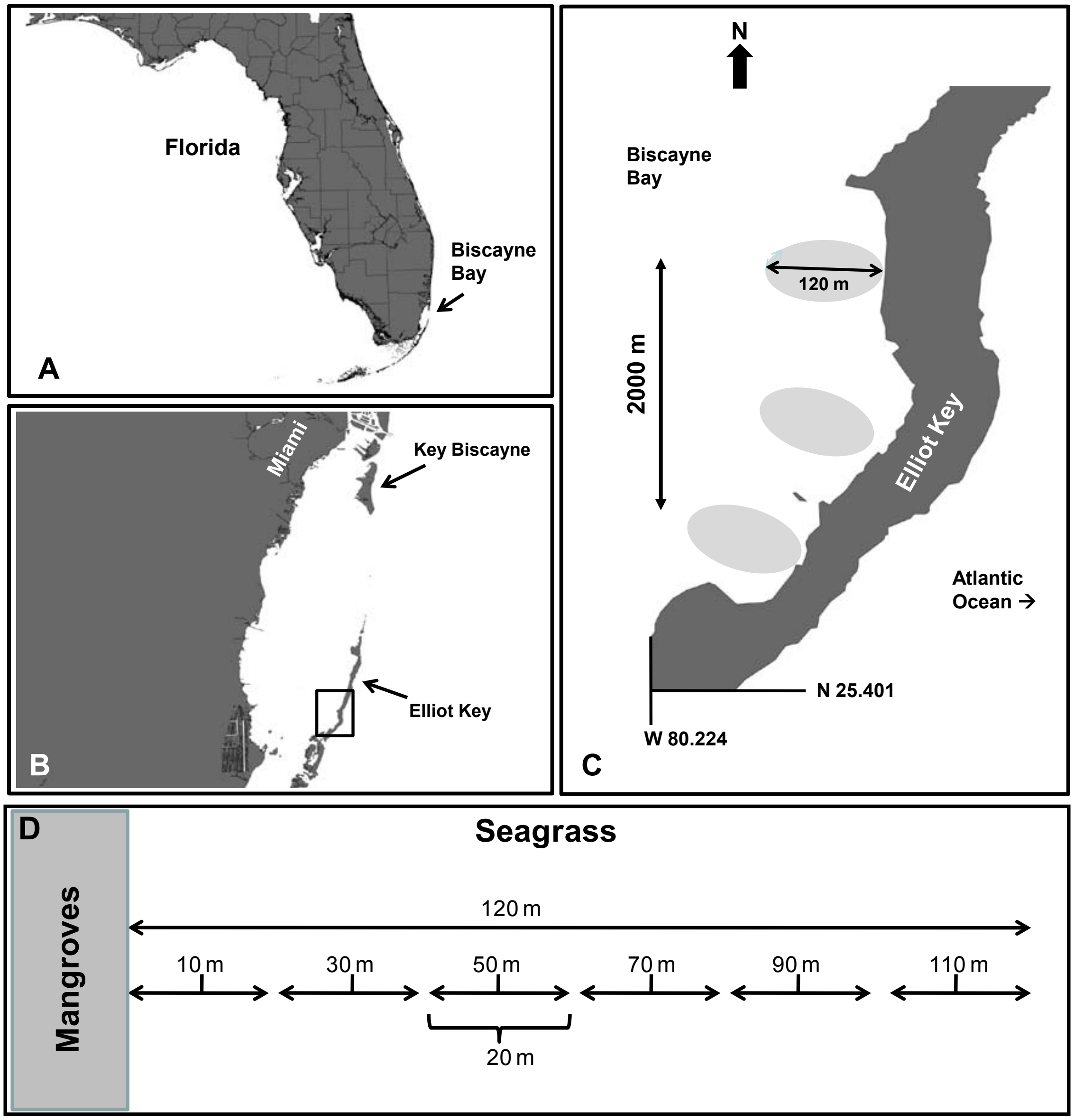


Figure 2.1. Study sites: (A) Map of Florida depicting location of Biscayne Bay; (B) position of study area (black square) on leeward side of Elliott Key within Biscayne Bay; (C) location of sampling transects within the study area; and (D) 120 m distance gradient with 20 m sampling intervals demarcated. The midpoints of the sampling intervals correspond with positions of beach seine bags.

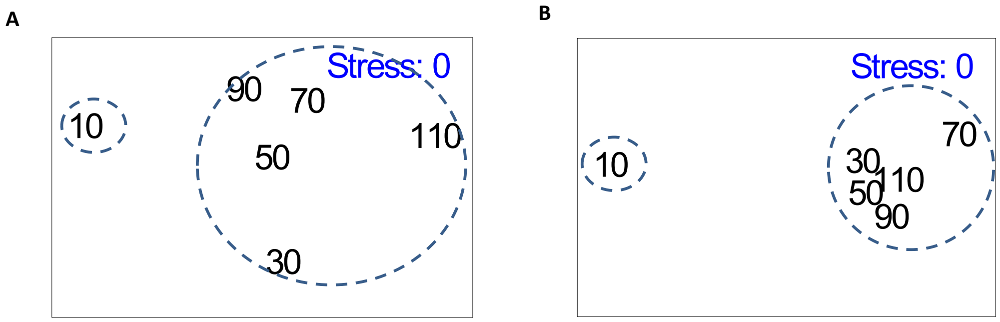


Figure 2.2. Nonmetric multidimensional scaling (MDS) plots revealing that samples nearest the mangroves separate from the rest in both the dry (A) and wet (B) season. Dashed lines indicate cluster analysis grouping of samples at about 80 % similarity. Numerical values indicate distance from the mangrove-seagrass shoreline. Success of MDS is measured by a stress coefficient. Stress < 0.05 gives an excellent representation with no prospect for misinterpretation.

Figure 2.3. Relative density-distance patterns for early-juveniles: (A, B) gray snapper; (C, D) bluestriped grunts; (E, F) seabream; and (G, H) great barracuda. Open symbols indicate dry season and solid symbols wet season. Symbol shapes correspond with different transects. Values are standardized (zero centered) transect-specific mean (± 1 standard error) fish densities (per 142 m^2). Solid lines and associated R^2 values indicate significant distance patterns ($P < 0.05$). Dashed lines and associated R^2 values indicate marginally significant distance trends ($0.05 < P < 0.1$).

Fig. 2.3

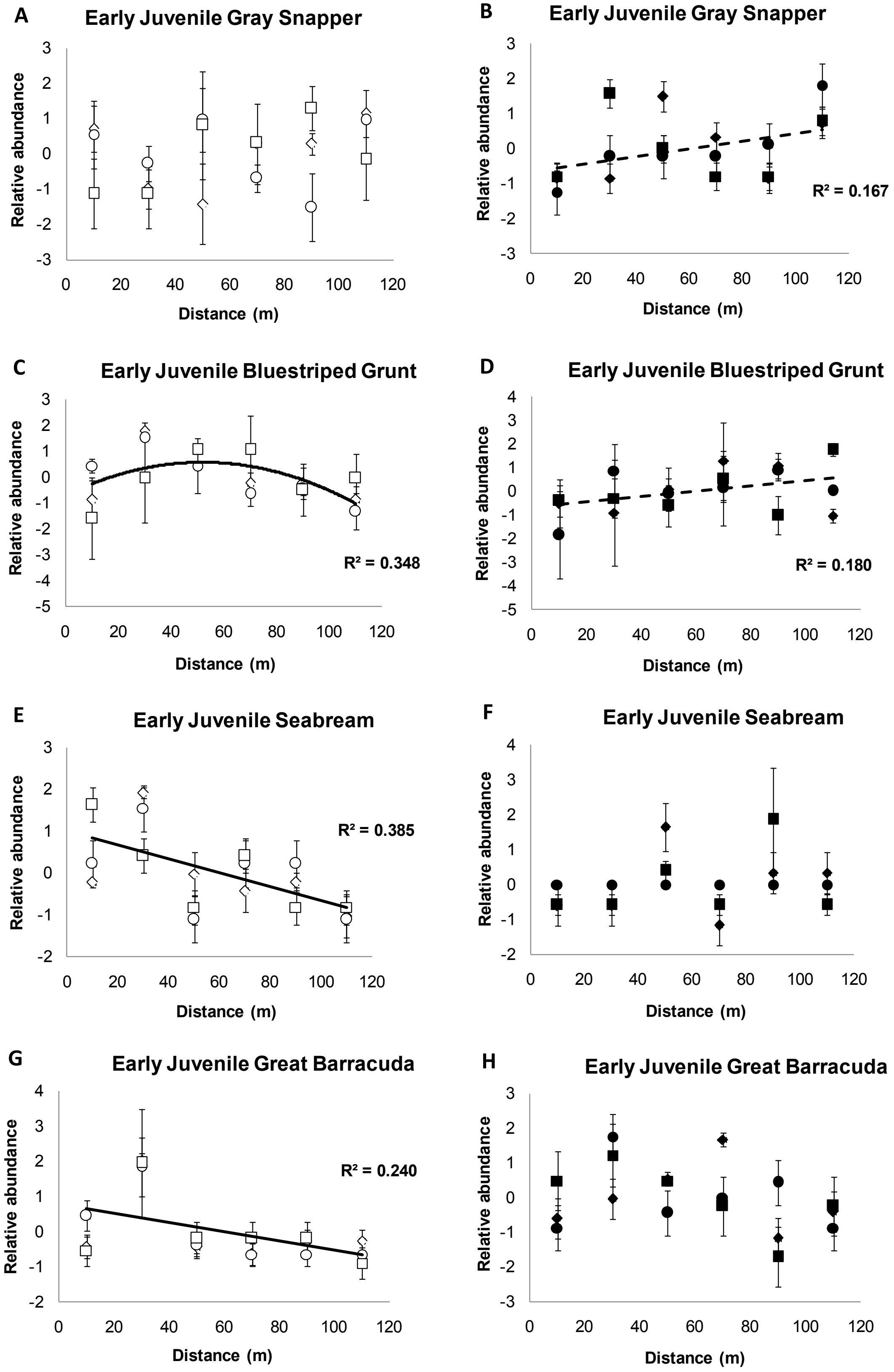
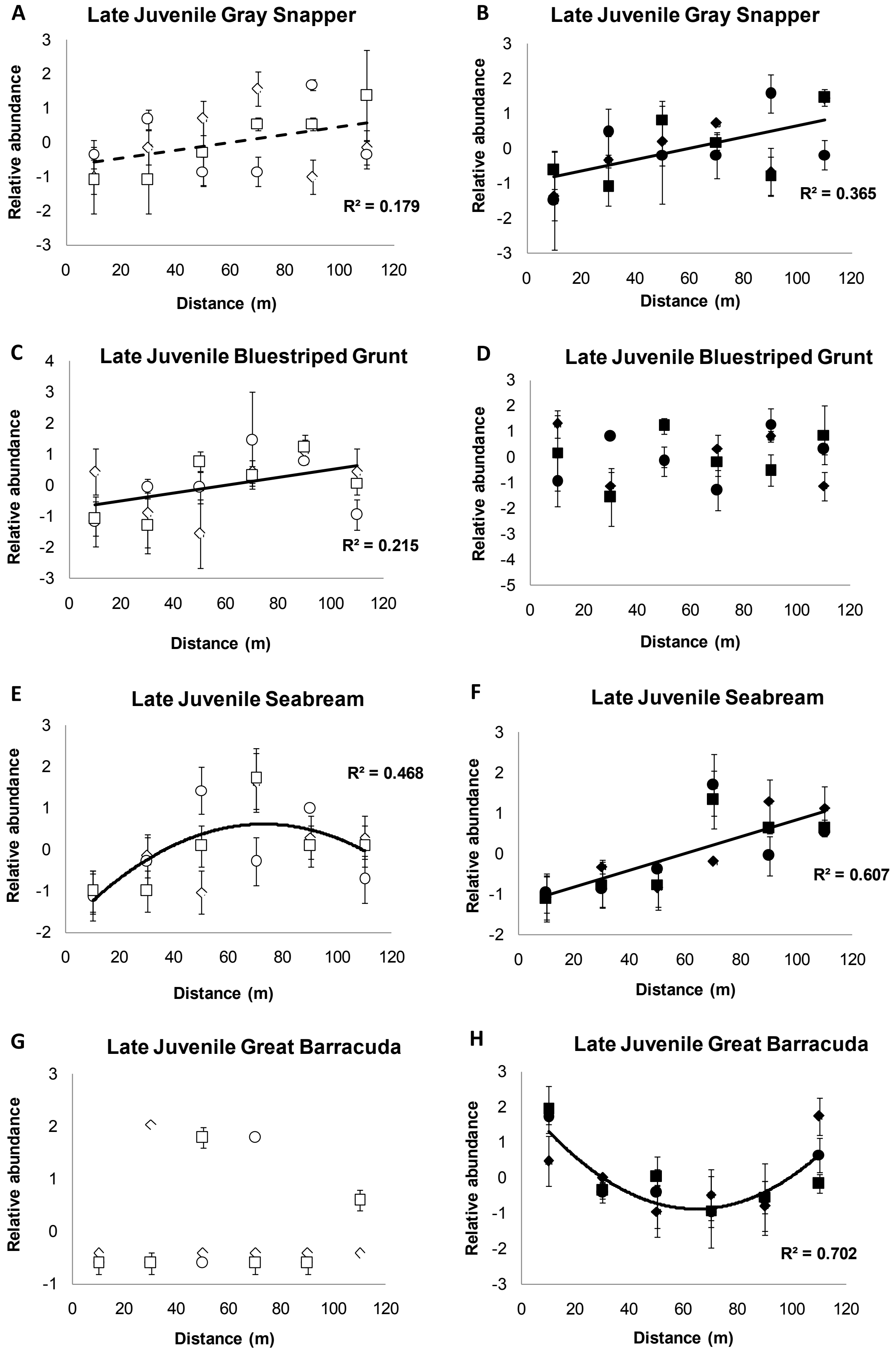

A
Early Juvenile Gray Snapper
Relative abundance
3
2
1
0
-1
-2
-3
0
20
40
60
80
100
120
Distance (m)
B
Early Juvenile Gray Snapper
Relative abundance
R² = 0.167
Distance (m)
C
Early Juvenile Bluestriped Grunt
Relative abundance
R² = 0.348
-4
-5
Distance (m)
D
Early Juvenile Bluestriped Grunt
Relative abundance
4
R² = 0.180
Distance (m)
E
Early Juvenile Seabream
Relative abundance
R² = 0.385
Distance (m)
F
Early Juvenile Seabream
Relative abundance
Distance (m)
G
Early Juvenile Great Barracuda
Relative abundance
R² = 0.240
Distance (m)
H
Early Juvenile Great Barracuda
Relative abundance
Distance (m)

Figure 2.4. Relative density-distance patterns for late-juveniles: (A, B) gray snapper; (C, D) bluestriped grunts; (E, F) seabream; and (G, H) great barracuda. Open symbols indicate dry season and solid symbols wet season. Symbol shapes correspond with different transects. Values are standardized (zero centered) transect-specific mean (± 1 standard error) fish densities (per 142 m^2). Solid lines and associated R^2 values indicate significant distance patterns ($P < 0.05$). Dash lines and associated R^2 values indicate marginally significant distance trends ($0.05 < P < 0.1$).

Fig. 2.4


A
Late Juvenile Gray Snapper
Relative abundance
Distance (m)
R² = 0.179
B
Late Juvenile Gray Snapper
Relative abundance
Distance (m)
R² = 0.365
C
Late Juvenile Bluestriped Grunt
Relative abundance
Distance (m)
R² = 0.215
D
Late Juvenile Bluestriped Grunt
Relative abundance
Distance (m)
E
Late Juvenile Seabream
Relative abundance
Distance (m)
R² = 0.468
F
Late Juvenile Seabream
Relative abundance
Distance (m)
R² = 0.607
G
Late Juvenile Great Barracuda
Relative abundance
Distance (m)
H
Late Juvenile Great Barracuda
Relative abundance
Distance (m)
R² = 0.702
0
20
40
60
80
100
120

Chapter 3. Seasonal diet and feeding habits of juvenile fishes foraging along a subtropical marine ecotone

Summary

Relatively few studies have examined seasonal diet variation and trophic relationships among fishes foraging in shallow subtropical waters. In the present study, I sampled consecutive wet and dry seasons within Biscayne Bay, Florida (USA), to examine seasonal diet and feeding habit variation in juvenile gray snapper (*Lutjanus griseus*), bluestriped grunt (*Haemulon sciurus*), seabream (*Archosargus rhomboidalis*) and great barracuda (*Sphyraena barracuda*) - four of the Bay's most abundant secondary-tertiary consumers. I found significantly lower feeding intensity during the dry season compared to the wet, which is likely related to lower water temperatures during the former season. Gray snapper fed on a variety of small fishes and crustaceans, while bluestriped grunt fed primarily on caridean shrimp. Seabream fed almost exclusively on vegetation and great barracuda was almost entirely piscivorous. Seasonal shifts in major food resource use generally did not correspond with changes in relative abundance of food supply. Seasonal trophic niche breadth differences were evident for gray snapper, great barracuda and bluestriped grunt; niche breadth was equivalent between seasons for seabream. Based on seasonal food supply in the environment, niche breadth values did not match basic theory predictions, which state that niche breadth should expand as preferred food resources become scarce. Given the seasonal variation in diet and feeding habits, it is important to incorporate seasonal variation when modeling the trophodynamics of shallow subtropical systems or characterizing them as essential fish habitats (i.e., feeding and nursery grounds).

Background

Studies of diets and feeding patterns can contribute to an understanding of ecological interactions and community structure (e.g. Winemiller 1989; Krebs 1998; Nagelkerken et al. 2006; Layman et al. 2007). Dietary ecology and feeding habits can be explored by quantifying variation in resource use, feeding intensity and trophic niche breadth. Individuals are predicted to shift resource use in response to food availability in the environment (Stephens and Krebs 1986). Trophic niche breadth can be influenced by a variety of factors, including food diversity (Layman et al. 2007) and intraspecific competition (Svanback and Bolnick 2006); however, basic theory predicts that trophic niche breadth should expand as preferred food resources become scarce (Emlen 1966; Schoener 1971; Sephens and Krebs 1986; Rodel et al. 2004). For fishes, feeding intensity is thought to decrease at lower temperatures (Tyler 1971) due to lower metabolic demands.

Although a number of studies have investigated fish feeding patterns and trophic dynamics in tropical and subtropical marine environments (e.g. Randall 1967; Harrigan et al. 1989; Layman and Sillman 2002), most quantitative trophic studies involving fishes in these systems have either grouped diet data across seasons and/or have not analyzed data to investigate whether seasonal fish diet patterns exist (e.g. Lugendo et al. 2006; de la Moriniere et al. 2003; Nagelkerken and Vandervelde 2004; Nagelkerken et al. 2006; Snodgrass et al. 2008). However, studies from mostly temperate marine and tropical freshwater systems have shown that seasonal changes in resource availability and environmental conditions can influence fish feeding patterns (Winemiller et al. 1989;

Jepsen et al. 1997; Peterson and Winemiller 1997; Laidre and Heide-Jorgenson 2005; Taniniata et al. 2008).

The present study focuses on seasonal diet and feeding patterns of late-stage juvenile gray snapper (*Lutjanus griseus*), bluestriped grunt (*Haemulon sciurus*), seabream (*Archosargus rhomboidalis*) and great barracuda (*Sphyraena barracuda*) within subtropical Biscayne Bay, Florida (USA). These fishes were selected because they are among the most abundant species in the bay (Serafy et al. 2003) and two have economic importance in the region's recreational fishery and dive tourism industry (i.e., great barracuda and gray snapper). Biscayne Bay's wet season is characterized by relatively warm water temperatures (~30 ^{o}C) and high salinity variation and its dry season by cooler temperatures and low salinity variation (Serafy et al. 2003). Given predictable seasonal variation in environmental conditions, my specific objectives were to examine for seasonal differences in feeding intensity, diet composition and trophic niche breadth. Based on theoretical predictions, I investigated the following questions for juveniles of the four focal species: (1) Is feeding intensity lower in the cool, dry season? (2) Does trophic resource use shift with food abundance? (3) Does trophic niche breadth vary inversely with seasonal food abundance?

Materials and Methods

Study site and physical habitat measurements

This study was conducted along the eastern boundary of southern Biscayne Bay, Florida, USA, along the leeward side of Elliott Key, between latitudes N 25.4271^{o} and N 25.4064^{o} (Fig. 1). Sampling was conducted during two consecutive seasons (wet season:

July – October, 2007; dry season: January-April, 2008) by seine netting along three, 120 m-long transects that extended perpendicularly from shore (Fig. 3.1C). Water temperature and salinity were measured along the three 120 m-long transects using YSI ® multi-probe instruments (600XL and 650 MDS). Water depth was measured using a 1 cm demarcated polyvinyl chloride pole.

Fish and food collections

Center-bag seine nets (21.3 m long, 1.8 m high, 3 mm mesh) were used to collect fishes and to quantify their potential prey items along the three 120 m-long transects (Chapter 2). Seine nets were hauled parallel to shore, against the current (or wind, if stronger) and pursed such that a standardized area of 142 m^2 was sampled with each haul. Sampling was conducted in darkness, from 0.5-2.0 h after sunset and within 2.5 hrs of low tide. All collected fishes and invertebrates were identified to species and measured to the nearest mm total length (TL). To permit stomach content analysis, focal fishes were removed from seines immediately after capture and preserved to reduce post-capture digestion that could result in loss of dietary information (Bowen 1996). To halt digestive processes and preserve stomach contents for laboratory analyses, focal fishes were placed in a container of ethanol (80-90 %), a slit was made in the animal's body cavity to accelerate preservation, and containers were then refrigerated. Because seagrass and macroalgae have been previously reported as the primary food items for seabream (Vega-Cendejas and Arreguin-Sanchez 2001), I also quantified vegetation cover every 20 m along the three 120-m transects. This was achieved by estimating the areal percentage of seagrass and algae within 50 cm x 50 cm quadrats (6-10 quadrats per distance-transect). This method was chosen to be consistent with existing aquatic vegetation monitoring programs in the region (Fourqurean et al. 2001; Browder et al. 2009).

Fish Diet

Stomachs were removed from each individual by severing the esophagus, the first few millimeters of the intestine, and the mesentery at its dorsal point of attachment (Bowen 1996). Stomachs were carefully opened by slitting them lengthwise with fine scissors. The presence or absence of food items within individuals was recorded since the percentage of fish with empty stomachs in each season can be used as a metric to compare seasonal feeding intensity (e.g., Laidre and Heide-Jorgenson 2005). Contents of individual stomachs were then sorted and identified to the lowest possible taxonomic level. Volumes of individual food items were quantified by measuring water displacement of food items in graduated cylinders following Winemiller (1990).

Data Analyses

To determine the adequacy of the number of collected fishes for diet description, cumulative food resource curves were created for each species-season combination following Maia et al. (2006). Seasonal differences in fish feeding intensity (i.e., the percentage of fishes with empty stomachs) were compared statistically using chi-square analysis. To quantify the relative importance of different food items seasonally in the diets of the focal fishes, I calculated the percent by volume (% *V)* of different food items in fish stomachs (following Bowen 1996; Cortes 1997). Percent volume (or weight) of different food items, compared to percent numbers or occurrence, is the better metric for quantifying the relative importance of different food items towards a fish's nutrition since it is the only, of the widely used metrics, which quantifies food types in directly comparable units (Bowen 1996). Hybrid indices combining all three metrics (e.g. index of relative importance, IRI) are also commonly used; however, Bowen (1996) suggests that these should be avoided since the summing and multiplication of percentages that are dimensionless ratios produces numbers of no definable meaning. Seasonal differences in use of major food resources were compared statistically using Kruskal-Wallis tests in which 'experimental wise' error rate was held at the $P < 0.1$ level using the Bonferroni method (Sokal and Rohlf 1987).

Seasonal differences in dietary niche breadth (*w*) was calculated for each species using Levins' formula (Levins 1968): $w = 1/\sum (p_j)^2$, where p_j is the proportion of individuals found using resource j. Dietary niche breadth values were compared for all species in both seasons. To examine for seasonal differences in food abundance, I compared mean densities of the predominant food items individually and in combination between seasons using t-tests in which 'experimental wise' error rate was held at the $P < 0.1$ level using the Bonferroni method. Because seabream consumed seagrass and macroalage, I also compared mean vegetation cover along my transects, between seasons, using t-tests. All analyses were conducted on SAS (1990) statistical software.

Results

Abiotic variables

Table 3.1 presents seasonal summaries of abiotic data collected. Water temperature ranges during fish sampling were distinct between seasons (wet season: 29.36 - 33.95 °C; dry season: 19.96 - 27.08 °C), whereas seasonal ranges for the other environmental variables overlapped substantially.

Fish Diets

A total of 134 nocturnal seine samples (62 wet season; 72 dry season) yielded 229 specimens (74 dry season; 155 wet season) of juvenile gray snapper, bluestriped grunt, seabream and great barracuda for stomach content analysis (Table 3.2). Cumulative food resource curves (Fig. 3.2) for each species-season combination showed a trend toward an asymptote, suggesting that the number of stomachs analyzed in this study was adequate for accurately describing the diet of each focal species in both seasons. Across all four focal species, there were significantly more individuals with empty stomachs in the dry season compared to the wet (Table 3.2).

Gray snapper exhibited the most diverse diet (Table 3.3A; Appendix B). In the dry season, mojarras (*Eucinostomus spp.)*, pink shrimp (*Penaeus duorarum)* and caridean shrimp constituted about 60 % of gray snapper diet. However, in the wet season, their diet was made up of a greater variety of crustaceans and teleosts, with gulf toadfish (*Opsanus beta*), hardhead silversides (*Atherinomorus stipes*), caridean shrimp, blue crab (*Callinectes sapidus*), mojarras, rainwater killifish (*Lucania parva)* and pink shrimp accounting for 60% of food items consumed. Of the primary prey items consumed, significantly more silversides were consumed in the wet season versus dry; however, there was no statistically significant seasonal difference in gray snapper consumption of pink shrimp, caridean shrimp, rainwater killifish, blue crabs or mojarras.

For bluestriped grunt, a large amount of unidentifiable, highly digested, material was found in their stomachs, likely due to the relatively rapid digestion of invertebrate skeletons (Table 3.3B; Appendix B). Of the identifiable items, caridean shrimp and vegetation accounted for 60 % of their diet in the dry season, whereas caridean shrimp and vegetation constituted about 50 % of bluestriped grunt diet in the wet season. This seasonal difference in the amount of caridean shrimp and vegetation consumed by bluestriped grunt was not statistically significant.

Aquatic vegetation, particularly seagrass *Thalassia testudinum* and macroalgae, dominated the diet of seabream in both seasons (*%V*=76.92 dry, 86.36 wet) (Table 3.3C; Appendix B). This difference emerged as statistically significant.

The diet of great barracuda was composed almost exclusively of teleosts in both seasons (Table 3.3D; Appendix B). In the dry season, hardhead silverside and rainwater killifish constituted 72 % of barracuda diet. However, in the wet season, their diet was made up of a greater variety of teleosts, with *Anchoa* sp., redfin needlefish (*Strongylura notate*), mojarras and hardhead silversides accounting for 78 % of food items consumed. Of the primary prey items consumed, significantly more silversides were consumed in the wet season versus dry; however, there was no significant seasonal difference in barracuda consumption of mojarras and rainwater killifish.

Food abundance in the environment & consumption by fishes

Table 3.4 presents seasonal summaries of environmental abundances of major food items consumed by the focal fishes. Significant seasonal differences in mean abundances of silversides, mojarras and pink shrimp were found at my site (Table 3.4). In terms of aggregate food abundances (i.e., all food types combined for a particular species), I did not find any significant seasonal differences.

For gray snapper, seasonal shift in consumption of silversides, rainwater killifish, pink shrimp and caridean shrimp corresponded with a shift in their environmental abundance (Fig. 3.3A). In contrast, the respective abundances of mojarras and blue crabs showed a declining trend from the dry to the wet season, while their importance in gray snapper diet was equivalent with a tendency for increase. For bluestriped grunt, consumption of caridean shrimp was highest in the dry season, when environmental abundances were lowest (Fig. 3. 3B). Bluestriped grunt consumption of vegetation was highest in the dry season, while mean vegetation cover at my site was equivalent with a tendency for increase in the dry season. For seabream, ingestion of vegetation (their primary food) was significantly higher in the wet season, although mean vegetation cover was similar in both seasons (Fig. 3.3C). Consumption of silversides and rainwater killifish by great barracuda was higher in the dry season, while abundances of silversides and rainwater killifish in the environment tended to be higher in the wet season (Fig. 3.3D). Abundances of mojarras declined from the dry to the wet season, while their importance in great barracuda diet tended to be higher in wet.

Trophic Niche Breadth

Trophic niche breadth was higher in the wet season versus the dry for gray snapper and great barracuda (Fig. 3.4). In contrast, niche breadth of bluestriped grunt was higher in the dry season. For seabream, trophic niche breadth was similar between seasons.

In terms of examining if niche breadth varies inversely with seasonal food abundance in the environment, trophic niche breadth of gray snapper increased from the dry to the wet season; but, their food supply tended to show the opposite pattern (Fig 3.5A). For great barracuda, trophic niche breadth and food supply were both higher in the wet, compared to the dry season (Fig 3.5B). Trophic niche breadth of both bluestriped grunt and seabream was higher in the dry season, while their food supply showed a similar trend (Fig 3.5C, D).

Discussion

In the present study, I conducted a diet analysis of juvenile gray snapper, bluestriped grunt, seabream and great barracuda inhabiting the shallows of subtropical Biscayne Bay, Florida. Gray snapper was a generalist forager, feeding on a variety of small fishes and crustaceans, while bluestriped grunt fed primarily on caridean shrimp and in the dry season, also vegetation. Seabream fed mostly on vegetation and great barracuda was almost entirely piscivorous. These feeding habits are consistent with previous studies from nearby areas (gray snapper: Odum 1970; Starck and Schroeder 1970; Harrigan et al. 1989; Layman and Silliman 2002; bluestriped grunt: Randall 1967; Sierra et al. 2001; Layman and Silliman 2002; de la Moriniere et al. 2003; seabream: Vaughan 1976; Sierra et al. 2001; Vega-Cendejas and Arreguin-Sanchez 2001; Nagelkerken et al. 2006; great barracuda: de Sylva 1963; Randall 1967; Schmidt 1989; Lugendo et al. 2006). Because seasonal changes in resource availability and environmental conditions can influence fish feeding patterns, I analyzed my diet data for seasonal differences in feeding intensity, diet composition and trophic niche breadth to address the following three questions.

Is fish feeding intensity lower in the cool dry season?

For all focal fishes, feeding intensity was significantly lower during the dry season when water temperatures were about 8 ^{o}C cooler than the wet season. My data are consistent with others' suggesting fish feeding rates decrease as water temperature drops

(Tyler 1971). Jardas et al. (2004) reported that feeding intensity of horse mackerel, *Trachurus trachurus*, collected from the Adriatic Sea was lower in the winter due to both reduced food abundance and lowered fish metabolism. Because aggregate food abundances did not vary substantially across seasons at my site for all four focal species (Table 3.4), I hypothesize that reduced feeding intensity during the dry season was primarily due to their depressed metabolic rates.

Diet studies from back-reef systems rarely report the percentage of fish sampled with empty stomachs. Of those that have presented this information, relatively high percentages of fishes sampled with empty stomachs have been found. Previous studies have reported that between 52 % (Starck and Schroeder 1970) and 69 % (Randall 1967) of gray snapper sampled had empty stomachs, as did between 44 % (Randall 1967) and 47 % (Schmidt 1989) of great barracuda and 43% of bluestriped grunt sampled (Randall 1967). In contrast, in this study (Table 3.2), I found relatively lower proportion of fishes with empty stomachs, especially during the wet season. This may be due to two factors. First, I used a sampling method that permitted rapid removal of fish from gear and immediate preservation, which minimized post-capture digestion (Bowen 1996). Second, and perhaps most important, all my sampling took place at night – a time when the focal fish species are likely foraging (Rooker and Dennis 1991; Nagelkerken et al. 2000; Chapter 2). Most studies examining stomach contents of nearshore fishes have made collections during daylight hours, which is a time when many mangrove and reef associated species, such as snappers and grunts, predominantly shelter in mangroves and are not, for the most part, feeding. My results are consistent with those reported by Odum (1970) who also conducted some diel sampling using seine nets, fish traps and poison in nearby Florida Bay area. Odum (1970) found that nocturnal sampling resulted in nearly 30 % more gray snapper with stomach contents present (empty ~ 20 % day vs. 5 % night).

Does seasonal fish resource use shift in response to food abundance?

For gray snapper, in four of six cases a seasonal shift in individual diet items corresponded with a food abundance shift in the environment (Fig. 3.3A). For bluestriped grunt, trends in resource use and environmental abundance were opposite to expectations of foraging in proportion to food supply (Fig. 3.3B). For seabream, ingestion of vegetation was significantly higher in the wet season, although mean vegetation cover was similar across seasons (Fig. 3.3C). For great barracuda, seasonal differences in consumption of individual diet items did not correspond with seasonal differences in food abundance in the environment (Fig. 3.3D). My data suggest that for the most part, shifts in seasonal food abundance are not driving shifts in fish resource use at my study site. One factor that may influence seasonal resource use at my site is competition. The mangrove shorelines of Biscayne Bay are inhabited by a diverse group of juvenile fishes which may be competing for food resources (Serafy et al. 2003; Serafy et al. 2007). Winemiller (1989) studied the feeding habits of nine piscivores from a diverse tropical fish assemblage in a Venezuelan creek. He suggested that during certain times of year, competition among fishes was high and this was ultimately driving their resource use. Another unmeasured variable that may have influenced seasonal fish feeding decisions at my site was predation risk. If predation risk varies spatially or seasonally, foragers should forego foraging opportunities for relative safety (see Lima and Dill 1990; Lima 1998 for reviews). For example, Dahlgren and Eggleston (2000) found that in Bahamian tidal creeks, juvenile Nassau Grouper (*Epinephelus striatus*) trade-off food for safety by feeding in algal clumps offering relatively less food, but which are safer from predators. Recent studies are challenging the notion that shallow, back-reef habitats, including mangroves and seagrass beds, harbor low piscivore densities (Baker and Sheaves 2006; Newman et al. 2007; Dorenbosch et al. 2009; Payne and Gillanders 2009; Unsworth et al. 2009). Studies currently underway at my site suggest that nocturnal predation risk to juvenile fishes is relatively high (Chapter 4). Future experiments manipulating both food and predation risk at my site may provide valuable insights into fish foraging decisions.

Does fish trophic niche breadth increase when food abundance seasonally decreases?

Although there have been recent advances in our understanding of factors influencing trophic niche breadth (e.g. Svanback and Bolnick 2006), basic theory predicts that trophic niche breadth should expand as food abundance decreases (Emlen 1966; Schoener 1971; Sephens and Krebs 1986; Rodel et al. 2004). This is because when food is scarce, foragers cannot afford to bypass available prey items. Several studies have obtained results consistent with this hypothesis (e.g. McKaye and Marsh1983; Rodel et al. 2004). Examining seasonal feeding habitats of piscivorous fish in a swamp-creek in Venezuela, Winemiller (1989) found that fish niche breadth increased seasonally when fish population densities were highest and availability of invertebrate prey was reduced. However, my data generally failed to support this scenario (Fig. 3.5). In fact, for great barracuda, bluestriped grunt and seabream, there was a tendency for the opposite pattern: higher trophic niche breadth in the season where food abundance was also higher. Only trophic niche breadth of gray snapper was higher in the season when food supply tended to be lower, but the seasonal differences in their food supply were not statistically significant. The lack of consistency between my results and basic theoretical predictions may be due to the fact that seasonal food abundances may not be limiting at my site. Individuals are predicted to only add new prey types to their diet as preferred prey become scarce. My data may reflect that densities of focal fish food are relatively high during both seasons, despite apparent seasonal differences.

The results of this study have implications for fishery management and conservation. Recent work has aimed at evaluating effects of habitat change on trophodynamics. For example, working in Bahamian Tidal creeks, Layman et al. (2007) found that trophic niche width of gray snapper declined due to the loss of food diversity following anthropogenic habitat fragmentation. Biscayne Bay has lost over 80 % of its mangrove fringe habitats; my study area within the Bay has not yet been similarly impacted by any noticeable anthropogenic habitat modifications (Milano et al. 2007). However, the present study provides baseline data on fish feeding intensity, diet composition and niche breadth to compare against any possible future ecosystem changes at my site. Data from the current project may also be useful for those developing trophic models as tools for understanding multi-species fisheries (e.g. Christensen and Pauly, 1992; Walters et al., 1997). Based on my diet data, I constructed simple trophic diagrams for both the wet and dry season (Fig. 3.6). The food webs presented here may be useful for future studies exploring predator-prey interactions at this site, investigating impacts of environmental change or for testing various environmental or anthropogenic scenarios using ecosystem models. These types of models and other modeling approaches are expected to be more heavily utilized as management agencies move towards more ecosystem-oriented approaches to resource management.

Table 3.1. Mean and range of abiotic environmental variables measured at the study site in dry and wet season: water temperature, salinity and depth.

	Dry Season			**Wet Season**		
Env. Variable	**Mean ± SE**	**Min**	**Max**	**Mean ± SE**	**Min**	**Max**
Temperature (ºC)	23.9 ± 0.28	19.96	27.08	32.19 ± 0.25	29.36	33.95
Salinity (ppt)	37.8 ± 0.09	36.37	38.85	36.5 ± 0.27	34.16	38.75
Depth (cm)	80.9 ± 2.47	49.00	116.00	94.06 ± 2.85	55.00	120.00

Table 3.2. Sample sizes and size ranges of late-juvenile fishes collected at night for stomach content analysis. Collection seasons are indicated. Numbers in parenthesis indicate percentage of empty stomachs. P-values indicate seasonal difference in proportion of fish with empty stomachs (i.e., feeding intensity) based on chi-square analysis.

Species	Size range	Wet Season	Dry Season	Total	P value
Gray snapper	10.4 - 31.0 cm TL	49 (8 %)	25 (48 %)	74 (22 %)	< 0.0001
Bluestriped grunt	9.1 - 23.6 cm TL	20 (30 %)	18 (67 %)	38 (47%)	< 0.02
Seabream	10.1 - 23.2 cm TL	56 (0 %)	22 (27 %)	78 (7 %)	< 0.0001
Great barracuda	11.2 - 33.0 cm TL	30 (3 %)	9 (33 %)	39 (10 %)	< 0.009

Table 3.3. Seasonal diet compositions of late-juvenile gray snapper (A), bluestriped grunt (B), seabream (C) and great barracuda (D) collected at night in Biscayne Bay, Florida (USA). Values are the percent by volume (% *V)* contribution of different food items in fish diets.

Table 3.3

(A) *Lutjanus griseus*		
Food items	**Dry Season**	**Wet Season**
Teleosts		
Atherinomorus stipes	0.00	11.83
Eucinostomus spp.	2.84	4.94
Lucania parva	0.00	4.24
Floridichthys carpio	0.00	0.26
Opsanus beta	0.00	23.15
Unknown or other	34.09	21.37
Crustaceans		
Penaeus duorarum	34.09	1.31
Caridean shrimp	24.15	9.28
Callinectes sapidus	0.00	5.14
Amphipod	0.00	0.05
Unknown or other	0.00	13.04
Echinoderm	0.00	0.13
Vegetation	1.70	2.37
Other	0.00	0.03
Unknown Material	3.13	2.85

(B) *Haemulon sciurus*		
Food items	**Dry Season**	**Wet Season**
Crustaceans		
Caridean shrimp	15.38	47.67
Amphipod	15.38	0.00
Unknown or other	23.08	7.77
Mollusc	0.00	0.52
Vegetation	30.77	1.04
Other	0.00	0.52
Unknown Material	15.38	42.49

(C) *Archosargus rhomboidalis*		
Food items	**Dry Season**	**Wet Season**
Teleosts		
Atherinomorus stipes	0.00	0.61
Crustaceans		
Caridean shrimp	22.62	1.60
Amphipod	0.00	0.10
Unknown or other	0.45	0.15
Mollusc	0.00	0.02
Vegetation	76.92	86.36
Other	0.00	1.84
Unknown Material	0.00	9.31

(D) *Sphyraena barracuda*		
Food items	**Dry Season**	**Wet Season**
Teleosts		
Atherinomorus stipes	64.62	41.25
Eucinostomus spp.	0.00	5.82
Lucania parva	6.46	0.86
Strongylura notata	0.00	13.69
Anchoa sp.	0.00	17.12
Unknown or other	27.63	16.09
Crustaceans		
Carridean shrimp	0.00	0.68
Unk or other	0.16	0.00
Vegetation	0.16	1.61
Unknown Material	0.97	2.88

Table 3.4. Mean seasonal abundance and range of main food resources (individually and aggregate) for focal species collected from the environment at my study site. GS = gray snapper, BSG = bluestriped grunt, SB = seabream, GB = great barracuda. * indicates significant seasonal difference in environmental food supply based on t-tests in which ‘experimental wise’ error rate was held at the P < 0.1 level using the Bonferroni method. NS = not significant

	Dry Season				**Wet Season**				
Food type	**Mean**	**Std Error**	**Min**	**Max**	**Mean**	**Std Error**	**Min**	**Max**	**Significance**
Atherinomorus stipes	44.34	6.28	1.00	346.00	89.37	7.64	2.00	237.00	*
Eucinostomus spp.	58.94	4.50	0.00	167.00	40.68	5.01	0.00	244.00	*
Lucania parva	15.26	1.63	0.00	71.00	16.44	3.41	0.00	160.00	NS
Penaeus duorarum	32.46	4.20	0.00	153.00	17.05	2.20	0.00	88.00	*
Caridean shrimp	172.01	16.51	0.00	877.00	140.00	23.47	0.00	922.00	NS
Callinectes sapidus	0.29	0.08	0.00	3.00	0.08	0.03	0.00	1.00	NS
Vegetation	91.73	1.13	40.00	100.00	89.66	1.10	25.00	100.00	NS
GS Aggregate	323.31	23.29	59.00	1197.00	304.57	29.62	13.00	1038.00	NS
BSG Aggregate	172.01	16.51	0.00	877.00	140.00	23.47	0.00	922.00	NS
SB Aggregate	91.73	1.13	40.00	100.00	89.66	1.10	25.00	100.00	NS
GB Aggregate	118.55	8.65	10.00	479.00	146.49	11.56	3.00	391.00	NS

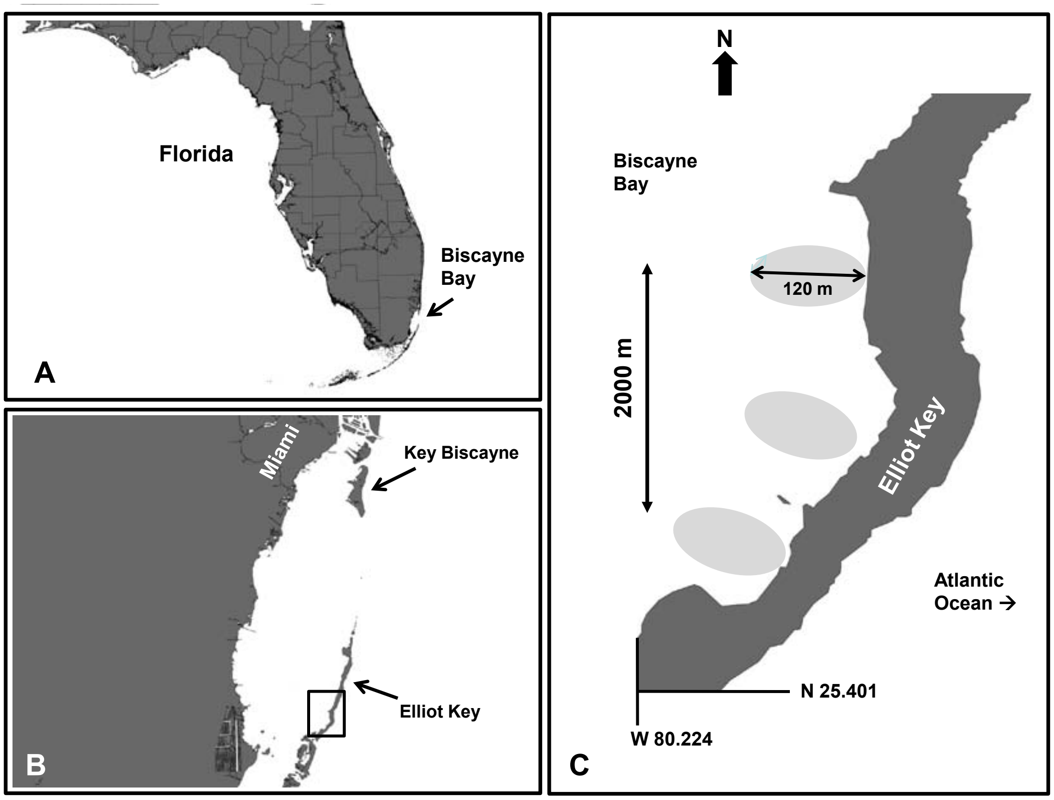


Figure 3.1. Study sites: (A) Map of Florida depicting location of Biscayne Bay; (B) position of study area (black square) on leeward side of Elliott Key within Biscayne Bay and (C) location of sampling transects within the study area.

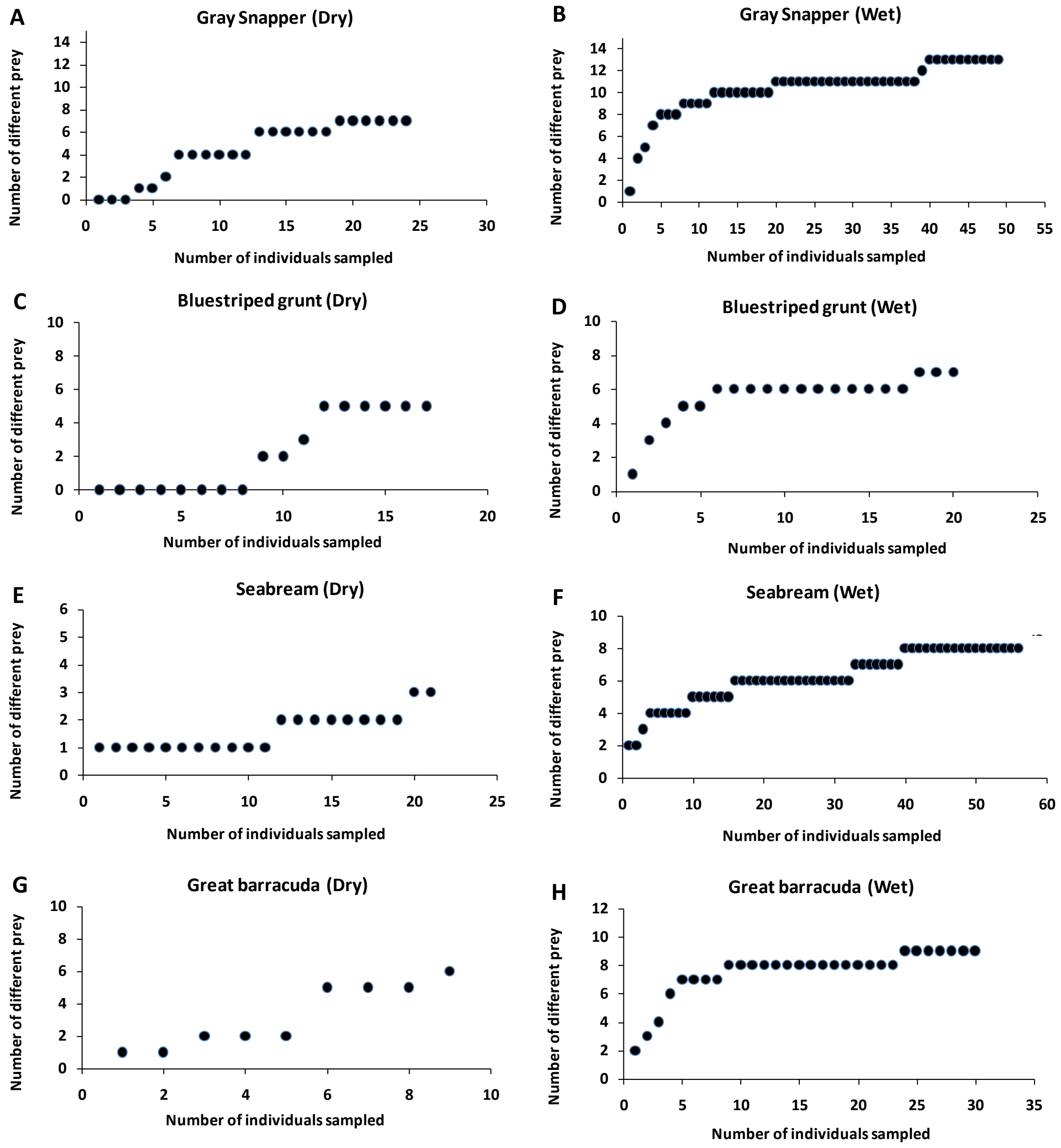


Figure 3.2. Cumulative food resource curves for stomachs analyzed of gray snapper (A, B), bluestriped grunt (C, D), seabream (E, F) and great barracuda (G, H). Wet and dry seasons are indicated.

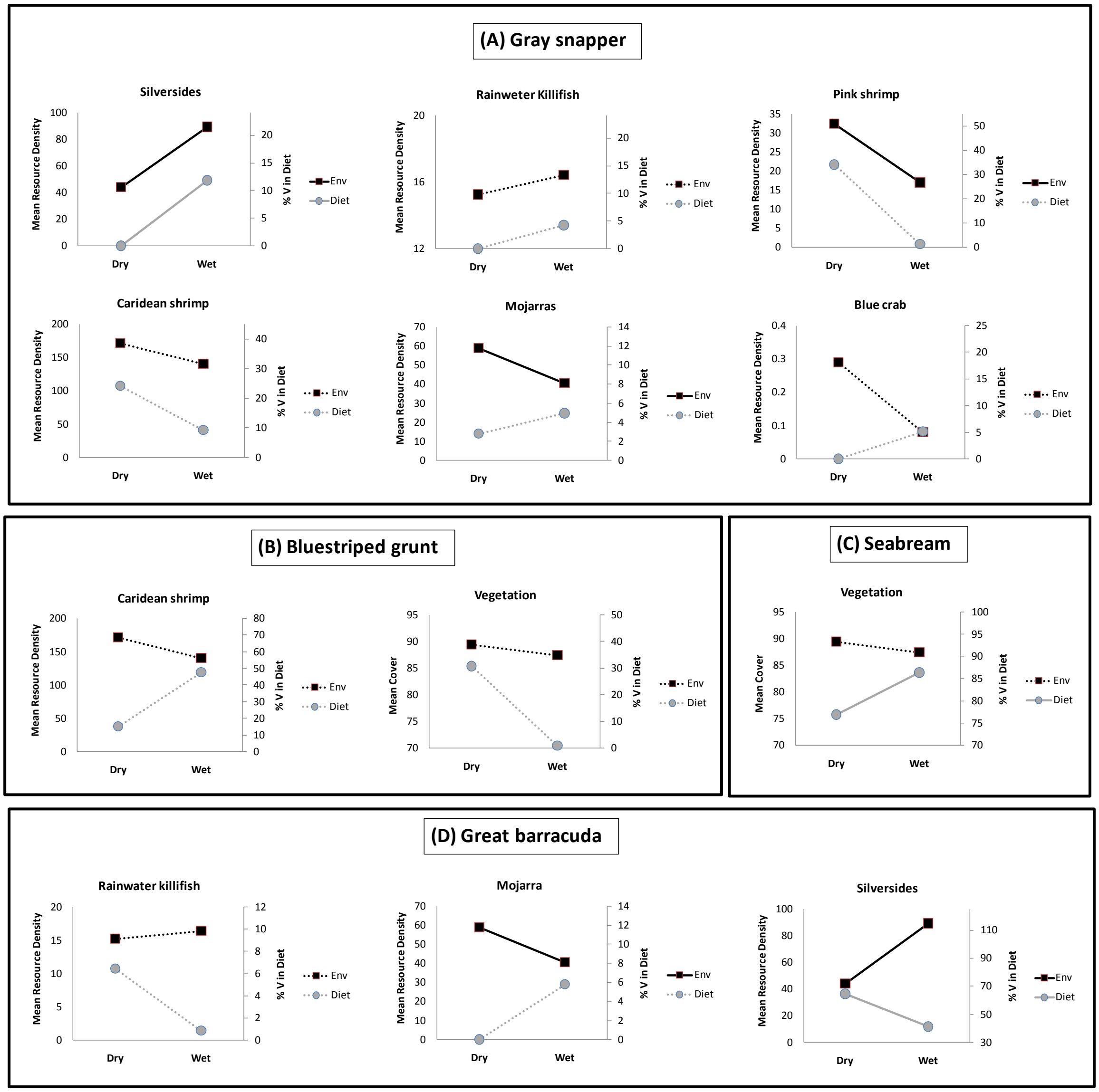


Figure 3.3. Plots comparing seasonal abundance of fish primary food items in the environment relative to seasonal consumption of these food items by gray snapper (A), bluestriped grunt (B), seabream (C) and great barracuda (D). Consumption data correspond to the contribution by volume of different food items to the diets of the focal fishes based on the data presented in Table 3.3. Food supply values correspond with data presented in Table 3.4. Solid lines indicate significant seasonal differences in which ‘experimental wise’ error rate was held at the P < 0.1 level using the Bonferroni method. “Diet” refers to consumption values of food items in the diet; “Env.” refers to food supply values in the environment.

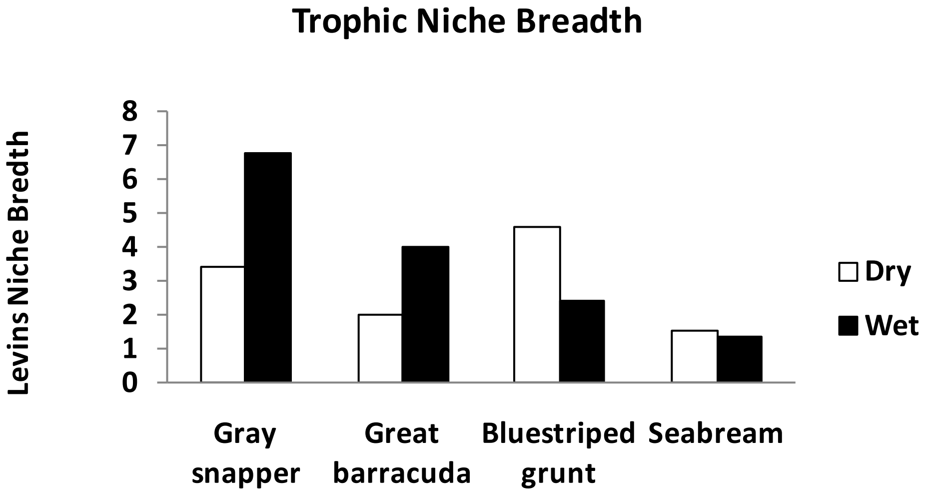


Figure 3.4. Levins' index of trophic niche breadth calculated for gray snapper, seabream, bluestriped grunt and great barracuda in Biscayne Bay, Florida (USA). Dietary niche breadth values were calculated on the percent by volume contribution of different food items in fish diets.

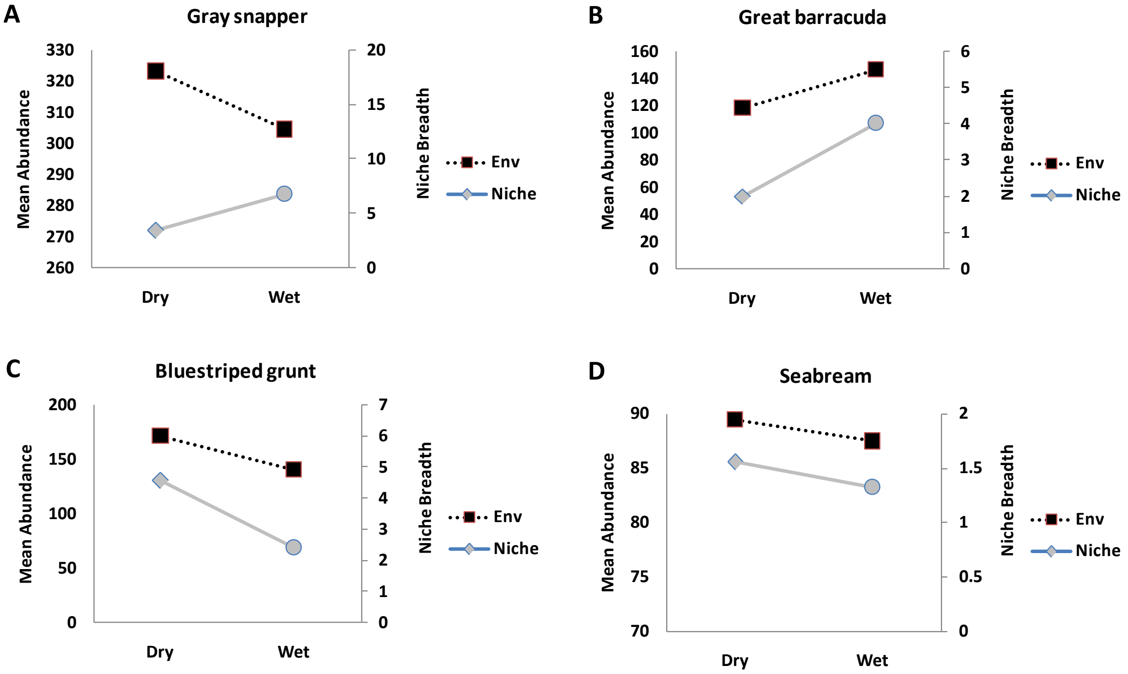


Figure 3.5. Plots comparing seasonal aggregate abundance of primary food items in the environment relative to trophic niche breadths of gray snapper (A), great barracuda (B), bluestriped grunt (C) and seabream (D). Niche breadth values correspond with data presented in Fig. 3.3; food supply values correspond with data presented in Table 3.4. Solid lines indicate significant seasonal differences in which 'experimental wise' error rate was held at the P < 0.1 level using the Bonferroni method."Niche" refers to fish niche breadth values; "Env." refers to food supply values in the environment.

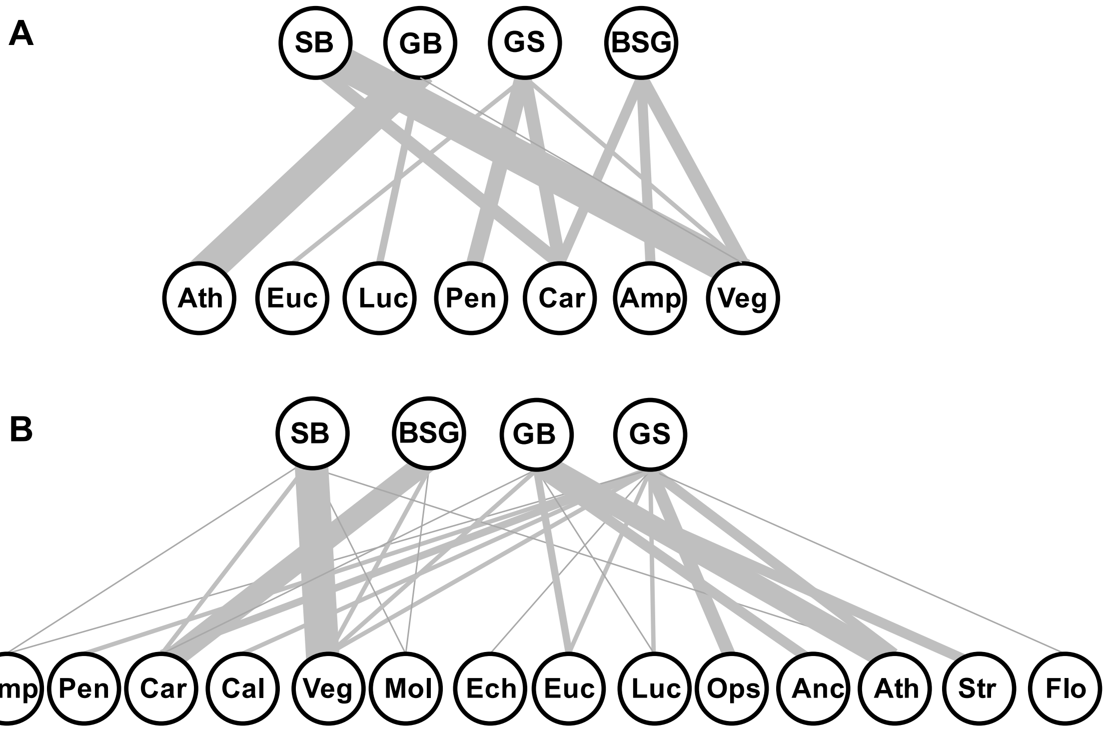


Figure 3.6. Preliminary simple trophic model of focal fishes and their prey from Biscayne Bay, Florida (USA), in the dry season (A) and wet season (B). Focal fishes (top) are arranged from left to right in order of increasing trophic niche breadth based on data presented in Fig. 3.3. The width of linking lines, correspond to the contribution by volume of different food items to the diets of the focal fishes based on the data presented in Table 3.3. GS = gray snapper, BSG = bluestriped grunt, SB = seabream, GB = great barracuda. Abbreviations for food types (bottom) are the first three letters of species names listed in Table 3.3.

Chapter 4. Relative predation risk for juvenile fishes along a subtropical mangrove-seagrass ecotone

Summary

Many fishes shelter in mangrove habitats by day and forage mostly in seagrass beds by night. This pattern of diel habitat use has been attributed to a predator avoidance strategy, whereby predation risk is reduced by alternating between the cover afforded by prop-roots during the day and darkness at night. I employed a series of diel tethering experiments in Biscayne Bay (Florida, USA) to empirically (1) examine whether relative predation pressure on fishes is lower at night than during the day; and (2) compare relative predation pressure on fishes at different distances from the mangrove-seagrass ecotone. Pinfish (*Lagodon rhomboides*) ranging 10 to 17 cm total length were tethered during day and night at 10, 50 and 110 m distances from the mangrove-seagrass ecotone. Pinfish removal rates at night were twice as high as during the day, which tends to contradict the idea that darkness provides "cover" during nocturnal foraging in seagrass. Predation losses were highest nearest the mangrove edge and decreased with increasing distance from shore. My results agree with those of other tethering studies that marine ecotones, or transition zones between refuges and feeding sites, can be areas of high predation pressure for fishes; there is less agreement among tethering studies that predation in nearshore habitats is higher at night than by day.

Background

Seagrass beds and mangroves are widely recognized as nursery habitats for a variety of coastal fishes, especially for species that occupy coral reefs as adults (Adams et al. 2006a; Blaber 2007; Nagelkerken et al. 2008). Many fishes shelter in mangrove prop-roots by day, but at night disperse into adjacent seagrass beds to feed (Starck and Schroeder 1970; Rooker and Dennis 1991; Nagelkerken et al. 2000). These nocturnal movements are presumed to primarily occur due to high food supply and lowered predation risk at night, with darkness providing cover during foraging; however, this assumption has not been empirically tested in mangrove-seagrass systems. Throughout the literature, fishes such as snappers (*Lutjanidae*) and grunts (*Haemulidae*) are cited to forage in seagrass at night, presumably taking advantage of reduced predation risk and increased prey availability as their invertebrate prey emerges from the substrate at night (e.g. Starck and Davis 1966, Nagelkerken et al. 2000; Valdes-Munoz and Mochek 2001; Unsworth et al. 2007).

Reduced predation pressure in mangrove-seagrass habitats is hypothesized to be one of the underlying factors behind the relatively high fish densities found in these habitats (reviewed by Adams et al. 2006a; Blaber 2007; Nagelkerken et al. 2008). Commonly cited factors presumed responsible for lower predation risk within and near mangroves include increasing levels of turbidity, shade, and, structural complexity, which are thought to provide shelter from predators and decrease predator foraging efficiency (Blaber and Blaber 1980; Robertson and Blaber 1992; Laegdsgaard and Johnson 2001). Closer to the prop-roots, fish fleeing distance to mangrove refuges is thought to be reduced and water depths tend to be shallower, which may restrict predator access (Shulman 1985; Rypel et al. 2007; Blaber 2007). Most previous studies, which have been primarily diurnal, have consistently reported increasing fish densities closer to, as opposed to far from, mangroves (e.g. Jelbart et al. 2007; Newman et al. 2007; Unsworth et al. 2008). However, direct field-based evidence evaluating how predation risk varies spatially in seagrass beds in relation to mangrove proximity is lacking.

Ecotones, or habitat transition zones, are recognized as hunting corridors for predators in a variety of systems (Decamps and Naiman 1988; Ries and Sisk 2004). Organisms are likely at highest risk from predation when crossing ecotones between sheltered and feeding patches, due to the high concentration of individuals in refuges and predictability of their foraging movements. For example, off the coast of South Africa, hunting white sharks (*Carcharodon carcharias*) patrol fur seal (*Arctocephalus pusillus pusillus*) refuge entry and exit points in attempts to ambush seals as they leave for, and return from, foraging (Martin et al. 2005; Hammerschlag et al. 2006; Martin et al. 2009). Although previous studies in a variety of habitats (e.g., reefs, Shulman 1985) have reported predation pressure to be high near ecotones, or habitat edges, this has not been previously reported in mangrove-seagrass habitats and is at odds with results of most published fish abundance surveys that indicate highest fish densities nearest the mangroves (Jelbart et al. 2007; Newman et al. 2007; Unsworth et al. 2008).

In Chapter 2, I examined abundance patterns of fishes in subtropical Biscayne Bay, Florida, USA - a marine system rimmed by mangroves (mostly *Rhizophora mangle*) that transition into dense seagrass (mostly *Thalassia testudinum*). I found lowest nocturnal densities of several late-stage juvenile fishes foraging near the mangrove-seagrass ecotone relative to further (up to 120 m) offshore. I hypothesized this fish distribution pattern may reflect avoidance of a predator-rich ecotone, which is consistent with the notion that transition zones between sheltered and feeding patches are high risk areas (Chapter 2).

Tethering experiments provide a means of assessing relative risk to juvenile fishes in nearshore environments by measuring predator encounter rates (McIvor and Odum 1988; Aronson and Heck 1995; Baker and Sheaves 2007). Of 22 fish tethering studies in nearshore environments published over the past 24 years (Table 4.1, 4.2), most have been conducted exclusively during the day (77 %), used small (< 10 cm total length, TL) fishes (91 %) and compared removal rates either between different habitats types, substrates or depths (81 %). Diurnal tethering studies have reported that removal rates tend to be lower in mangroves and seagrass beds versus reefs, lower in shallow versus deeper waters, and lower in areas of high versus low vegetation abundance. Only 13 % of studies have directly compared diel differences in risk and none have exclusively focused on predation pressure to juveniles >10 cm TL. However, fishes >10 cm TL correspond to sizes classes best-known to make diel mangrove-seagrass migrations. Also, no studies to date have reported diurnal or nocturnal patterns of predation risk to juvenile fishes in seagrass beds as they relate to proximity from mangrove-seagrass ecotone, despite the fact that predation risk has long been assumed as one of the important factors driving day/night shifts in fish habitat use (Starck and Davis; 1966; Nagelkerken et al. 2000; Nagelkerken et al. 2001; Valdes-Munoz and Mocheck 2001; de la Moriniere et al. 2002; Unsworth et al. 2007).

The present study builds on my previous work in subtropical Biscayne Bay (Florida, USA) by employing a series of tethering experiments to empirically: (1) examine whether relative predation pressure on fishes is lower at night than during the day; and (2) compare relative predation pressure on fishes at different distances from the mangrove-seagrass ecotone. I examined for diel and distance patterns of predation pressure by tethering pinfish (*Lagodon rhomboides*) ranging 10 to 17 cm TL, a length range which corresponds to the size classes of fishes best-known to make diel migrations among seagrass and mangrove habitats.

Material and Methods

Study site

This study was conducted from July to September, 2008, along the eastern boundary of southern Biscayne Bay, Florida, USA, along the leeward side of Elliott Key between latitudes N 25.4271º and N 25.4064º (Fig. 4.1). Sampling was focused along three, 120 m-long transects that extended perpendicularly from shore and shared the following characteristics: (1) consistently high seagrass and macroalgae bottom cover (mean: 90 % ± 8.0 SD); (2) consistently shallow depths (mean: 97 cm ± 14 SD) out to 120 m from shore; and (3) stable salinity (mean: 37 ± 1.5 SD) and temperature (mean: 32ºC ±1.2 SD) due to its close proximity to oceanic waters. Additionally, seine net sampling indicated that fish assemblage composition and structure at each transect was very similar (Chapter 2). Consistency in the above characteristics across transects limited the possibility that within- and between- transect variation may cloud relationships between relative predation rates and distance from the mangrove shoreline.

Tethering apparatus, design and pilot studies

Tethering experiments have the potential for simple and higher-order artifacts (*sensu* Peterson & Black, 1994) that can confound results. Simple artifacts include alterations in tethered-fish behavior and health, or encounters with predators that may result in changes in tethered fish survivorship. Higher-order artifacts occur when there is an interaction between the tethering technique and treatment as the effect of tethering on prey vulnerability is assumed to be constant across all treatments. I employed a tethering design aimed at minimizing both types of artifacts. .

Juvenile pinfish were used as bait for two reasons. First, pinfish ranging in size from 10 to 20 cm TL – the size class of fishes best known to make diel migrations between seagrass and mangroves (e.g. Rooker and Dennis 1991; Nagelkerken et al. 2000) – were readily available from commercial suppliers. Second, pilot studies indicated pinfish were relatively robust to the tethering process both physically and behaviorally (see below).

The tethering technique I employed was modified from Ellis and Bell (2004). The gear consisted of: (1) a 2 m-long (11.34 kg test) monofilament center line with a 226.8 g lead weight attached at one end and a small, plastic float attached to the other; and (2) a 1 m –long (11.34 kg test) monofilament tether line. Deployment was carried out in three steps. First, the center line was positioned by pushing the weight into the sediment, allowing the float to sit at the surface. Second, to secure the tether line to a pinfish, one end of the line was threaded through the mouth, out through the operculum, and was tied to form a loose loop, just forward of the pinfish's snout. Compared with more invasive fish attachment techniques, which require hooking or suturing the tether line to the fish (Table 1), the method I employed minimizes tissue damage and the release of body fluids, which could inflate detection and/or vulnerability of tethered prey to predators or scavengers. Finally, to secure the tether to the center line, it was connected to the center line using a snap-swivel (0.5 g). This snap-swivel attachment permitted pinfish to move freely in a vertical cylinder, with a 2-m diameter, from the seagrass to the water surface.

To further minimize interactions between our tethering technique and treatment (which commonly occurs in experiments where predation rates are compared between habitats that differ considerably in physical structure), I conducted all experiments such that the treatments (day-night, distance from prop-roots) were compared within a single habitat type (seagrass beds) with consistently high seagrass cover and blade lengths, uniform depths and stable salinity and temperature regimes.

Prior to my study, I made a series of qualitative laboratory and field observations to evaluate my tethering set-up. Tethered pinfish were held in outdoor, fiberglass tanks (2.3 x 1.9 x 0.7) and monitored with video cameras for 24 hours for changes in condition or behavior as well as to determine if the fish could break from tethers in the absence of predators. During monitoring, no fish died or exhibited signs of injury. Additionally, no fish broke or escaped from their tether lines. During field evaluations, tethered fish maintained equilibrium and showed no signs of erratic swimming behavior. Pinfish routinely swam from the substrate, in and out of seagrass, to the water's surface without entanglement. Tethered pinfish were also observed schooling with conspecifics. No tethering artifacts were observed that would prevent comparison of relative predation rates in seagrass beds versus distance from shore or between day and night.

To determine appropriate soak time, I conducted a series of preliminary tethering experiments at 10, 50 and 110 m distances from shore using soak times of 60, 90 and 120 minutes. In total, I conducted 111 experiments: 60 min. soak (n=36), 90 min. soak (n=42) and 120 min. soak (n=33). I found that 90 and 120 minute deployments resulted in uniformly large proportions of tether losses at all distances from shore due to eventual predation, suggesting that these soak times were too long to resolve predation rate differences among the three distances from shore. On the other hand, 60 min. soak times were optimal among those examined, providing enough time for predation to occur, yet sufficiently brief to resolve distance differences in tether losses.

Tethering experiments

To examine relationships between fish survival and proximity to mangroves, tethered pinfish were deployed at distances of 10, 50, and 110 m from the mangrove shoreline by day and by night. At deployment, pinfish were measured to the nearest mm TL. An experimental trial was composed of a group of six tethered pinfish deployed at each of the three distances from shore (Fig. 4.1D). In each trial, I randomized the sequence in which pinfish were deployed at each distance from shore. Within each distance, pinfish were spaced 10 m apart. All tethers were retrieved after 60 min., with an absence of the pinfish (or presence of a severed fish or predator on the line) scored as a predation event. All experiments occurred within 2.5 hrs of low tide. Daytime tethering began 60 to 90 min. after noon in full daylight; nocturnal tethering began > 0.5 hours after sunset, in complete darkness. Diel and distance differences in predation loss were assessed using Chi-square analysis (SAS, 1990). Throughout, statistical significance was declared at the $P < 0.05$ level.

Qualitative predator identification efforts

Three complementary techniques were used to qualitatively identify potential predators of mangrove-dwelling fishes at our study site. First, several piscivores were caught by swallowing tethered pinfish, without breaking the line. At retrieval, these predators were identified and measured for TL. Second, five tethering experiments (two during day and three at dusk) were conducted with accompanying underwater video cameras. Underwater video cameras were placed in the seagrass facing the tether and left recording for 60 min.; tethering experiments were run as described above. Predators observed preying on tethered pinfish were recorded on videotape, identified and TL estimated. Finally, 20 nocturnal gillnet collections were conducted along the three transects at our study site. Gillnet gear specifications (180 x 3 m, 4 5/8" stretched mesh, weighted) and survey procedures followed those used by Heupel et al. (2006) and Wiley and Simpfendorfer (2007). This procedure is highly selective for particular nearshore predators, such as juvenile sharks (Heupel et al. 2006, Wiley & Simpfendorfer 2007). Gill-netted animals were identified, measured for TL and released.

Results

Tethering experiments

In total, 234, 60-minute tethering deployments were conducted (126 during the day and 108 at night) using 10 to 17 cm TL (mean = 12.13 cm ± 1.4 SD) pinfish. Of the 234 deployments, 87 (37 %) predation events were tallied (i.e., tethered fish were either missing or found severed). Predation rates ranged from 10 % at the furthest distances from shore (110 m) during the day to nearly 70 % at distances nearest the mangroves (10 m) at night. During the day, predation losses decreased significantly with increasing distance from shore ($P < 0.009$, Fig. 2a). Similarly, nocturnal predation losses significantly decreased with increasing distance from the prop-roots ($P < 0.01$, Fig. 2b). Removal rates were approximately twice as high at night compared to the day ($P < 0.0001$).

Qualitative predator identification efforts

During experiments, five piscivores were caught on tethers by swallowing tethered pinfish without breaking the line, permitting their identification. During the day, this included two gray snapper, *Lutjanus griseus* (30 cm each), one great barracuda, *Sphyraena barracuda* (45 cm), one houndfish, *Tylosurus crocodilus* (87 cm), and one nurse shark, *Ginglymostoma cirratum* (45 cm). No predators were caught on tether lines at night. In the five tethering deployments monitored by video, two nurse sharks (approx. 100 cm) were filmed during the day and three juvenile lemon sharks, *Negaprion brevirostris* (approx. 100 cm each), were observed removing tethered pinfish at dusk. Nocturnal gill-netting yielded six juvenile lemon sharks, ranging from 74 to 122 cm TL (mean: 91.2 cm ± 17.5 SD), and 20 bonnethead sharks, S*phyrna tiburo*, ranging in size from 68 to 85 cm TL (mean: 76.4 cm ± 4.6 SD). All lemon shark catches were within 60 m of the mangroves; 60 % were within 40 m of shore. In contrast, 90 % of bonnethead sharks were caught between 120 and 160 m from shore.

Discussion

Reduced predation risk at night is commonly invoked as one of the main reasons for nocturnal movement and feeding in seagrass beds by fishes that shelter in mangrove habitats by day (e.g. Starck and Davis 1966; Nagelkerken et al. 2000; Valdes-Munoz and Mochek 2001). Reduced predation pressure in mangrove-seagrass habitats is also hypothesized to be one of the underlying factors behind the relatively high fish densities found in these habitats (reviewed by Blaber 2007; Nagelkerken et al. 2008). Despite an increasing number of empirical studies from a variety of systems showing that predation pressure is high near habitat edges (Decamps and Naiman 1988; Ries and Sisk 2004), this has not been previously reported in mangrove-seagrass habitats and is at variance with results from most published fish abundance surveys that reveal highest fish densities near, as opposed to far from, the mangroves (e.g. Jelbart et al. 2007; Newman et al. 2007). In the present study, I found that predation rates on 10 to 17 cm TL pinfish at night were nearly twice as high compared to the day, which is inconsistent with the notion that darkness provides "cover" during foraging bouts into seagrass beds. I found fish mortality due to predation was highest nearest the mangrove edge, decreasing with increasing distance from shore.

There have been several recent efforts to identify and describe general patterns of predation pressure to fishes in nearshore environments (Table 4.1, 4.2). Sizes of fishes used in different tethering experiments have ranged from < 3 cm TL (Nakamura and Sano 2004) to a maximum of about 10 cm TL (Laurel et al. 2003; Gorman et al. 2009). However, fishes >10 cm TL correspond to sizes classes best-known to make diel mangrove-seagrass migrations (e.g. Rooker and Dennis 1991; Nagelkerken et al. 2000). Thus, caution should be exercised when generalizing about patterns of predation risk for fishes that make diel mangrove-seagrass migrations based on previous studies that used fish < 10 cm TL.

No studies to date have reported diurnal or nocturnal patterns of predation risk to juvenile fishes in seagrass beds as they relate to proximity from the mangrove-seagrass ecotone. However, four studies in nearshore environments compared diurnal versus nocturnal differences in predation rates (Fig. 4.3A; Danilowicz and Sale 1999; Linehan et al. 2001; Horinouchi, 2007; Baker and Sheaves 2007). While both Danilowicz and Sale (1999) and Horinouchi (2007) found higher removal rates of tethered fish at night in reef and estuarine habitats, Linehan et al. (2001) and Baker and Sheaves (2007) found the opposite pattern in shallow estuarine habitats (Fig. 4.3A). The diel variation in risk found among these studies could be related to a variety of factors that differed among studies, including sampling habitat, tethered prey species and size.

Although I could not find any tethering studies evaluating patterns of risk relative to mangrove ecotone proximity, I identified three experiments from two tethering studies (Shulman 1985 and Gorman et al. 2009) examining the relationship between predation rates and proximity to other nearshore ecotones (e.g. reef edge). My results of higher rates of predation rates at the mangrove-seagrass interface are consistent with those reported from the other nearshore ecotones (Fig. 4.3B). Shulman (1985) found that predation of small grunt species was 1.4 times higher at the coral reef edge, compared to just 20 m away. Similarly, Gorman et al. (2009) found that predation on age-0 Atlantic cod was more than twice as high at the seagrass-mud boundary compared to just 10 m away in either seagrass or mud habitat.

In Chapter 2, I hypothesized that either low food availability or increased predation risk was responsible for the low nocturnal densities of late- juvenile gray snapper, bluestriped grunt and seabream I found foraging near the mangrove-seagrass interface. The results of the present study support the hypothesis that the mangrove-seagrass interface and its surroundings may represent a gauntlet for fishes migrating to forage, especially at dusk or night when predators may have a visual advantage (Munz and McFarland 1973). This hypothesis is further supported by studies from nearby sites documenting that lemon sharks, one of the main predators identified in this study, tend to focus search efforts near the mangrove shoreline (Morrissey and Gruber 1993; Franks 2007). Thus, because of the risk associated with the area, fishes may avoid foraging at night near the mangrove-seagrass ecotone.

Sheaves (2005) suggested that studies examining the patterns and timing of fish movement through transition zones can indicate whether species are moving rapidly through dangerous zones or slowly as they follow the tide to feed. Further supporting evidence that the mangrove-seagrass ecotone is an area of high predation pressure - especially at night - comes from recent acoustic tracking of juvenile gray snapper (Luo et al. 2009). This study showed that at sunset, gray snapper migrate rapidly out of the mangroves in a synchronized fashion and do not forage in seagrass nearest the mangroves, but rather move as much as 500 m offshore, returning to the mangroves the following morning.

Predation risk can be decomposed into two components – the probability that a prey encounters a predator and the probability of death as a result of that encounter (Lima and Dill 1990; Hugie and Dill 1994). Probability of death given an encounter is often mediated by differences in habitat characteristics (e.g. amount of physical structure), escape ability and their interaction (Hugie and Dill 1994; Heithaus et al. 2009). Tethering experiments measure predator encounter rates (Peterson and Black 1994; Aaronson and Heck 1995). Given that I conducted all experiments within a single habitat type (seagrass beds) with uniform physical and abiotic variables across my transects, predator encounter rates are likely representative of overall predation risk to juvenile fishes along my distance gradient. However, I must consider that at the mangrove fringe, probability of fish escape back into the mangroves given an encounter with a predator may be higher compared to just several meters away. But, this notion is dependent on fish being able to detect predators patrolling the mangroves, which is likely hindered at night, when predators may have a visual advantage (Munz and McFarland 1973). Pending further studies on the fleeing and predator detection capabilities of vulnerable fishes, I conclude that at our site, as fish begin to migrate away to feed in adjacent seagrass beds, they are likely at high risk nearest shore as compared to further away.

In the present study, I was able to determine the identity of a number of potential predators at my study site. A variety of large piscivores removed tethered fish during the day, including great barracuda, gray snapper and nurse sharks. These species are known predators of small fishes in back-reef habitats (de Sylva 1963; Stark and Schroeder 1970; Castro 2000). During dusk, only juvenile lemon sharks were found removing pinfish. In my nocturnal gillnet surveys, juvenile lemon and bonnethead sharks were caught. Most lemon sharks were captured close to shore, while most bonnethead sharks were caught offshore (> 120 m). Lemon sharks are piscivorous (Newman 2003), while bonnethead sharks are omnivorous, feeding mainly on crustaceans (Bethea et al. 2007). Based on my preliminary results, and those reported from other nearby studies (e.g. Morrissey and Gruber 1993; Franks 2007), I hypothesize that juvenile lemon sharks patrolling the shoreline at night are primarily responsible for the elevated predation rates found closest to the mangroves at night. However, future studies are needed to adequately identify the full suite of predators in my study domain and reveal diel differences, if any.

Although in this study I attempted to minimize tethering artifacts, it is possible that some arose due to inherent limitations of the tethering approach. For example, a tethered pinfish may have struggled on the line, unduly attracting a predator that would otherwise not have normally detected, pursued or been able to capture a pinfish (Adams et al. 2004). However, because experiments were conducted using the same procedure in a single habitat type, I doubt that such artifacts would have varied with distance from shore or by time of day, thus preventing comparisons of *relative* predation rates in seagrass beds versus distance or between day and night.

It is worth considering that my nocturnal results are based on sampling that took place in complete darkness, but still relatively early in the night. Thus, it is possible that predation pressure during this period may not be the same as much later in the night or just before dawn the next morning. Likewise, it is possible that predation pressure varies over the course of the day; I recommend, therefore, that future work investigate if and how predation pressure changes in relation to mangrove proximity over the entire 24 hr cycle. Until then, however, my results support the idea that the mangrove-seagrass ecotone is a high risk area for fishes that conduct diel migrations between mangroves and adjacent seagrass beds.

Prolonged soak times have the potential to reduce differences between tethering treatments due to eventual predation. Additionally, long soak times increase the likelihood of fish fatigue, injury or death, which can result in tether losses due to scavenging or removal by organisms that would otherwise not prey upon un-tethered fish. For example, Dorenbosch et al. (2009) observed tether removals by non-piscivorous fishes, which they suggested may have caused on overestimation of predation pressure. Soak times in the reviewed studies ranged from less than 30 minutes (Laurel et al. 2003; Gorman et al. 2009) to 192 hours (Halpin 2000). Based on my results, I recommend conducting a pilot study to determine optimal soak times for the system under investigation. Several recent studies have used tether-timers to generate survival curves (e.g. Danilowicz and Sale 1999; Chittaro et al. 2005). In terms of reducing issues associated with prolonged soak times, I suggest such devices would be most valuable when determining which tethers are preyed upon the fastest among the different treatments.

Conclusions

It has been long cited that mangrove-fishes were foraging at night under the cover of darkness, in large part, because of both reduced predation risk and high prey availability. However, this study suggests that risk in mangrove-seagrass habitats is significantly higher at night. This result is consistent with those reported from the reef, where predation rates on tethered juvenile grunts were higher at night (Dailowicz and Sale 1999). I propose that nocturnal foraging migrations of mangrove-associated fishes in seagrass beds are in fact driven primarily by enhanced food abundance at night and that fish foraging during these times incur a cost of enhanced predation risk.

My results suggest that the mangrove-seagrass ecotone is likely an area of high risk to juvenile fishes (10-20 cm TL) migrating from the mangroves to forage in adjacent seagrass. Although this study is the first to investigate such patterns across a mangrove-seagrass distance gradient, my results are consistent with other studies in different nearshore environments (e.g. Shulman1985; Gorman et al. 2009). These results support the notion imparted by Sheaves (2005) that transition zones between refuges and feeding areas are potentially predictable "hot spots" in space and time where animals are most vulnerable to predation.

Table 4.1. Chronological list of 22 studies using fish tethering experiments in nearshore habitats published over the past 24 years

Source	Location	Prey Species	Fish Size (cm)	Fish Attachment	Tether Line Length (cm)	Tether Anchor	Distance b/w Tethers (m)
Shulman, 1985	St. Croix, USVI	*Haemulidae spp.*	3.2 avg SL	mono, through posterior ventral musculature	25	pole	NR
McIvor & Odum, 1988	Virginia, USA	*Fundulus Heteroclitus*	4-6.5 TL	mono, through lower jaw	100	pole	NR
Rozas & Odum, 1988	Virginia, USA	*F. Heteroclitus*	4-5.5 SL	mono, through lower jaw	70	pole	≥2
Ruiz et al., 1993	Chesapeake Bay, USA	*F. Heteroclitus*	4-5	mono, through skin anterior of dorsal	20	buried rod	2
Danilowicz & Sale, 1999	Teague Bay, US Virgin Islands	*Haemulon flavolineatum*	3-4 TL	mono, through dorsal musculature	20	timer	5
Dahlgren & Eggleston, 2000	Great Exuma, Bahamas	*Epinephelus striatus*	3.9-7.3 TL	mono, through lower jaw	30	pole	10
Halpin, 2000	Rhode Island, USA	*F. Heteroclitus*	5-7 TL	mono, Through lower jaw, mouth-operculum loop	50	pole	NR
Linehan et al., 2001	Newfoundland, Canada	*Gadus morhua, G. ogac*	4.6-5.8 SL	Hook, through caudal peduncle	50	monofilament	NR
Laurel et al., 2003	Newfoundland, Canada	*Gadus spp.*	6.5-10.6 SL	hook, through caudal peduncle	50	monofilament	3-25
Adams et al., 2004	Florida, USA	*Lagadon rhomboides*	2-5 SL	mono, through muscle between anal fin and spine	30	pole	5
Ellis & Bell, 2004	Florida, USA	*Cyprinodon variegatus*	NR	mono, mouth-operculum loop	25	monofilament	1.5
Ellis & Bell, 2004	Florida, USA	*C. variegatus*	NR	mono, mouth-operculum loop	25	monofilament	≥1
Manderson et al., 2004	New Jersey, USA	*Pseudopleuronectes americanus*	3-5 SL	mono, mouth-operculum loop	75	chain	3
Nakamura & Sano, 2004	Ryukyu Islands, Japan	*Stethojulis & Apogon spp.*	2.96, 2.86 avg TL	mono, through caudal or abdominal vertebrate	100	buried peg	NR
Chittaro et al., 2005	Turneffe Atoll, Belize	*H. chrysargyreum*	3-6 TL	hook, through dorsal musculature	NR	pole	≥4
Baker & Sheaves, 2007	Northern Australia	*Various*	<10 FL	mono, through lower jaw	35	NR	≥20
Horinouchi, 2007	Miura Peninsula, Japan	*Acentrogobius spp.*	3.0-3.5 TL	NR, to caudal peduncle	40	buried peg	NR
Rypel et al., 2007	Andros Island, Bahamas	*Eucinostomus spp.*	3-9 SL	mono, through hole cut in snout	100	pole	varied
Rypel et al., 2007	Andros Island, Bahamas	*Eucinostomus spp.*	3-9 SL	mono, through hole cut in snout	100	pole	varied
Dorenbosch et al., 2009	Curacao, Netherlands Antilles	*H. flavolineatum*	3.1-4.5 TL	Mono, through lower jaw	50	pole	≥10
Gorman et al., 2009	Newfoundland, Canada	*Gadus spp.*	4.5-10.5 SL	hook, through caudal peduncle	50	monofilament	NR
Gorman et al., 2009	Newfoundland, Canada	*Gadus spp.*	4.5-10.5 SL	hook, through caudal peduncle	50	monofilament	NR
Present Study	Southeast Florida, USA	*L rhomboides*	12.13 avg TL	mono, mouth-operculum loop	100	monofilament	10

Table 4.2. Review of experimental designs employed in 22 nearshore fish tethering experiments published over the past 24 years

Source	No. Experiments	Soak Time (hr)	Habitat type(s)	Factor(s) compared	Time of Day
Shulman, 1985	64	1	Exposed sand near reef	Proximity to reef	Day
McIvor & Odum, 1988	90	2-3	Tidal marsh (depositional and erosional banks)	Depth; Habitat	Day
Rozas & Odum, 1988	80	2-3	Tidal creeks with SAV	Presence/Absence of SAV	Day
Ruiz et al., 1993	NR	1.5	Shallow non-vegetated subestuary	Depth	Day
Danilowicz & Sale, 1999	330	0.5-3	Reef	Time of Day, Side of Reef	Day; Night; Crepuscular
Dahlgren & Eggleston, 2000	120	8.25-9.25	Tidal Creeks with mangroves, seagrass and coral	Algae cover	Day; Crepuscular
Halpin, 2000	78	120-192	Pond; creek; shallow subtidal; mudflat; channel	Habitat	Day; Night
Linehan et al. 2001	576	0.42	Sand & Gravel, Eelgrass	Depth; Day/Night; Presence/Absence of SAV	Day; Night; Crepuscular
Laurel et al., 2003	1116	0.25	Eelgrass patches, Sand	Patch size, Substrate	Day
Adams et al., 2004	120	1-4	Seagrass	Algae cover	Day
Ellis & Bell, 2004	600	1-5	Sand w/ algae	Depth	Day
Ellis & Bell, 2004	352	1-1.3	Mangrove	Shade; Structure; ShadexStructure	Day
Manderson et al., 2004	239	4	Sand bar close to deep habitat	Depth	Crepuscular
Nakamura & Sano, 2004	128	1	Coral, Seagrass	Habitat, Use of shelter	Day
Chittaro et al., 2005	20	1.5	Mangrove, Seagrass, Reef	Habitat, Time of Day, Sites	Day
Baker & Sheaves, 2007	183	2-3	Shallow sand	Depth; Day/ Night; Moon phase; Tide State	Day; Night
Horinouchi, 2007	160	8-17.5	Seagrass, Sand	Substrate; Day/Night	Day; Night
Rypel et al., 2007	180	0.5	Mangrove	Depth	Day
Rypel et al., 2007	128	0.5	Mangrove tidal creek	Depth; tidal stage	Day
Dorenbosch et al., 2009	203	1.5	Mangrove, Seagrass, Reef	Habitat	Day
Gorman et al., 2009	490	0.25	Eelgrass patches	Patch size	Day
Gorman et al., 2009	1145	0.25	Mud, Eelgrass	Edge effects	Day
Present Study	234	1	Seagrass	Distance from shore; Day vs Night	Day; Night

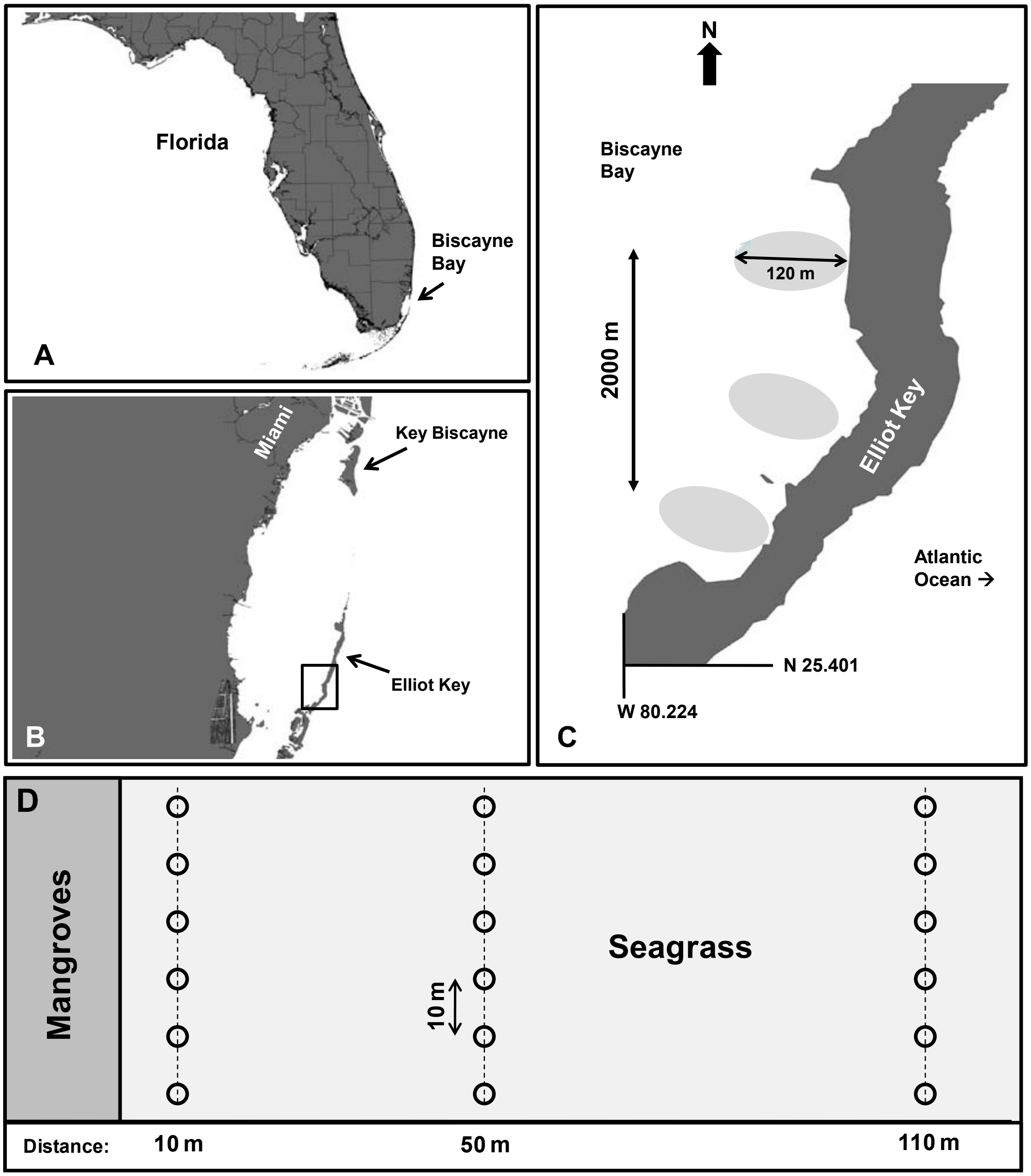


Figure 4.1. Study sites: (A) Map of Florida depicting location of Biscayne Bay; (B) position of study area (black square) on leeward side of Elliott Key within Biscayne Bay; (C) location of sampling transects within the study area; (D) Birdseye view of experimental set-up along the sampling transect. An experimental trial was composed of a group (open circles) of six tethered pinfish deployed at 10, 50 and 110 m distances from shore. Within each distance, pinfish were spaced 10 m apart. Depths were consistently shallow across the transect, averaging 90 cm ± 22.3 SD at 10 m from shore to 122 cm ± 18 SD at 110 m from shore.

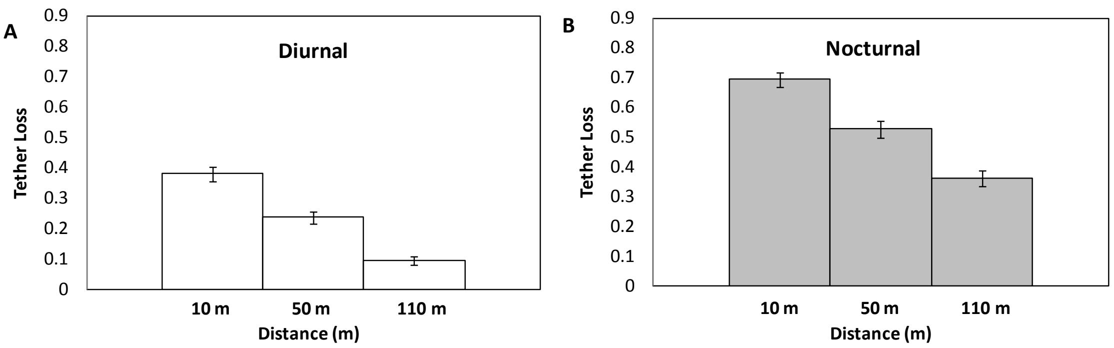


Figure 4.2. Predation losses (percent predation) of tethered pinfish in relation to mangrove proximity during the day (A) and night (B). Error bars indicate ± 1 standard error.

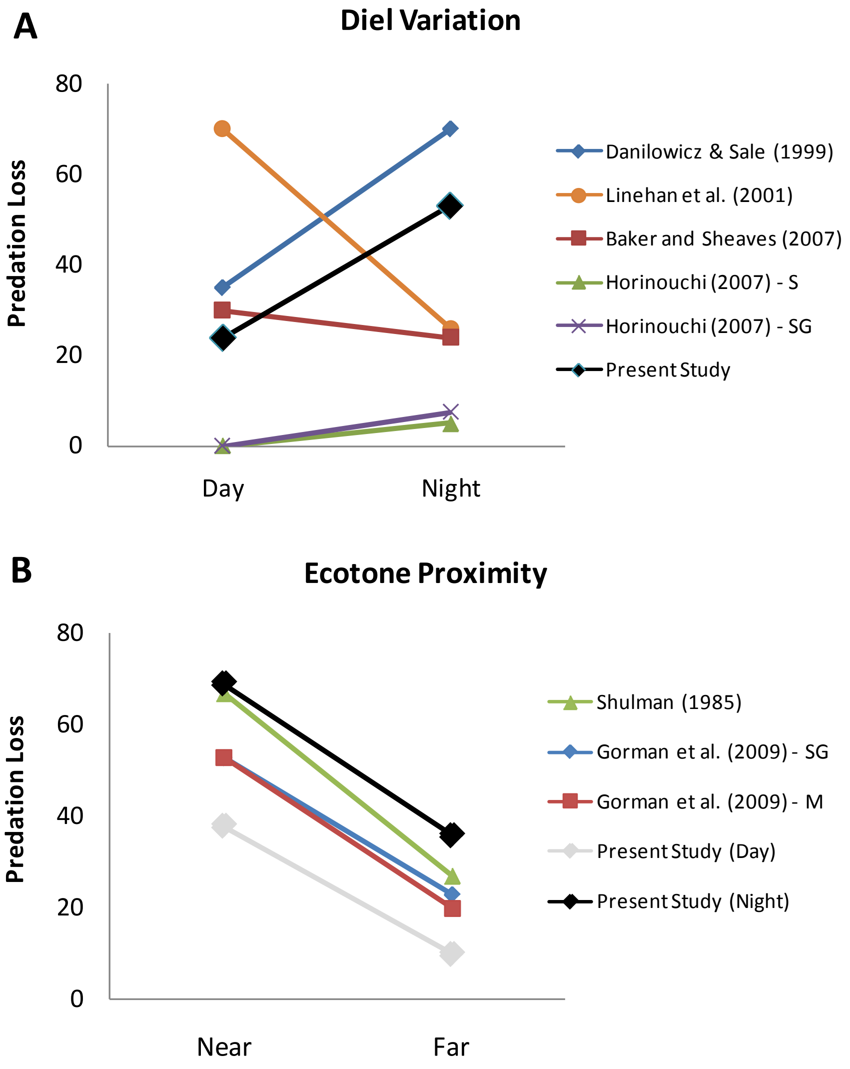


Figure 4.3. Trends in relative predation pressure in nearshore habitats (A) during the day versus night, and (B) in relation to distance from ecotone, based on data from published studies. Note that the lines are not intended to indicate continuous trends or to contrast differences in study predation rates, but rather as a means of comparing relative trends among studies. Studies with multiple experiments are indicated. In (A), the “S” and “SG” identifiers in Hironouchi (2007) refer to results from experiments in sand and seagrass respectively. In (B), the “SG” and “M” identifiers in Gorman et al. (2009) refer to results from experiments in seagrass and mud, respectively. Predation values from Baker and Sheaves (2007) were extrapolated from their data; values from Danilowicz and Sale (1999) were averages of ranges provided; values from Gorman et al. (2009) were determined by averaging across study sites.

Chapter 5. The influence of predation risk and food supply on nocturnal fish foraging distributions along a subtropical mangrove-seagrass ecotone

Summary

The combined effects of food availability and predation risk on fish habitat use have received little attention along subtropical shorelines, which serve as nursery habitats for a variety of economically important fishes. In subtropical Biscayne Bay, Florida (USA), I investigated the influences of food and predation risk on nocturnal habitat use by gray snapper (*Lutjanus griseus*), bluestriped grunt (*Haemulon sciurus*), and seabream (*Archosargus rhomboidalis*) along a distance gradient, spanning from the mangrove-seagrass ecotone to 120 m from shore. Seine and submerged vegetation sampling were used to determine distribution patterns of fishes and their food resources. Tethering experiments were used to explore gradients in predation pressure. I used these data to test *a priori* predictions of fish distributions relative to food and risk that were generated from foraging theory: (1) fishes will be distributed across the distance gradient in proportion to their food supply (i.e., ideal free distribution, IFD); or (2) fishes will avoid high risk areas such that their abundances will be lower than predicted by food resources in high-risk habitats (i.e., food-risk trade-off). Results indicated that none of the fishes were distributed according to IFD. Seabream and gray snapper avoided foraging close to the mangrove edge, where their food was most abundant, but risk was highest. Bluestriped grunt responses to spatial variation in food supply and risk were less clear; they appeared to forage randomly across the distance gradient. My results suggest that fish generally avoid the risky mangrove-seagrass ecotone, but responses to spatial

variation in food and predation risk are species-specific and may be dependent on their specific anti-predator tactics or are influenced by factors I did not measure.

Background

Predators can affect prey distribution and abundance through direct mortality (Krebs and Davies 1984; Morin 1999) and through risk effects (Werner et al. 1983; Brown et al. 1999; Creel and Christianson 2008), such as altering prey behavior and habitat use. While foraging, most animals are susceptible to predation because behaviors that enhance foraging opportunities typically also increase predation risk (e.g., increased activity levels; discussed in Lima and Dill 1990; Lima 1998). Moreover, habitats that contain the greatest food resources are often the most dangerous (Sih 1980; Brown 1988; Brown and Kotler 2004). Thus, a trade-off often exists between foraging opportunities and the risk of predation (Sih 1980; Lima and Dill 1990; Houston et al. 1993). By sacrificing feeding rate for safety (e.g. shifting to safer but less profitable feeding patches) in response to risk, mesoconsumers can impact the behaviors and abundances of other organisms, which can initiate trophic cascades (Creel and Christianson 2008; Heithaus et al. 2008). Thus, understanding how mesoconsumers respond to food-risk trade-off is important for predicting how they, and their communities, are likely to respond to anthropogenic impacts (Morris 2003; Heithaus et al. 2008). For example, recent work in Prince William Sound, Alaska, suggest that harbor seals (*Phoca vitulina*) trade-off food for safety from Pacific sleeper sharks (*Somniosus pacificus*), by primarily foraging on herring (*Clupea pallasi*) in shallower, safer, waters, instead of mainly foraging in deeper, more profitable, waters on walleye pollock (*Theragra chalcogramma*)

(Frid et al. 2007). Shark removal by bycatch fisheries are predicted to cause seals to shift to deeper waters, thereby indirectly increasing consumption on walleye pollock and decreasing predation on herring (Frid et al. 2008).

The influence of food availability and predation risk on forager habitat use has received considerable theoretical and empirical attention. The ideal free distribution (IFD; Fretwell and Lucas 1970) is the basis of many habitat selection models and can be used as a null model for assessing factors influencing habitat use during foraging, including predation risk (e.g. van Baalen and Sablelis 1993; Heithaus et al. 2007b; Wirsing et al. 2008). The basic IFD model predicts that foragers will be distributed across habitat patches in proportion to their food supply and, therefore, the densities of foragers relative to their food availability (i.e., the ratio of relative foragers to their food densities) should be equal across habitats (Heithaus et al. 2007b; Wirsing et al. 2007b). If predation risk varies across habitats, however, most foragers will forego foraging opportunities to enhance their safety (see Lima and Dill 1990; Lima 1998; Brown and Kotler 2004 for reviews). This should lead to relative densities of foragers in safer habitats being greater than they would be in the absence of predation risk (e.g., dolphins, *Tursiops aduncus*, Heithaus and Dill 2002; perch, *Perca fluviatilis*, Bystrom et al. 2003; elk, *Cervus elaphus*, Ripple and Beschta 2007; harbor seals, *Phoca vitlina*, Frid et al. 2007). Numerous currencies have been proposed for optimizing the trade-off between predation risk and food availability (see Fraser and Gilliam 1987; Brown 1992; Brown and Kotler, 2004). In many situations, foragers - especially juveniles - may select the habitat that minimizes the ratio of predation risk (μ) to foraging rate (f) (i.e., minimize μ/f) (Gilliam and Fraser 1987; similar to pF in Brown 1992). Working in tidal creeks in the Bahamas, Dahlgren and Eggleston (2000) found that juvenile Nassau Grouper (*Epinephelus striatus*) shifted habitat use in a way that minimized μ/f; small juvenile grouper foraged in safer algal clumps, although food availability was higher in adjacent riskier habitats. However, because energy intake in habitats is usually density dependent, the quality of a given habitat will decline as more foragers accumulate in it, thereby increasing μ/f. Therefore, foraging animals are unlikely to all select the same habitat and individuals will begin selecting higher-risk habitats when foraging rewards offset the cost of increased predation risk (Brown and Kotler 2004). Furthermore, some individuals will select high-risk, but high-reward, habitats even if the value of μ/f is relatively high. For example, individuals in poor body condition often accept higher risk in order to forage in high quality habitats (McNamara and Houston 1987; Sinclair and Arcese 1995; Lima 1998; Heithaus et al. 2007a) and some age-sex classes that can benefit from increased body condition will take greater risks in order to realize fitness gains (e.g. Cresswell 1994; Brown and Kotler 2004).

The combined effects of food availability and predation risk on fish foraging behavior has been investigated via both laboratory (e.g. Abrahams and Dill 1989; Grand and Dill 1997) and field experiments (Werner et al. 1983), primarily in temperate, freshwater systems and during daylight hours. In contrast, relatively little attention has been directed towards fish foraging decisions in subtropical marine systems, especially at night when many species emerge from refuges to feed. Moreover, most studies investigating habitat use have typically examined foraging behavior in discrete habitat patches, for example, structurally complex “safe” habitats versus open ‘risky’ habitats (Lima and Dill 1990; Lima 1998). Few studies have examined the influences of food and risk along a habitat gradient that varies in relative safety and food availability (Thorson et al. 1998; Laundre et al. 2001; Hernandez and Laundre 2005; Van Der Merwe and Brown 2008). In addition, relatively few studies have simultaneously investigated the spatial responses of multiple prey species to the same predators, even though most systems contain a variety of species that may respond differently to the same predators (e.g. Vesakoski et al. 2008; Valeix et al. 2009; Heithaus et al. 2009).

Subtropical Biscayne Bay, Florida (USA) provides an opportunity to investigate the combined effects of food availability and predation risk on the nocturnal distributions of multiple fish species across their foraging landscape from the mangrove-seagrass ecotone. During daylight hours, a diverse group of juvenile fishes utilize the Bay's mangrove-fringed shorelines as shelter from predators (Serafy et al. 2003; Serafy et al. 2007). However at night, many fishes leave the safety of mangrove prop roots and cross over the mangrove-seagrass ecotone to forage in adjacent seagrass beds (Rooker and Dennis 1991; Nagelkerken et al. 2000). In the present study, I specifically investigate whether the distance at which three sympatric juvenile fishes - gray snapper (*Lutjanus griseus),* bluestriped grunt (*Haemulon sciurus*) and seabream (*Archosargus rhomboidalis*) – forage from mangrove edge across adjacent seagrass feeding habitat at night matches theoretical expectations based on food-only or food-safety currencies.

Materials and Methods

Study system and species

This study was conducted along the leeward side of Elliott Key, between latitudes N 25.43 and N 25.40 at the eastern boundary of southern Biscayne Bay, Florida (USA).

Sampling activities were focused along three 120 m-long transects that extended perpendicularly from shore (Fig. 5.1). Research was conducted from July-October in 2007 and 2008, corresponding with South Florida's wet season. Water temperature at the site ranges between 32.2-34.9 ºC. Across transects, seagrass and macroalgae bottom cover is high (range: 89-97 %) and depths are consistently shallow (range: 55.0-120.0 cm) out to 120 m from shore (Chapter 2, 3). Seine net sampling indicated that the composition and structure of fish communities was very similar among transects (Chapter 2).

I selected juvenile gray snapper, bluestriped grunt and seabream because (1) these species are among the most abundant and easily-identified at my site; (2) each is representative of a different trophic guild (seabream - herbivore, bluestriped grunt - crustacean zoobenthivore, gray snapper – generalist zoobenthivore); and (3) two have economic importance in the region's recreational fishery and dive tourism industry (gray snapper and bluestriped grunt).

I focused on late-stage juvenile fish ranging in size from 10-25 cm total length (TL) because this corresponds with the size class of fishes, such as snappers (*Lutjanidae*) and grunts (*Haemulidae*), known to make nocturnal foraging migrations between mangrove refuges and adjacent seagrass feeding habitats (e.g. Rooker and Dennis 1991; Nagelkerken et al. 2000; Chapter 2).

To examine the effects of food availability and predation risk on fish habitat use at my site, I first quantified patterns of fish distribution, food abundance and predation risk along the 120-m distance gradient. I then used these data to test *a priori* predictions of fish distributions relative to food and risk that were generated from foraging theory:

(1) fishes will be distributed across the distance gradient in proportion to their food supply (i.e., ideal free distribution); or (2) fishes will avoid high-risk habitats such that fish abundances will be lower than predicted by food resources in high-risk areas (i.e., food-risk trade-offs).

Fish distribution and food supply

Previous studies of late-stage juvenile fishes in my study site during the wet season revealed that gray snapper fed primarily on small fishes (hardhead silversides, *Atherinomorus stipes*; mojarras, *Eucinostomus spp*. and rainwater killifish, *Lucania parva*) and crustaceans (pink shrimp, *Penaeus duorarum,* and caridean shrimp) (Chapter 3). Bluestriped grunts fed almost exclusively on caridean shrimp, while seabream fed almost exclusively on seagrass (mostly *Thalassia testudinum*) and algae (Chapter 3).

I used center-bag seine nets (21.3 m long, 1.8 m high, 3 mm mesh) to assess distribution and abundance of both focal fish species and their potential invertebrate and fish prey along the distance gradient. Sampling occurred every 20 m along the three, 120 m-long transects. Seine nets were hauled parallel to shore, against the current (or wind, if stronger) and pursed such that a standardized area of 142 m^2 was sampled with each haul. At least two seine samples were collected simultaneously and the sequence at which each distance was sampled was chosen randomly. Sampling was conducted in complete darkness, at least 0.5 hrs after sunset and within 2.5 hrs of low tide. Each transect was visited on different days to enable the collection of three to four seine samples for each transect-distance combination (i.e., 9-12 samples per 20-m distance). Focal fishes and their food items were collected, counted and measured to the nearest mm total length (TL). Because seagrass and algae are the primary food sources of seabream at my site, I also quantified vegetation cover every 20 m along the three 120-m transects by estimating the percent cover of seagrass and algae within 50 cm x 50 cm quadrats (10 quadrats per distance-transect combination). This sampling method was chosen to be consistent with existing aquatic vegetation monitoring programs in the region (Fourqurean et al. 2001; Browder et al. 2009).

Predation risk

Nocturnal patterns in predator encounter rates at my site were assessed with tethering experiments (Chapter 4). Briefly, late-stage juvenile pinfish (*Lagodon rhomboides*) between 10-20 cm total length were tethered at 10 m, 50 m and 110 m from shore. All tethers were retrieved after 60 minutes, with an absence of the pinfish (or presence of a severed fish or predator on the line) scored as a predation event. To correspond with seine net sampling, all tethering experiments were conducted in darkness from 0.5-2.0 h after sunset and within 2.5 hrs of low tide.

Data analyses

Mean densities of gray snapper, bluestriped grunt and seabream were determined for each transect-distance combination using a delta-distribution mean estimator (Fletcher et al. 2005): a measure of fish density (hereafter just density) that separately considers the proportion of samples positive for a given fish species (i.e., frequency of occurrence) and its mean density when present (i.e., concentration). This approach was previously used to examine mangrove fish density patterns in Biscayne Bay (Faunce and Serafy 2007; Serafy et al. 2007; Faunce and Serafy 2008a,b). To reveal overall relative fish density-proximity patterns, I calculated relative fish densities at each distance from shore (*sensu* Heithaus et al. 2009) by dividing the mean fish density at each distance by the sum of mean fish densities across the 120-m distance gradient. Relative fish densities were calculated separately for all transects. Relations between relative fish density and distance were evaluated using regression analysis, applying linear and quadratic models.

Food available to foraging fishes was determined by using all food types frequently consumed by the focal fishes (i.e., prey items occurring in > 5 % of fishes collected; Chapter 3). Mean densities of prey fishes and invertebrates at each transect-distance combination were used to calculate food availability since their size composition did not vary significantly across the distance gradient (Table 5.1B). Food densities per sample were used to calculate mean densities of food resources for each transect-distance combination. To reveal overall relative food supply-proximity patterns, I calculated relative food densities at each distance from shore (*sensu* Heithaus et al. 2009) in the same manner as for relative fish density (i.e., mean food density per distance divided by the sum of mean food densities across the distance gradient). Because seabream consumed seagrass and macroalage, I also calculated relative vegetation cover in the same manner for each transect, by dividing mean vegetation cover at each distance from shore by the sum of mean vegetation cover across the 120-m distance gradient. Relationships between relative food densities and distance were evaluated via regression analysis, applying linear and quadratic models.

To test theoretical predictions of the links between food availability, predation risk, and forager abundance, I calculated the ratio of relative foragers to their food availability (referred hereafter as “relative foraging densities;” e.g., Heithaus et al. 2007b; Wirsing et al. 2007b) by dividing the relative abundance of foragers by the relative food abundance at each distance from shore. A ratio value of 1.0 across all distances indicates that fish habitat use is proportional to food abundance (an ideal free distribution); values below 1.0 indicate under-matching of resources (i.e., fewer foragers than predicted by food abundance and presumably higher intake rates per forager), while values above 1.0 indicate over-matching food resources (i.e., more foragers than predicted by food abundance and presumably lower intake rates). If foragers were distributed according to an IFD, I would expect all distances from mangroves to have relative forager densities of 1.0, but to deviate from this pattern if other factors (e.g., predation risk) were influencing nocturnal fish distributions. In cases where fish did not match an IFD, I investigated whether predation risk might be responsible for deviations from predictions by comparing tether predation losses at each distance from shore using data presented in Chapter 4. Relationships between predation rates and distance from shore were calculated using logistic regression.

To gain more insight as to whether fishes were distributed such that they were optimizing energy intake and safety, I calculated a proxy for μ/f at each distance from shore and compared these values with observed fish distributions. To calculate my estimates of μ/f, I divided the rate of predation loss in tethering experiments by relative food supply (*sensu* Dahlgren and Eggleston 2000). While this measure does not take into account density-dependent declines in food intake at a particular distance, it provides insight into the relative risks and gains available to fishes at each distance. I predicted that if fish were responsive to predation risk and shifted habitats in a way that minimizes the ratio of mortality risk to foraging rate, relative forager densities would be lowest (i.e., under 1.0) at distances with the highest value of my estimate of μ/f and vice versa. All statistical analyses were performed using SAS (1990) software.

Results

Sixty-two seine samples yielded 295 specimens of juvenile gray snapper, bluestriped grunt and seabream, ranging in size from 10.0 to 25.0 cm TL for gray snapper and bluestriped grunt and 10.0 to 20.0 cm TL for seabream. Gray snapper and seabream relative density significantly increased with increasing distance from shore (R^2=0.34, $P<0.01$, Fig. 5.2A; R^2=0.57, $P<0.0002$; Fig. 5.2E, respectively). In contrast, bluestriped grunt showed no significant change in density along the distance gradient (Fig. 5.2C).

Seining also yielded 5,609 potential food items of gray snapper and bluestriped grunt. For bluestriped grunt this included caridean shrimp (their primary prey); while, for gray snapper this included mojarra, rainwater killifish, hardhead silverside, pink shrimp and caridean shrimp (Table 5.1). Relative food density for both gray snapper and bluestriped grunt followed a parabolic distribution pattern along the distance gradient (R^2=0.47, $P<0.002$, Fig. 5.2B; R^2=0.55, $P<0.0009$; Fig. 5.2D, respectively; Table 5.1A) with lowest values at intermediate distances. A total of 178 quadrats provided estimates of vegetation cover (seabream food) along the distance gradient. Seabream food supply significantly decreased with increasing distance from shore (R^2=0.48, $P<0.002$, Fig. 5.2F; Table 5.1A). Similarly, vegetation height also decreased with distance from shore (Table 5.1B).

Logistic regression based on data from 108 tethering experiments revealed that predation loss significantly decreased with increasing distance from shore ($P<0.005$; Fig. 5.3) from 70 % nearest the mangroves (10 m) to 35 % at the furthest distances from shore (110 m).

Gray snapper habitat use relative to their food supply (i.e., Relative foraging densities) followed a parabolic distribution pattern (R^2=0.5, P<0.003, Fig. 5.4A), under-matching food supply near shore (0-40 m), over-matching food abundance at distances of 40-80 m from shore and matching food abundance at distances furthest from shore (80-120 m). Bluestriped grunt habitat use relative to their food abundance also followed a parabolic distribution pattern (R^2=0.43, P<0.005, Fig. 5.4C), approximately matching food abundance near shore (0-40 m), over-matching their food abundance between 40-80 m from shore, and slightly under-matching food supply furthest from shore (80-120 m). Seabream abundance relative to their food supply significantly increased with increasing distance from shore (R^2=0.66, P<0.001, Fig. 5.4E), under-matching their food supply near shore (0-40 m), and over-matching food supply at further distances (60-120 m).

For gray snapper and seabream, μ/f significantly decreased with increasing distance from shore (R^2=0.24, P<0.03, Fig. 5.4B; R^2=0.9, P<0.0001, Fig. 5.4F, respectively). For bluestriped grunt, μ/f followed a parabolic pattern with distance (R^2=0.45, P<0.02, Fig. 5.4D), with lowest values furthest from shore (80-120 m).

Discussion

A variety of factors influence animal distributions including food availability, predation risk and competition. All else being equal, foraging theory predicts that the distribution of foragers will match that of their food supply in the absence of predation risk; however, if risk varies across habitats, foragers will trade off food for safety from predators (Lima and Dill 1990; Lima 1998; Brown and Kotler 2004). Here, I investigated whether the nocturnal habitat use decisions of three sympatric juvenile fishes - gray snapper, bluestriped grunt and seabream - matched this theoretical expectation across a 120-m continuous distance gradient, extending from the mangroves (refuge) across adjacent seagrass (feeding) habitat, in subtropical Biscayne Bay, Florida.

If focal fishes were distributed across the distance gradient in proportion to their food (i.e., an ideal free distribution), relative forager densities, (i.e., the ratio of relative foragers to their food availability) at all distances from mangroves should have approximated 1.0. Instead, I found that distributions of all the focal fishes along the distance gradient were not proportional to that of their food. In fact, relative foraging densities of both seabream and gray snapper were lowest nearest the mangroves. It is worth considering that my measure of relative forager densities overestimates the abundance of fishes foraging nearshore since I would have captured both foragers and individuals departing to, and returning from, foraging further offshore. Thus, in a true IFD, I would expect relative forager densities to be slightly above 1.0 nearshore. Thus, all three species I sampled appear to concentrate their foraging at distances that do not maximize energy intake rates.

Seabream distributions were consistent with my μ/f predictions. They undermatched food resources nearshore and exhibited the highest densities in the safest habitats furthest from the mangroves. This pattern suggests that seabream travel far from shore in order to forage at a reduced risk of predation. Gray snapper avoided foraging in high-risk, but productive areas near mangroves. Consistent with my theoretical predictions, relative forager densities were lowest nearshore where μ/f was highest. However, further from shore, relative foraging densities did not show a strong match to my predictions (i.e., relative forager densities were not consistently highest where μ/f

values were lowest). The deviation from my predictions furthest from shore may be because my μ/f values do not take into account density-dependent declines in food intake, which are likely in my system. Offshore food resources may begin to become depleted or interference competition likely increases (Sutherland et al. 1988; Sutherland and Parker 1999), as more gray snapper forage there.

In contrast to gray snapper and seabream, bluestriped grunt did not appear to avoid foraging nearest the mangroves – although relative abundances were below that predicted by food abundance. Moreover, bluestriped grunt deviations from IFD along the distance gradient where not consistent with my μ/f predictions. Farthest from shore (where risk was lowest), bluestriped grunt slightly under-matched their food supply. The reasons for this pattern are unclear. Perhaps schooling by grunts (Hobson 1965) or other anti-predator tactics or adaptations (e.g., crypsis, vigilance) allow them to compensate for higher predator encounter rates nearshore.

Deviations from my predictions may arise because the measure of μ/f used does not quantify actual predation pressure for each species. Here, I used predation on tethered pinfish to assess predation pressure for all three focal species, which may be a source of error since spatial variability in predation pressure on pinfish may differ from that of other species. However, I believe removal rates on pinfish in this study likely reflect actual encounter rates with predators for all three focal species since pinfish, seabream, gray snapper and bluestriped grunt occupy the same habitat, have similar body forms and are characterized by similar length-frequency distributions within the study site. Moreover, all three species appear to at-least slightly under-match their food resources nearest the mangroves, where both tether removal rates and gillnet catch rates of predators are highest (Chapter 4). Divergence from my predictions may also arise since my measure of μ/f also does not quantify foraging rates for each species at a particular distance and instead uses food abundance as a proxy. It is possible that foraging rates of seabream (a herbivore) are correlated with its sessile and abundant food supply (vegetation), while those of gray snapper or bluestriped grunts at any particular distance are not correlated with abundances of their highly motile prey due to a variety of possible factors, including prey anti-predatory behaviors, interference competition, or differential prey selectivity by the fishes for particular food types.

Crossing ecotones between refuges and feeding patches should be risky for mesoconsumers because the concentration of individuals in refuges and predictability of their movements attract predators. For example, off the coast of South Africa, hunting white sharks (*Carcharodon carcharias*) patrol fur seal (*Arctocephalus pusillus pusillus*) refuge entry and exit points in attempts to ambush seals as they leave for and return from foraging (Martin et al. 2005; Hammerschlag et al. 2006; Martin et al. 2009). My results suggest that the mangrove-seagrass interface and its surroundings may similarly act as a gauntlet to fishes migrating to forage. Indeed, nearshore predators appear to focus search efforts near the mangrove shoreline (e.g. lemon sharks, *Negaprion brevirostris*; Morrissey and Gruber 1993; Franks 2007). Although the probability of fish escaping back into the mangroves during an encounter with a predator is relatively high at the mangrove fringe, at my closest sampling distance (10 m), this probability of escape may have declined such that it is similar to that across the rest of my distance gradient. Of course, escape to mangroves is dependent on fish being able to detect predators patrolling the mangroves, which may be hindered at night, when predators often have a visual advantage (Munz and McFarland 1973). Thus, I suggest that as fish begin to migrate away from shore to feed in adjacent seagrass beds, they are likely at high risk from predators patrolling the mangrove fringe with decreasing risk at further distances. Indeed, acoustic tracking of gray snapper (Luo et al. 2009) has revealed that at sunset, gray snapper migrate rapidly out of the mangroves in a synchronized fashion and do not forage in seagrass nearest the mangroves. For both gray snapper and seabream, selecting offshore foraging locations represents a substantial energetic opportunity cost since their food supply is greatest nearest the mangroves.

The present study is the first to explicitly investigate the influences of food availability and predation risk on nocturnal fish habitat use patterns along a continuous mangrove-seagrass distance gradient. My results indicate that while some species (e.g., seabream) appear to trade-off food for safety and forage away from the mangrove-seagrass ecotone where food abundance is highest, the responses of other species are less clear. For example, late-juvenile bluestriped grunt (a crustacean zoobenthivore) did not match theoretical expectations, foraging randomly across the distance gradient despite habitat spatial variation in food supply and predation risk.

Individual forager responses to variation in predation risk and food availability are not necessarily straightforward. Species may manage risk at a variety of spatial scales and behavioral tactics by employing a variety of complementary behaviors such as allocation of time spent foraging in different habitat patches as well as the use of apprehension or vigilance (Brown 1999; Brown and Kotler 2004). For example, in Shark Bay, Australia, foraging dugongs (*Dugon dugon*) shift habitat use at multiple scales (Wirsing et al. 2007 b, c) and change foraging tactics (Wirsing et al. 2007 a) in order to balance the conflicting demands of food acquisition and gaining relative safety from predators. At broad spatial scales, fewer dugongs forage in dangerous shallow habitats when shark predators are most abundant. However, those that do forage in shallow waters during dangerous time periods shift to feed in safer edge microhabitats and generally avoid the risky interior portions of seagrass banks. In addition, when risk is highest, dugongs employ a foraging tactic ("cropping"), which affords higher vigilance even though an alternate tactic ("excavation") provides higher energy intake rates, but renders dugongs more susceptible to predation. In my study, I only examined spatial responses to predation risk. However, fishes may be using other types of avoidance behaviors like schooling, cryptic coloration and vigilance to optimize energy gain and safety from predators. Future studies should investigate a diversity of predator avoidance tactics simultaneously to further elucidate the role of predation risk in shaping distribution patterns of fishes along the seagrass-mangrove ecotone.

Table 5.1. (A) Mean abundance and (B) length of different fish food items across the distance gradient. In (A), vegetation values are mean percent cover, in (B), vegetation values are mean canopy height. TL = total length in cm. Shrimp length measurements are post-orbital length. All caridean shrimp measured were between 0.2-0.5 cm. At our study site, gray snapper feed on hardhead silversides, rainwater killifish, pink shrimp, and caridean shrimp. Bluestriped grunts feed almost exclusively on caridean shrimp, while seabream feed almost exclusively on seagrass (mostly *Thalassia testudium*) and algae (Chapter 3). All values are means ± 1 standard error.

(A) Density vs Distance

Distance (m)	Hardhead silversides Mean No.	Mojarras Mean No.	Rainwater killifish Mean No.	Pink shrimp Mean No.	Caridean shrimp Mean No.	Vegetation Cover Mean Cover (%)
10	93.5 ± 17.8	32.4 ± 9.6	30.3 ± 15.2	17.9 ± 6.9	173.7 ± 57.5	96.1 ± 1.3
30	116.4 ± 25.4	53.7 ± 13.7	11.64 ± 3.8	16.9 ± 3.5	112.9 ± 51.5	94.4 ± 1.7
50	83.5 ± 21.5	39.9 ± 9.3	13.5 ± 9.2	14.3 ± 4.7	69.8 ± 22.5	89.5 ± 3.1
70	67.3 ± 12.6	28.0 ± 4.8	11.5 ± 4.1	17.3 ± 4.8	83.6 ± 31.0	91.5 ± 1.8
90	80.4 ± 15.7	32.8 ± 7.5	12.4 ± 6.2	18.17 ± 9.0	143.2 ± 46.0	83.3 ± 3.9
110	94.4 ± 14.9	56.5 ± 21.7	20.2 ± 7.4	18.2 ± 4.3	278.3 ± 98.8	83.2 ± 2.8

(B) Length (cm) vs. Distance

Distance (m)	Hardhead silversides Mean TL	Mojarras Mean TL	Rainwater killifish Mean TL	Pink shrimp Mean TL	Caridean shrimp Mean TL	Vegetation Height Mean TL
10	4.6 ± 0.9	4.7 ± 1.7	2.1 ± 0.3	1.5 ± 0.6	< 0.6	32.5 ± 1.7
30	4.5 ± 0.9	4.8 ± 1.7	2.1 ± 0.4	1.6 ± 0.5	< 0.6	36.2 ± 2.3
50	4.4 ± 0.9	4.9 ± 1.7	2.1 ± 0.3	1.4 ± 0.5	< 0.6	27.4 ± 1.0
70	4.4 ± 0.9	4.5 ± 1.5	2.1 ± 0.3	1.7 ± 0.6	< 0.6	27.7 ± 1.6
90	4.2 ± 0.9	4.5 ± 1.7	2.1 ± 0.3	1.6 ± 0.6	< 0.6	25.0 ± 1.3
110	4.4 ± 0.9	4.3 ± 1.8	2.1 ± 0.3	1.4 ± 0.6	< 0.6	24.8 ± 1.3

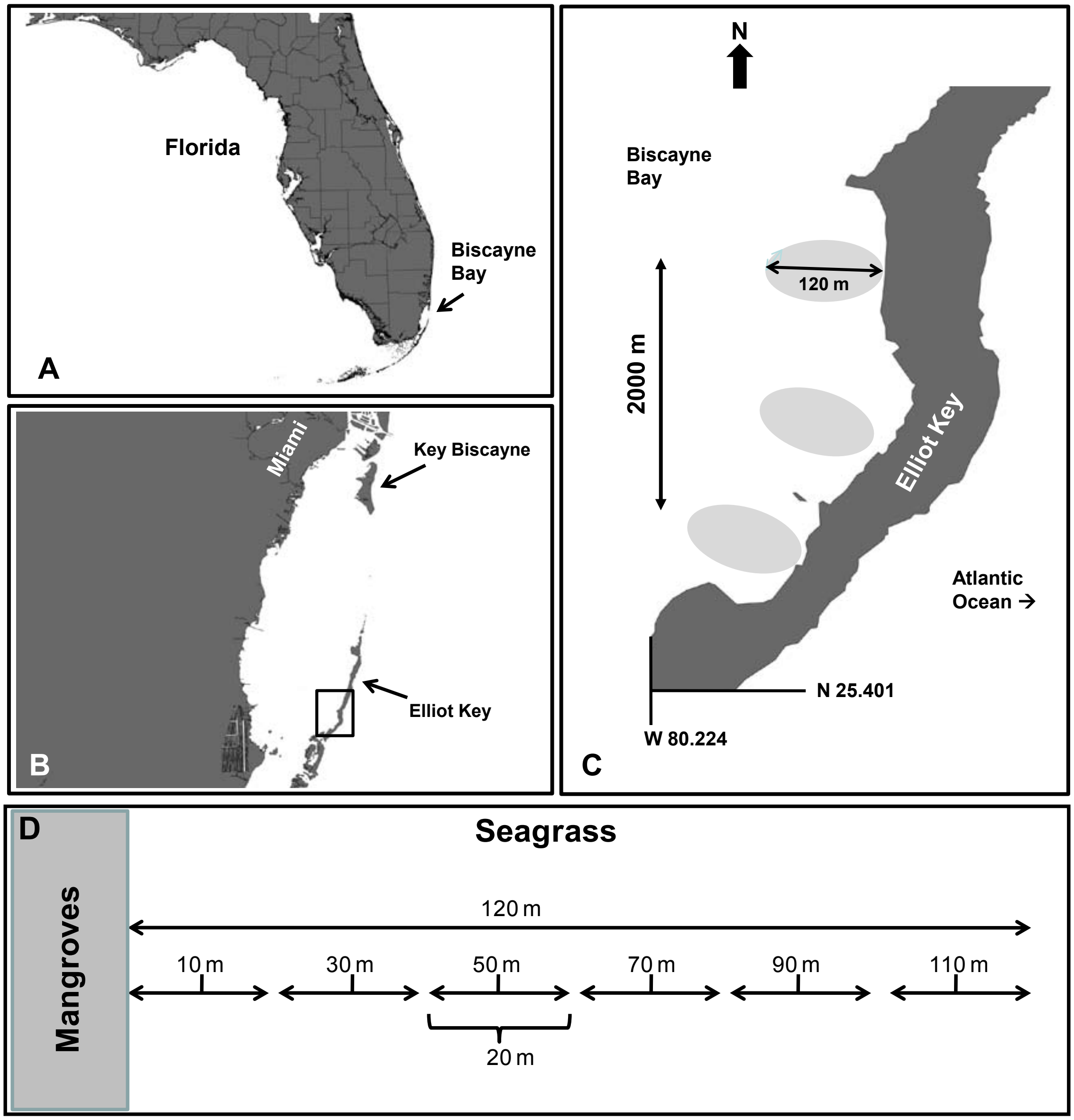


Figure 5.1. Study sites: (A) Map of Florida depicting location of Biscayne Bay; (B) position of study area (black square) on leeward side of Elliott Key within Biscayne Bay; (C) location of sampling transects within the study area; and (D) 120 m distance gradient with 20 m sampling intervals demarcated. The midpoints of the sampling intervals correspond with positions of beach seine bags.

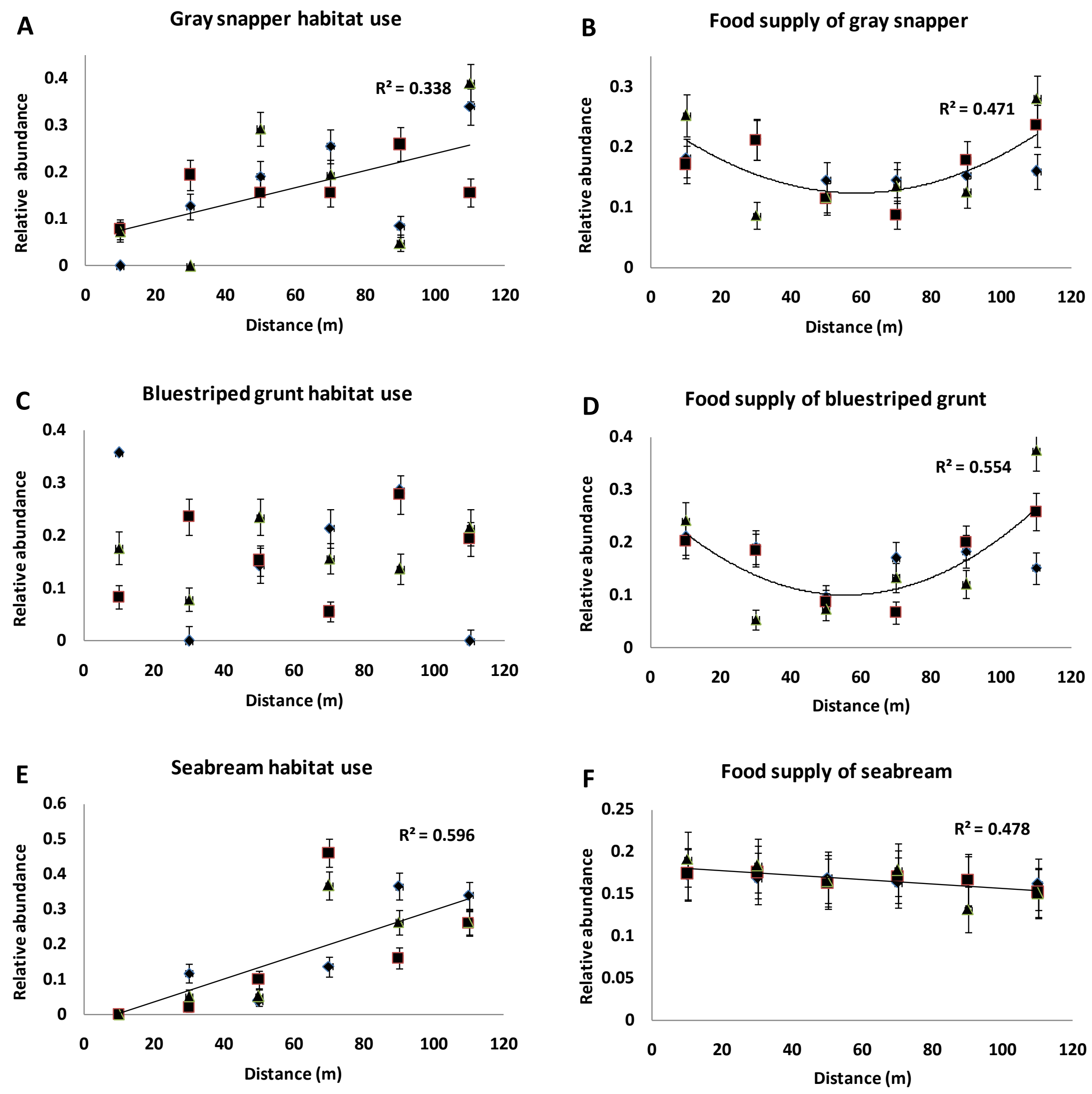


Figure 5.2. Relative density-distance patterns of juvenile gray snapper, bluestriped grunt, seabream (A, C, E) and their food supply (B, D, F). Values are transect-specific relative densities (± 1 standard error). Symbol shapes correspond with different transects. Solid lines and associated R^2 values indicate significant distance patterns ($P < 0.05$).

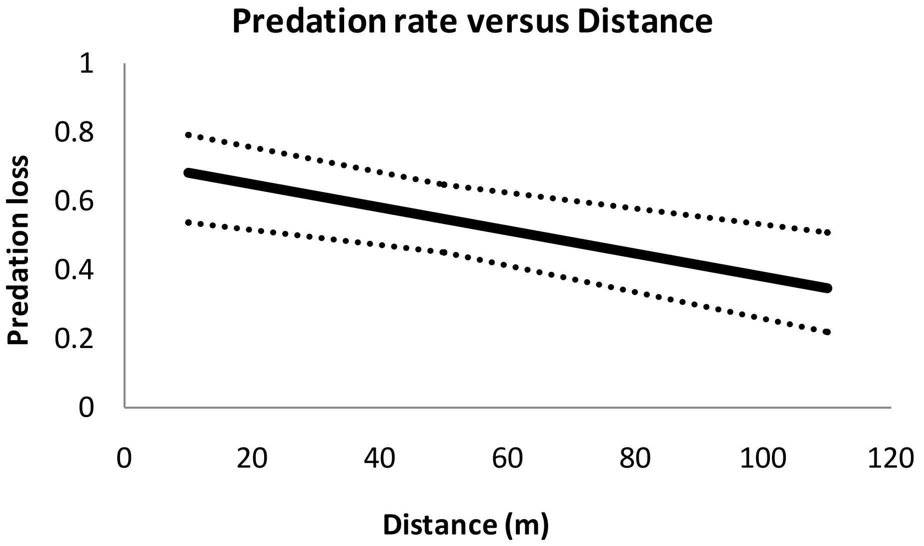


Figure 5.3. Significant fit of logistic regression relating predation losses of tethered pinfish against distance from shore. Dashed lines indicated upper and lower 95% confidence intervals.

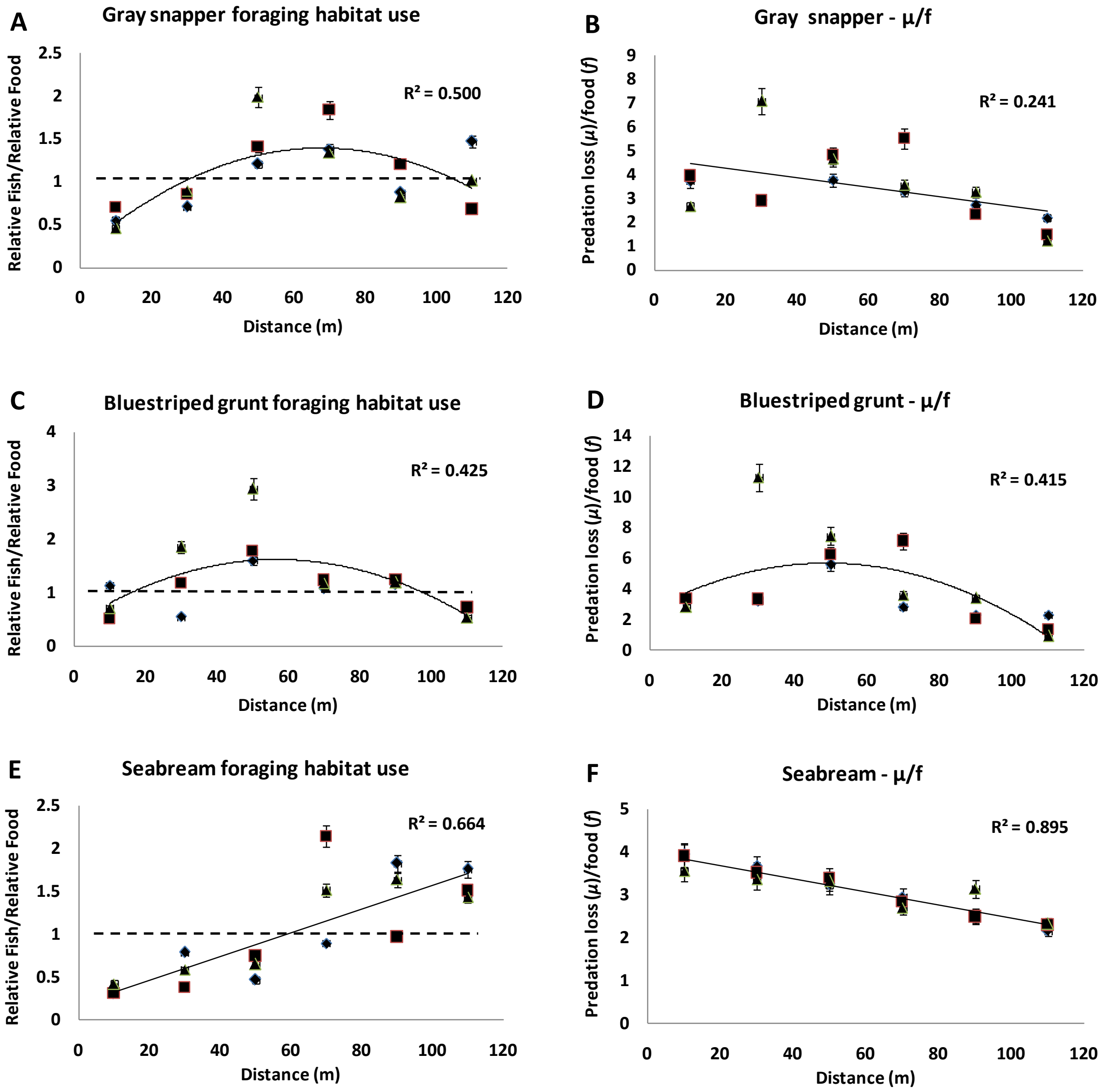


Figure 5.4. Examining the effects of food availability and predation risk on habitat use by gray snapper (A-B), bluestriped grunt (C-D) and seabream (E-F). Fish relative foraging densities along the 120-m distance gradient (A, C, E). A ratio value of 1.0 at all distances (dashed lines) indicates that fish habitat use is proportional to food abundance (an ideal free distribution). Values of predation risk (μ) divided by food supply (*f*) along the 120-m distance gradient (B, D, F). Solid lines and associated R^2 values indicate significant distance patterns ($P < 0.05$). Error bars represent 1 standard error.

Chapter 6. Overview, Conclusions and Future Research

Study overview

Animal distributions and densities are influenced by a variety of factors including physicochemical variability, food availability, predation risk and competition. All else being equal, foraging theory predicts that consumers will match their food supply under conditions of low predation risk; however, if risk varies across habitats, foragers will trade off food for safety from predators (Lima and Dill 1990; Lima 1998; Brown and Kotler 2004). Recent evidence suggest that the effects of predation risk on foraging behavior are context dependent (Schmitz 2007) and can be influenced by landscape features (e.g. distance from edge habitat) (Heithaus et al. 2009). However, studies examining risk-effects on fish habitat use have received little attention along subtropical shorelines, which serve as nursery habitats for a variety of economically important fishes. Sampling and observation of fishes in subtropical Biscayne Bay, Florida (USA) provide opportunities to investigate the response of multiple fish species to risk effects across their foraging landscape, spanning from the mangrove-seagrass ecotone into adjacent seagrass beds. To that end, this dissertation comprised an integrated set of quantitative studies which collectively tested *a priori* predictions (based on foraging theory) as to whether: (1) fishes were distributed across their foraging landscape in proportion to their food supply (i.e., ideal free distribution theory (IFD), Fretwell and Lucas, 1970); or (2) fishes avoided high-risk habitats such that relative abundances were lowest in habitats with relatively high-risk and *vice versa* (i.e., food risk tradeoffs, Gilliam and Fraser 1987). My results supported the notion of Heithaus et al. (2009) that landscape features can influence predator-prey interactions; specifically, I found that the mangrove-seagrass ecotone appeared to serve as a hunting corridor for predators that are presumably targeting the diel juvenile fish migration from mangroves to seagrass beds, and back again. Consequently, none of the focal fishes examined (gray snapper, *Lutjanus griseus*, bluestriped grunt, *Haemulon sciurus*, and seabream, *Archosargus rhomboidalis*) were distributed according to IFD. Seabream and gray snapper appeared to trade-off food for safety by avoiding foraging close to the mangrove-edge, where their food was most abundant, but risk was highest. In contrast, bluestriped grunt appeared to spatially forage randomly across the distance gradient. An overview of each chapter's objectives and major results is presented below:

Chapter 2: Nocturnal fish utilization of a subtropical mangrove-seagrass ecotone: stage-specific patterns of abundance in four species

- While diel fish migration between mangrove and seagrass habitats has been recognized since at least the 1960's, quantitative studies have focused mainly on *diurnal* patterns of fish distribution and abundance. The objective of this chapter was test the hypothesis that *nocturnal* fish abundances would decrease with increasing distance from shoreline. In general, previous work has revealed that fish abundances decline with increasing distance from mangroves; however, evidence for such a pattern at night, when most fishes are feeding, is scarce. To date, only three studies have reported nocturnal fish density patterns in seagrass beds at various distances from mangrove shoreline and their sampling design was not conducive for revealing the nature of nocturnal abundance-proximity relationships (e.g., linear or parabolic), if they existed.

- I conducted nocturnal fish sampling over two consecutive wet and dry seasons along a mangrove-lined shoreline in Biscayne Bay. The goal was to examine nocturnal habitat use patterns of early- and late-stage juvenile gray snapper, bluestriped grunt, seabream and great barracuda (*Sphyraena barracuda*). I used seine nets to sample at 20 m intervals along a 120 m- distance gradient extending from the mangrove edge across adjacent seagrass habitat.

- Results indicated that assemblage composition and structure differed significantly by season, likely influenced by temperature. However, within each season, the fish habitat use pattern at both the assemblage and species-specific level generally failed to support my working hypothesis of abundance decline with increasing distance from the ecotone. Data indicated that the nocturnal fish assemblage differed according to distance from shore, with the zone closest to the mangrove edge being the most distinct. Species-specific analyses revealed mostly uniform patterns of abundance with distance from shore for early juveniles. Except for the piscivorous great barracuda, the zone nearest the mangrove edge tended to harbor the lowest fish densities for late juveniles of all examined species.

Chapter 3: Seasonal diet and feeding habits of juvenile fishes foraging along a subtropical marine ecotone

- The objective of this study was to examine seasonal diet and feeding variation in late juvenile gray snapper, bluestriped grunt, seabream and great barracuda. The same seine collections were used to acquire the four focal fishes, their digestive tracts and to examine the relative abundance of their prey items. I specifically investigated for seasonal differences in feeding intensity, diet composition and trophic niche breadth.

- I found significantly lower feeding intensity during the dry season compared to the wet. Gray snapper fed on a variety of small fishes and crustaceans, while bluestriped grunt fed primarily on caridean shrimp. Seabream fed almost exclusively on vegetation and great barracuda was almost entirely piscivorous. Seasonal shifts in major food resource use generally did not correspond with changes in relative abundance of food supply. Seasonal trophic niche breadth differences were evident for gray snapper, great barracuda and bluestriped grunt, while niche breadth was equivalent between seasons for seabream. Based on seasonal food supply in the environment, niche breadth values did not match foraging theory predictions, which state niche breadth should expand as preferred food resources become scarce. Finally, based on the dietary information obtained in this effort, simplified, season-specific trophic web diagrams were generated.

Chapter 4: Relative predation risk for juvenile fishes along a subtropical mangrove-seagrass ecotone

- The objective of this study was to investigate diel patterns of predation pressure in seagrass beds as they relate to proximity to the mangrove-seagrass ecotone. I conducted a series of tethering studies to specifically test the hypotheses that predation pressure: (1) increases with increasing distance from shore; and (2) is lower at night than during the day.

- I found no support for the above hypotheses. Results indicated that predation rates were highest nearest the mangrove edge and decreased with increasing distance from shore. Additionally, fish mortality due to predation at night was nearly twice as high compared to the day. My results are consistent with previous studies in marine environments which have shown that ecotones are areas of high predation risk to fishes. In contrast, there is less conformity among studies that predation in nearshore habitats is higher at night than by day.

Chapter 5: The influence of food supply and predation risk on nocturnal fish distributions along a subtropical mangrove-seagrass ecotone

- The objective of this integrative chapter was to examine the combined effects of food supply and predation risk on nocturnal fish distribution patterns along their foraging landscape, spanning from the mangrove-seagrass ecotone to 120 m from shore. Data from chapters 2, 3 and 4 were used to specifically test hypotheses based on classical foraging models for late juveniles. These were: (1) fishes (late juveniles of seabream, gray snapper and bluestriped grunt) will be distributed across the distance gradient in proportion to their food supply (i.e., ideal free distribution, IFD, Fetwell and Lucas 1970); or (2) fishes will avoid high-risk habitats such that relative abundances are lowest in habitats with relatively high-risk and *vice versa* (Gilliam and Fraser 1987).

- Results indicated that late juvenile gray snapper, bluestriped grunt and seabream were not distributed along the distance gradient in proportion to the food supply (i.e., not an IFD). Seabream and gray snapper avoided foraging nearest the mangrove-edge, presumably exchanging food for safety; but, offshore, gray snapper abundance relative to their food supply was not highest where risk was lowest. In contrast, bluestriped grunt did not match theoretical expectations and appeared to forage randomly across the distance gradient despite variation in both food supply and risk.

Conclusions

The present study is the first to investigate the influences of food availability and predation risk on nocturnal fish habitat use patterns along a continuous mangrove-seagrass distance gradient. Based on the results presented above, the broad conclusions of this study are:

1) Season is an important factor influencing fish distribution patterns as well as feeding habits. Sampling, dietary analysis and trophic modeling needs to be seasonally resolved in this subtropical environment.
2) Nocturnal sampling revealed distribution patterns that were unexpected and unlike those found during the day. I suspect fewer patterns of fish decline with distance from the mangrove edge will emerge as more nocturnal, as opposed to diurnal, fish density data are collected. Reliance on strictly diurnal observations, especially with respect to shoreline fish feeding dynamics, may be misleading.
3) Upon analysis, significant species- and stage-specific variation in nocturnal fish distributions emerged. Even within the study area examined, generalizing abundance patterns for one species or life-stage to another would be erroneous.

4) Contrary to the findings of most diurnal studies, I found that the zone nearest the mangrove-seagrass ecotone was an area of relatively high risk to juvenile fishes. This suggests that the ecotone represents a hunting corridor for nearshore fish predators, especially at night.
5) Fish distributions patterns did not match their food supply (i.e., not an Ideal Free Distribution); while some species appeared to trade-off food for safety, not all focal fishes exhibited consistent matches to classic food-risk trade-off model predictions, despite spatial gradients in predation pressure and food supply.

Opportunities for study expansion and future research

Beyond the several questions that were specifically addressed in this dissertation, many more emerged over the course of this work. Below I present several additional questions that remain unresolved and that represent opportunities for study expansion as well as uncharted research territory for the future.

Field sampling expansion:

Given available resources, I would recommend that future studies examine fish density patterns beyond the 120 m rage investigated in this study. Recent acoustic tracking of gray snapper in Biscayne Bay has demonstrated that these fishes forage as much as 500 m from shore (Luo et al. 2009). Moreover, work from nearby areas has shown that juvenile lemon sharks (*Negaprion brevirostris*), an important predator of the focal fishes at my site, move as far as 1 km m offshore (Franks 2007). Thus, I would plan to sample to at least 500 m from shore. This would require a gear type that would not be limited by depth, such as a boat-deployable purse seine. In conjunction, I would suggest that future research continue to employ tethering experiments to measure gradients in predation pressure, since this is an easy and inexpensive means of assessing relative predation pressure by measuring predator encounter rates (McIvor and Odum 1988; Aaronson and Heck 1995; Baker and Sheaves 2007). I would also recommend expanded sampling along the eastern margin of Biscayne Bay as well as include the western shoreline. The western margin of Biscayne Bay is interspersed with creeks and freshwater canals making the nearshore salinity regime variable compared to the eastern margin of the Bay (Serafy et al. 1997, 2003). Thus, it is possible that fish and predator distance-distributions along the mainland shoreline may be influenced by salinity. Including sampling along the mainland would also complement existing fish (Serafy et al. 2007; Faunce and Serafy 2008b), invertebrate (Browder et al. 2009) and aquatic vegetation (Lirman et al. 2008) monitoring programs currently underway.

Throughout the present study, all sampling took place relatively early in the night, within a 2 hr period. Thus, it is possible that fish and predator distributions during this period may not be the same as much later in the night or just before dawn the next morning. Likewise, sampling over the course of the day may also reveal fine-scale temporal patterns of distribution that differ from those found here. Thus, in the future, I would recommend sampling throughout the day and night to investigate if and how fish distributions may change over the course of 24 hours. Such an effort would be highly resource intensive, but would likely begin to better reflect the feeding strategies and tactics of shoreline dwelling fishes. Similarly, in this study, I examined how predation risk in only one season (wet) influenced the spatial foraging behavior of three late-juvenile fish species (gray snapper, seabream, bluestriped grunt). Comparable future studies are also needed over the course of the year to examine if and how seasonal variation in predation risk influences fish foraging. Future studies might also consider examining more fish species and life-stages than examined in this research, although such expansion would need to be accompanied by substantially greater sampling and laboratory resources than were available here.

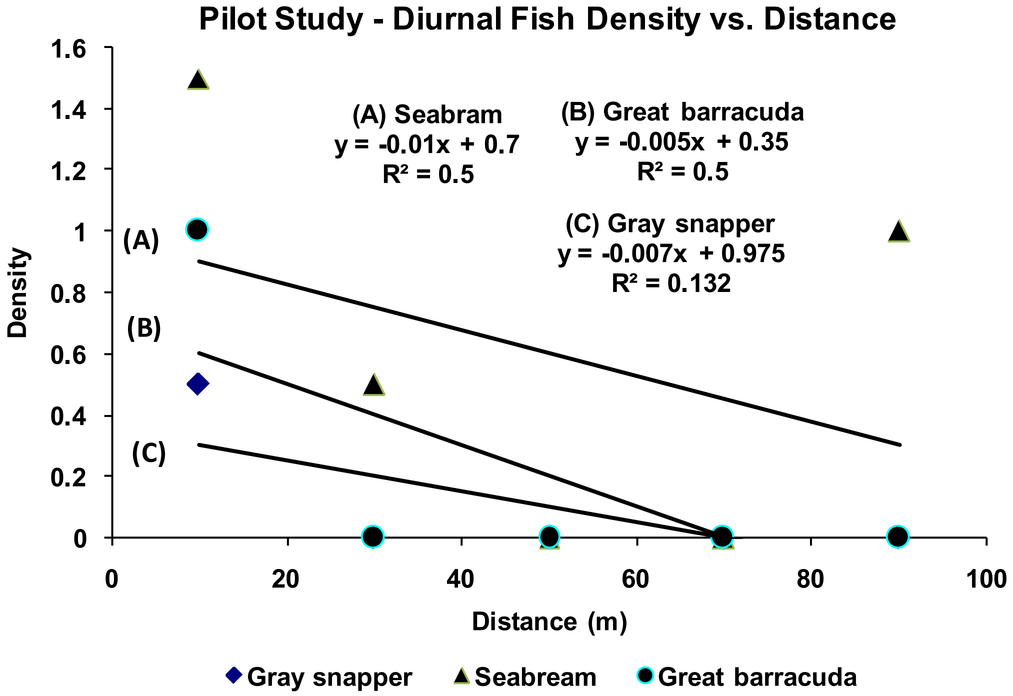
Other research avenues:

Predation risk is a product of two components: the probability that a prey organism encounters a predator and the probability of its death as a result of that encounter (Lima and Dill 1990; Hugie and Dill 1994). Probability of death given an encounter can be influenced by habitat characteristics (e.g., amount of physical structure), escape ability and their interaction (Hugie and Dill 1994). However, most studies just examine predator encounter rates in their overall assessment of predation pressure and do not consider landscape features and their interaction with prey escape abilities (Heithaus et al. 2009). In this study I found that predator encounter rates at my closest sampling distance to the mangroves (10 m) were the highest; but, it is possible that at the mangrove fringe, the probability of fish escape back into the prop-roots given an encounter with a predator may possibly be higher compared to just several meters away. Thus, overall risk to fishes may be quite low at the fringe despite high predator encounter rates near the mangroves. Future field and laboratory work is needed to evaluate fish detection and escape probability given encounters with predators at my site in order to fully quantify predation risk to juvenile fishes. This could be accomplished by setting up a mesocosm experiments in the laboratory where I could simulate the mangroves and seagrass beds and then construct simple communities (e.g. predator + fish consumer + food resource) and manipulate predator densities and compare fish escape responses at various distances from the mangrove fringe. With proper planning, this might be accomplished in the field, where an area is fenced off and numbers of predators, fishes and food resources are manipulated. However, use of a mesocosm may be more practical. In either case, an underwater video surveillance system with LED cameras (e.g., Luo et al. 2009) could be set up at various intervals from real or simulated prop-roots to monitor possible escape behaviors (i.e., darting into the prop roots or seagrass blades) at the mangrove edge compared different distances from shore. This could be done in conjunction with an automated fish detection system using stationary passive integrated transponder (PIT) technology (Zydlewski et al. 2001) such that a “gateway” of PIT sensors could quantify fine-scale habitat use and movements of PIT-tagged fishes and possibly their predators (Adams et al. 2006b). Such a combination of underwater video surveillance and PIT technology have been previously used to assess fish movements, including a lutjanid snapper, relative to mangroves in an estuarine salt marsh creek (Meynecke et al. 2008).

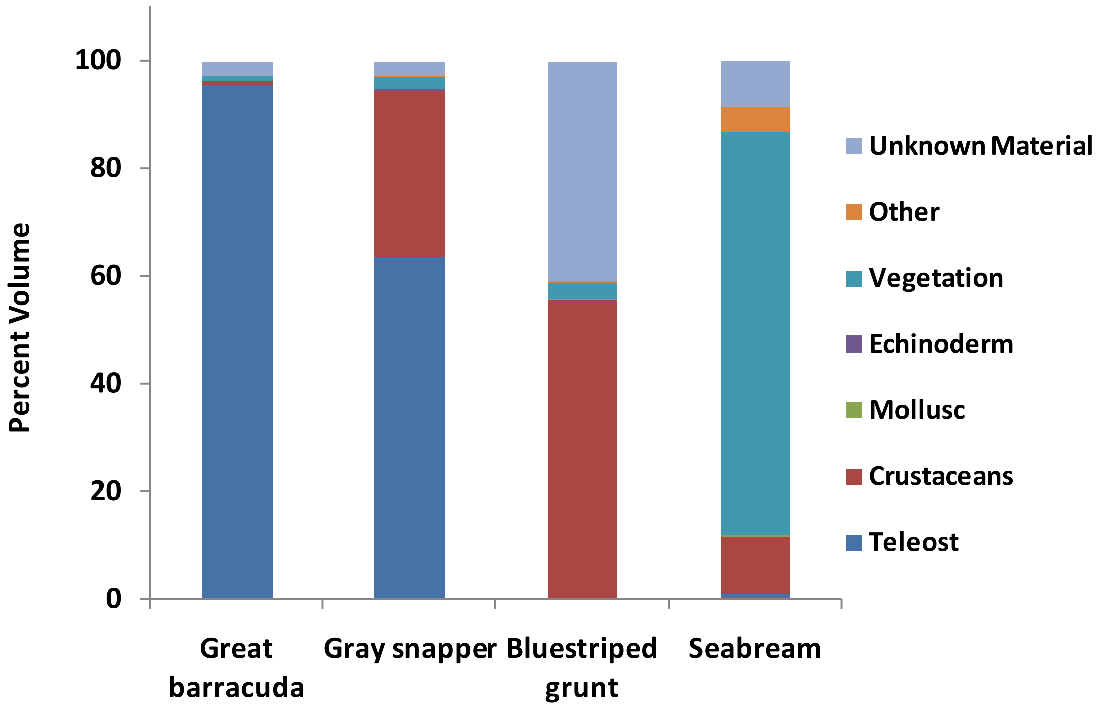
In the present study, I only examined *spatial* responses by the focal fishes to predation risk. However, fishes may be using other types of avoidance behaviors like schooling, cryptic coloration and vigilance to optimize energy gain and safety from predators (Brown and Kotler 2004). Future studies could investigate a diversity of predator avoidance tactics simultaneously to further elucidate the role of predation risk in shaping distribution patterns of fishes along the seagrass-mangrove ecotone. One method for doing so could involve tethering fish along the 120 m distance gradient as in this study; however, in addition, an observer and/or video array could visually monitor fish behaviors before, during, and after an encounter with a predator. Rypel et al. (2007) used a similar method to visually monitor predators approaching and attacking tethered mojarra (*Eucinostomus* spp.) in a Bahamian tidal creek. In addition, some recent technologies are available that could be used for examining fish anti-predatory behavior. For example, animal-borne video devices (known as "crittercams") are available that can provide continuous video recordings from the predator's viewpoint (Heithaus et al. 2001; Marshall et al. 2007). Until the systems are further miniaturized, "crittercams" for the sizes of fish that were the emphasis of my dissertation seem unlikely in the near future. However, if "crittercams" were attached to a predator species at my site (e.g. lemon shark), in an appropriate mesocosm, anti-predatory behaviors of fishes encountered by the predator could be examined in fine detail. For example, when a predator encounters a potential fish prey, one could potentially capture a range of anti-predator responses from charging the predator, changing color patterns, or retreating to the mangroves etc.

In summary, back-reef habitats such as mangroves and seagrass beds are nursery areas for a variety of fishes and invertebrates. There is a growing demand for predictive models in these nursery habitats for development of effective management strategies that maximize ecosystem production and diversity (e.g. Beck et al. 2001; Adams et al. 2006a; Dahlgreen et al. 2006). However, these models have largely overlooked the role of predation risk in structuring marine communities due to a lack of understanding of species interactions. The present study is the first to investigate the influences of food availability and predation risk on nocturnal fish habitat use patterns along a continuous mangrove-seagrass distance gradient. Results indicated that fish generally avoided the risky mangrove-seagrass ecotone, but responses to spatial variation in food and predation risk were species-specific and may be dependent on their specific anti-predator tactics or influenced by factors I did not measure. These results provide new insights that may be helpful for predicting how both predators and prey are likely to respond to anthropogenic ecosystem changes and for developing effective conservation and management strategies.

Appendix A. Results of diurnal seine sampling in Biscayne Bay, Florida (USA). Density-distance patterns of late-stage seabream, *Archosargus rhomboidalis* (A), great barracuda, *Sphyraena barracuda* (B) and gray snapper, *Lutjanus griseus* (C). Sampling revealed density declines with distance. See Chapter 2 for further details on sampling and analysis.



Appendix B. Percent composition by volume of different taxa in the diets of the four focal fishes from Biscayne Bay, Florida.



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VITA

Neil Hammerschlag was born in Johannesburg, South Africa on April 9, 1979, but grew up in Toronto, Canada. He received his Honors Bachelors of Science degree in Ecology at the University of Toronto in 2002. In 2004, Neil graduated with his Masters degree in Marine Biology from Nova Southeastern University. In fall 2004, he began his doctoral research in marine biology and fisheries at the University of Miami's Rosenstiel School of Marine and Atmospheric Science. Neil's current research interests focus on understanding how predator-prey interactions structure communities, particularly those involving sharks. Neil established and co-directs the University of Miami's South Florida Student Shark Program, a multi-disciplinary education and research program providing practical-hands-on marine field research experiences for high school and undergraduate students.

Permanent Address: 1500 Bay Road Apt 660, Miami Beach, Florida, 33139