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The Influence of Body Size on the Ecology of Coastal Fish Predators in The Bahamas

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FLORIDA INTERNATIONAL UNIVERSITY

Miami, Florida

THE INFLUENCE OF BODY SIZE ON THE ECOLOGY OF COASTAL FISH PREDATORS IN THE BAHAMAS

A dissertation submitted in partial fulfillment of the
requirements for the degree of
DOCTOR OF PHILOSOPHY
in
BIOLOGY
by
Caroline M. Hammerschlag-Peyer

2011

To: Dean Kenneth G. Furton
College of Arts and Sciences

This dissertation, written by Caroline M. Hammerschlag-Peyer, and entitled The Influence of Body Size on the Ecology of Coastal Fish Predators in The Bahamas, having been approved in respect to style and intellectual content, is referred to you for judgment.

We have read this dissertation and recommend that it be approved.

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ABSTRACT OF THE DISSERTATION

INFLUENCE OF BODY SIZE ON THE ECOLOGY OF COASTAL FISH PREDATORS IN THE BAHMAS

by

Caroline M. Hammerschlag-Peyer

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Miami, Florida

Professor Craig A. Layman, Major Professor

Body size is a fundamental structural characteristic of organisms, determining critical life history and physiological traits, and influencing population dynamics, community structure, and ecosystem function. For my dissertation, I focused on effects of body size on habitat use and diet of important coastal fish predators, as well as their influence on faunal communities in Bahamian wetlands. First, using acoustic telemetry and stable isotope analysis, I identified high variability in movement patterns and habitat use among individuals within a gray snapper (*Lutjanus griseus*) and schoolmaster snapper (*L. apodus*) population. This intrapopulation variation was not explained by body size, but by individual behavior in habitat use. Isotope values differed between individuals that moved further distances and individuals that stayed close to their home sites, suggesting movement differences were related to specific patterns of foraging behavior. Subsequently, while investigating diet of schoolmaster snapper over a two-year period using stomach content and stable isotope analyses, I also found intrapopulation diet variation, mostly explained by differences in size class, individual behavior and temporal variability. I then developed a hypothesis-testing framework examining intrapopulation niche variation between size classes using stable isotopes. This framework can serve as baseline to categorize taxonomic or functional groupings into specific niche shift scenarios, as well as to help elucidate underlying mechanisms causing niche shifts in certain size classes. Finally, I examined the effect of different-sized fish predators on epifaunal community structure in shallow seagrass beds using exclusion experiments at two spatial scales. Overall, I found that predator effects were rather weak, with predator size and spatial scale having no impact on the community. Yet, I also found some evidence of strong interactions on particular common snapper prey. As Bahamian wetlands are increasingly threatened by human activities (e.g., overexploitation, habitat degradation), an enhanced knowledge of the ecology of organisms inhabiting these systems is crucial for developing appropriate conservation and management strategies. My dissertation research contributed to this effort by providing critical information about the resource use of important Bahamian fish predators, as well as their effect on faunal seagrass communities.

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PREFACE

The following chapters have been published.

CHAPTER II

Hammerschlag-Peyer CM, Layman, CA (2010) Intrapopulation variation in habitat use by two abundant coastal fish species. Marine Ecology Progress Series 415: 211-220, doi: 10.3354/meps08714 www.int-res.com/abstracts/meps/v415/p211-220/

CHAPTER IV

Hammerschlag-Peyer CM, Yeager LA, Araújo MS, Layman, CA (2011) A hypothesis-testing framework for studies investigating ontogenetic niche shifts using stable isotope ratios. PLoS ONE 6(11): e27104, doi:10.1371/journal.pone.0027104 www.plosone.org/article/info%3Adoi%2F10.1371%2Fjournal.pone.0027104

CHAPTER I

INTRODUCTION

In his classic book, Elton (1927) proposed that body size has a fundamental effect on the organization of animal communities. His observation has been widely supported, with body size emerging as a primary structuring mechanism within and across many levels of biological organization (Peters 1983, Kerr & Dickie 2001, Brown et al. 2004, Yvon-Durocher et al. 2011). At the individual level, for instance, body size determines many key life history processes and physiological characteristics, such as growth rate, metabolic rate, consumption rate, predation risk, energetic requirements and resource utilization ability (Peters 1983, Werner & Gilliam 1984, Persson 1988, Brown et al. 2004). Likewise, body size also mediates the occurrence and consequences of the interactions among organisms (Brooks & Dodson 1965, Rudolf 2006), and thus affects population density (Blackburn et al. 1993, Dalerum & Angerbjorn 2005), species distributions (Brown et al. 1993, Greenwood et al. 1996), secondary production (Jennings et al. 2002), food web structure and dynamics (Cohen et al. 2003, Akin & Winemiller 2008), and structure and function of communities and ecosystems (Marquet et al. 1990, Hildrew et al. 2007).

Ecological studies that examine how body size affects resource use have focused on variation among species and the resulting implications (Blackburn et al. 1996, Robertson 1998, Cromsigt & Olff 2006, Bumrungsri et al. 2007, Langkilde & Shine 2007, Storms et al. 2008). Yet, effects of body size on resource use variation within species can also influence important aspects of population dynamics and community structure (Werner & Gilliam 1984). For instance, populations with large body size ranges are often characterized by strong ontogenetic shifts in resource use, leading to distinct functional size classes within a population that, for instance, can cause interactions with other species to shift between competition and predation (Wilbur 1988, Jennings et al. 2001, Woodward & Hildrew 2002, De Roos et al. 2003, Rudolf 2006).

As resource use can change during ontogeny, driving differences in resource use among ontogenetic stages (i.e., size or age classes), variation in resource use among individuals can also exist within a single ontogenetic stage (Bolnick et al. 2003, Araujo et al. 2011). Changing resource use within an ontogenetic stage has been called “individual specialization” and specifically is defined as the feeding behavior of an individual that causes its dietary niche to be significantly smaller than the population niche for reasons not attributable to its sex, body size, or age classes (Bolnick et al. 2003). Individual specialization has been identified in a number of diverse taxa (Ringler 1983, Magurran 1986, Schindler et al. 1997, Bolnick et al. 2003, Araujo et al. 2011), and can have important evolutionary, ecological and conservation implications (Bolnick et al. 2003).

The primary focus of my dissertation is to examine how resource use (i.e., diet and habitat use) can change during ontogeny within a predator population, as well as to investigate how resource variation among individuals may differ within size classes. In addition, my dissertation research examines the community level effects of predator body size variation, by exploring how different-sized predators can affect faunal community structure in seagrass beds. The central organizing principle of my dissertation research is the role of body size in driving ecological variation within shallow Bahamian coastal ecosystems, using abundant meso-predators as model organisms. The outline of my dissertation is as follows:

Chapter II examines whether movement patterns and habitat use of two abundant coastal predators (schoolmaster snapper, *Lutjanus apodus*, and gray snapper, *L. griseus*) change with body size, and if there is evidence of specialization in habitat use among conspecifics in a Bahamian wetland system. To do so, I used acoustic telemetry and stable isotope analysis. With this chapter, I attempt to provide a framework for future research to examine the variation in habitat use within marine populations, as well as to recognize its ecological importance. This study has been published in Marine Ecology Progress Series.

Chapter III focuses on how diet varies within and between size classes of schoolmaster snapper (*L. apodus*) in a Bahamian wetland system, as well as examines whether sampling period (i.e., year and season) influences their feeding behavior. I employ stable isotope ratios, direct diet information and simulation modeling as suite of complementary tools to examine underlying resource use variation. The findings of this research may add evidence that marine populations do not use their resources homogeneously, contrary to what is often tacitly assumed.

In Chapter IV, I generate a hypothesis-testing framework to examine ontogenetic niche shifts using stable isotope analysis. The majority of research that has applied stable isotope ratios to examine ontogenetic niche shifts used qualitative methods, or quantitative approaches that analyzed isotope elements separately. Yet, multivariate analyses are useful in depicting the characteristics of dietary changes through ontogeny because they can offer an enhanced understanding of shifts in niche width, niche position and niche overlap, which are critical factors in examining changes in resource use. Specifically, in this study, I (1) generate specific criteria to identify three main ontogenetic niche shift scenarios, and (2) provide an empirical example for illustration purposes. This study can be a baseline for future studies on ontogenetic niche shifts and can also be applied to investigate variation in resource use among other groupings (e.g., sex, phenotype). This study has been published in PLoS ONE.

Chapter V focuses on how different-sized fish predators affect the species composition and structure of seagrass epifauna in a shallow Bahamian system. To do so, I perform a small- and medium-scale exclusion experiment, utilizing mesh sizes that exclude different-sized predator individuals. This study is one of the first to investigate predator effects in subtidal seagrass systems when predator access is restricted to relatively small time windows during the daily tidal cycle.

Overall, each chapter of this dissertation concentrates on a different aspect related to body size in coastal fish predators. My dissertation provides valuable information on intrapopulation variation in diet and habitat use driven by differences in body size and/or individual feeding behavior, as well as offers a better understanding of the effect of different-sized fish predators on their faunal communities in important seagrass systems. Generally, my findings suggest the importance of incorporating resource variation based on differences in body size and individual behavior into the study of coastal fish populations, since this kind of variation is typically overlooked in traditional conservation and management strategies.

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CHAPTER II

INTRAPOPULATION VARIATION IN HABITAT USE BY TWO ABUNDANT COASTAL FISH SPECIES

Abstract

Decline of marine fisheries has become one of the most severe global environmental crises. In typical fishery management efforts, fish populations are often treated as homogeneous units, thereby tacitly ignoring potential intrapopulation variation within taxonomic groupings. I used acoustic telemetry and stable isotope analysis to examine movement patterns of 20 gray snapper (*Lutjanus griseus*) and 20 schoolmaster snapper (*L. apodus*) in a Bahamian tidal creek and wetland. In particular, I examined 1) if intrapopulation variation existed in fish habitat use and movement patterns, 2) whether that variation was a function of body size, and 3) if there was evidence of specialization in habitat use among individuals. I found that movement varied substantially among individuals, but was independent of body size. Some individuals exhibited frequent, repeated, movements to certain areas of the study site. The $\delta^{13}C$ values of individual snapper were significantly related to movement metrics, suggesting that movement differences were related to specific patterns of foraging behavior. My findings suggest the importance of incorporating intrapopulation niche variation into the study of coastal fish populations, a source of variation that is often overlooked in traditional conservation and management strategies.

Introduction

Overexploitation of marine fishes is considered one of the most critical global environmental crises (Jackson et al. 2001, Worm et al. 2006). Stocks of economically and ecologically important species have been drastically reduced through commercial and recreational fisheries (Coleman et al. 2004, Lotze & Worm 2009). Although large pelagic predators are especially susceptible to declines (Pauly et al. 1998, Heithaus et al. 2008), populations of coastal mesopredators such as groupers (Serranidae) and snappers (Lutjanidae) are also threatened by overexploitation (Willis et al. 2001, Nieland et al. 2007, Graham et al. 2008). For example, populations of Nassau Grouper, *Epinephelus striatus*, have declined by up to 60% over the last three decades and the species has been added to the IUCN Red List (Baillie & Groombridge 1996, Sadovy 1997).

To provide a template for developing conservation and management strategies, scientists usually seek to identify broad generalities that define the "typical" individual of a particular population. Individuals are assumed to possess generally the same behavioral or feeding traits during certain life stages or size classes, and thus a population is treated as a homogeneous unit from a management perspective. One well-known example are juvenile grunts (Haemulidae) in Teague Bay, U.S. Virgin Islands, which rest over coral heads during the day and move to seagrass beds at night as a group (Meyer et al. 1983). Similarly, gray snapper, *Lutjanus griseus*, in Biscayne Bay, Florida have been observed to move in groups from mangroves during the day to seagrass beds at night (Luo et al. 2009). With respect to ontogeny, individuals of many reef fishes are assumed to go through predictable sequences of habitat utilization (Nagelkerken et al. 2000). For instance, larval French grunts, *Haemulon flavolineatum*, in Piscadera Bay, Curaçao settle in sand/rubble habitat at the mouth of bays, move further into the bay to utilize mangroves and seagrass beds as juveniles, and then shift to coral reefs as adults (Huijbers et al. 2008).

Despite the common perspective that individuals of a population are homogeneous units, substantial intrapopulation variation in behavior has been shown to occur across diverse taxonomic groups and may have important evolutionary, ecological and conservation implications (Van Valen 1965, Roughgarden 1972, 1974, Schindler et al. 1997, Bolnick et al. 2003). From a management perspective, focusing only on the core habitats for a population may ignore those individuals that utilize alternative habitats or food sources. Ignoring intrapopulation variation in habitat use can be especially problematic when variation among individuals is a function of body size or age, so that a demographically important subset of the population is not considered (Durell 2000, Bolnick et al. 2003). Recognizing intrapopulation variation in fishery management plans may facilitate preserving species' ecological, phenotypic and genetic diversity (Moritz 1994, Coates 2000, Smith et al. 2001, Bolnick et al. 2003).

The aim of this study was to examine potential variation in habitat use and movement patterns among individuals of two ecologically and economically important nearshore snapper populations. Specifically, I investigated 1) if variation in habitat use and movement patterns occurred among individuals of gray snapper (*Lutjanus griseus*) and/or schoolmaster snapper (*L. apodus*), 2) whether that variation was a function of body size (a well-acknowledged mechanism of intrapopulation variation) , and 3) if there was evidence of specialization in habitat use for either focal population. I used acoustic telemetry to directly explore the movements of fishes at an individual level, as well as stable isotope ratios to provide indirect information as to potential feeding patterns. I endeavored to provide a framework for future research that acknowledges variation in behavioral attributes and foraging within marine populations.

Materials and Methods

Study System and Species

Broad Creek (26°29’35”N, 77°02’34”W) is an estuarine tidal creek located on the east side of Abaco Island, The Bahamas (Fig. 1). Tidal creeks in The Bahamas range in size from several hectares with maximum low tide depths of 1 m, to thousands of hectares with maximum depths >10 m (Layman et al. 2007, Rypel et al. 2007, Valentine-Rose et al. 2007b); Broad Creek falls at the lower end of this range. The system has a semi-diurnal tidal regime and a mean daily tidal amplitude of ~0.8 m. There is little freshwater input to this system and thus it is marine-dominated throughout its extent (Valentine-Rose et al. 2007a).

Broad Creek consists of extensive, shallow, intertidal, flats. These flats primarily are composed of a silt substrate with interspersed mangroves (mainly *Rhizophora mangle*). The most prevalent benthic habitat types are seagrass beds (primarily *Thalassia testudinum*), submerged mangrove prop roots (mostly *R. mangle*), hard bottom with soft corals (mostly *Gorgonia* spp.) and sand. At low tide, water depths >~0.3 m are only found in two pools (~10 m in diameter) in the northwest corner of Broad Creek (Fig. 1). The tidal pools are depressions in the karst substrate that stay inundated even at the lowest tides, thereby providing habitat for fishes at all tidal phases (Rypel et al. 2007, Valentine-Rose et al. 2007b). The majority of the creek area (>99%) is <0.3 m at low tide, depths that are generally too shallow for adult and sub-adult snapper to traverse (Rypel et al. 2007).

Gray snapper, *Lutjanus griseus* (Linnaeus 1758), and schoolmaster snapper, *Lutjanus apodus* (Walbaum 1972), are abundant generalist fish predators that coexist in many nearshore ecosystems in the tropics and subtropics of the Atlantic (Starck & Schroeder 1971, Allen 1985). In Broad Creek, as is common in shallow creeks of The Bahamas, these fishes typically inhabit deeper pools or deep mangrove-lined shorelines, herein referred to as "home sites" (e.g., A and B in Fig. 1). Individual fish may leave these home sites with rising water during flood tides, likely to feed, and they typically return to the home sites as water levels fall with the ebbing tide (Rypel et al. 2007). These repeated daily movements to and from the home sites in Broad Creek provide a unique opportunity to quantitatively evaluate individual level variation in local scale movement patterns.

Tagging and Tracking

Twenty gray snapper and 20 schoolmaster snapper were caught in home site A and B at low tide between April 20-28 2009 using baited hooks and fish traps. Sizes were representative of those fishes found in these systems (Layman et al. 2007, Luo et al. 2009). Small acoustic transmitters (V7, Vemco Ltd., Nova Scotia, Canada; 19mm x 7mm, 1.6g in air, 77-day battery life), which pinged every 15-45 seconds, were surgically implanted into each fish. Each transmitter had a unique code to identify individual fish. Individual fish were anesthetized in a mixture of fresh sea water and clove oil (active ingredient: eugenol), a commonly used fish anesthetic (Sladky et al. 2001, Hiscock et al.

2002, Parsons et al. 2003, Cotter & Rodruck 2006), and measured for standard length (SL). The transmitter was inserted into the body cavity through a 10-mm incision made between the pelvic and anal fins following a procedure similar to Nowak and Quinn (2002). The incision was closed with two stitches using a C-curved needle with attached suture. A small sample of the dorsal fin tissue (~1 cm^2) was removed from each fish for stable isotope analysis (see below) before the fish was transferred to a cooler with fresh sea water for recovery. After ~1 hour the fish were released at the capture location. Fin clips were transported on ice to a field station, stored in a freezer and later processed at Florida International University.

To quantify presence/absence patterns at the two home sites, one stationary omnidirectional hydrophone (VR2, Vemco Ltd., Nova Scotia, Canada) was placed at each location. The receivers were secured to cinder blocks and placed on the substrate in the middle of both home sites at ~1.5 m low tide depth. Since both home sites were surrounded by dense mangroves, detection ranges did not extend beyond the edges of the pools (C. Hammerschlag-Peyer, *unpublished data*).

To estimate movement outside the home sites, tagged fish were located from an inflatable Zodiac boat using a hand-held receiver and hydrophone (VR100, Vemco Ltd., Nova Scotia, Canada). The hydrophone was situated in the water column about halfway between the substrate and water surface to avoid acoustic disturbances. Once a fish was detected, the coordinates of its position and time of detection was recorded by the manual receiver. Mobile tracking was conducted every day at high tide for an entire lunar cycle, from April 26 to May 24 2009. Because most parts of the creek are largely intertidal (and thus very shallow at low tide with no fish movement) manual tracking was conducted two hours before until two hours after high tide. Tracking paths were chosen haphazardly each session.

Data Analysis

The continuous data from stationary receivers was categorized into “time in” and “time out” of the home site for each individual fish. If an individual was not detected by a stationary receiver for more than 60 min, the fish was considered to have left the tidal pool. For each fish, the home site, date, time in and time out were identified. Tracking with the manual receiver was used to identify the location of fish outside the home sites during each daily high tide. If more than one location fix (outside of the home sites) was obtained for an individual per tidal cycle, I used the fix with the highest detection strength (dB) as an estimate of its most precise location during that given detection period. This procedure eliminated the problem of autocorrelation of successive detections (Van den Avyle & Evans 1990, Sackett et al. 2007).

To determine mean distance moved, maximum distance moved and furthest distance away from the home sites for each individual, the stationary and mobile tracking data were combined. Euclidean distance between two successive locations (typically between a home site and the strongest detection from the manual receiver) was estimated using ArcMap GIS version 9.3.1 (ESRI 2008). The mean distance moved of an individual was calculated by dividing its total distance moved during the study period by the total number of tidal cycles in which a movement of that individual occurred (e.g., Roth & Greene 2006, Carfagno & Weatherhead 2008). The maximum distance moved of an individual was the longest distance it moved during a single tidal cycle. This measure usually included a movement from one of the tidal pools to some location in the tidal creek and then back to a tidal pool during the same tidal cycle. The furthest distance away from the home sites was the greatest distance that a fish was ever detected away from the home sites during the study period.

Activity space was defined as the area a fish utilized during daytime tracking for the duration of the entire study period. It was estimated using minimum convex polygon (MCP), i.e., the area of the smallest convex polygon that contains all observed positions of an individual fish (Anderson 1982). The MCP estimations were obtained using Animal Movements extension (Hooge & Eichenlaub 1997) for ArcView GIS version 3.2 (ESRI 1999). Areas of MCP that extended onto land were clipped using ArcMap Geoprocessing tools. The total activity space of each population was calculated by combining movement data for all 20 individuals of each species.

Fin tissues were analyzed for their $\delta^{13}C$ values as $\delta^{13}C$ reflects long term diet and thus may be used to indicate foraging areas (Layman 2007). In Bahamas tidal creek systems, prey $\delta^{13}C$ values vary predictably from upper reaches of creeks systems to creek mouths (C. Layman and C. Hammerschlag-Peyer, *unpublished data*). Snapper prey are relatively enriched in $\delta^{13}C$ at the creek mouth relative to prey typically found in the upper reaches of creeks (see Fig 4), and thus $\delta^{13}C$ values of snapper fin tissue may reflect long-term feeding in particular parts of the creek system. Analysis followed Post et al. (2007) and was conducted at the Yale Earth System Center for Stable Isotopic Studies (ESCSIS). All stable-isotope values are reported in the δ notation where $\delta^{13}C = [(R_{sample}/R_{standard}) - 1] \times 1000$, and where R is $^{13}C/^{12}C$.

Statistical Analysis

For some individuals, I had a small number of observations because a fish may have died or left the study area. Linear regression revealed that all of my response measures were not significantly related to sample size when individuals with less than nine observation points were excluded from each analysis ($p>0.05$), so each of these individuals was excluded. Additionally, it is also important to note that the number of individuals for a given analysis sometimes differed because of the way the individual observation points were used. For example, while two data points of each fish were used in the analysis of activity space and individual specialization, the same two points resulted in only one distance estimate for that fish. Hence, 14 gray and 15 schoolmaster snapper were used for the activity space and individual specialization analysis (see below), and nine gray and nine schoolmaster snapper for distance analysis.

Movement distances and activity space were examined as a function of body size using linear regression in SigmaPlot 10.0. When necessary to meet model assumptions, data were $\ln(x+0.5)$ transformed. Frequency histograms of movement distances and activity space were performed in R version 2.9.2. I examined a potential relationship between activity space and $\delta^{13}C$ using linear regression.

Individual Specialization

Recent studies have shown that intrapopulation variation in resource use can exist at a single ontogenetic life history stage (Bolnick et al. 2003). Individual specialization, defined as an individual whose (dietary) niche is significantly smaller than the niche of its population for reasons not attributable to its sex, body size, or discrete morphology, has been identified in a number of diverse taxa (Ringler 1983, Magurran 1986, Schindler et al. 1997, Bolnick et al. 2003). One way to infer the occurrence of individual specialists in a population is by examining components of niche variation following Roughgarden (1972, 1974, 1979). In this approach, the population's total niche width (TNW) in terms of resource use is subdivided into a within-individual component (WIC) and a between-individual component (BIC). Individual specialists occur in a population when the TNW consists mostly of the BIC, such that WIC/TNW is small (Roughgarden 1972, 1974, 1979). Most studies on individual specialization have focused on differences in diet and morphology (Bolnick et al. 2003, Araujo et al. 2007, Svanbäck & Bolnick 2007, Svanbäck et al. 2008, Quevedo et al. 2009). Herein, I extend this framework to examine movement data.

In this analysis, the tidal creek was divided into seven zones (the equivalent of individual diet items in traditional specialization studies) according to their habitat composition (Fig. 2), water depth, and distance from home site A and B (Fig. 1). To calculate WIC/TNW, I used the number of detections of an individual fish in each zone during the entire study period. Individual specialization is likely to be present if the WIC/TNW value differs significantly from a null expectation. To this end, the movement-based WIC/TNW value for each population was tested against a null-model using a non-parametric Bootstrap Monte Carlo simulation. Calculations were performed in IndSpec1 (Bolnick et al. 2002).

Results

The 20 gray snapper implanted with a transmitter had a mean SL of 168.5 ± 43.4 mm (mean ± SD; range 111-276 mm; Table 1) and schoolmaster snapper had a mean SL of 148.3 ± 33.7 mm (range: 110-272 mm). On the basis of otolith readings, the body size range in this study included fish of age 1 to 7 for gray snapper (Rypel & Layman 2008) and 2 to 8 for schoolmaster snapper (A. Rypel, University of Alabama, *unpublished data*), including sexually mature individuals (>185-195 mm SL for gray snapper, Starck & Schroeder 1971, and >250 mm FL for schoolmaster snapper, Munro 1983). According to length-weight regressions from tidal creeks on Abaco Island (C. Hammerschlag-Peyer, *unpublished data*), the SL range corresponded to body weights 39-533 g for gray snapper and 37-571 g for schoolmaster snapper. A total of 295,621 individual detections were recorded for these 40 fishes by stationary and manual receivers. All individuals were detected at least once by the stationary receivers at the home sites, and 17 gray and 18 schoolmaster snapper were detected using the manual receiver outside the home sites. Body size had no significant effect on any habitat use measure in both gray and schoolmaster snapper (Table 2). Most schoolmaster snapper stayed in the vicinity of the home sites throughout the study period. Only three of the 20 schoolmaster snapper and seven of the 20 gray snapper were detected outside the zones immediately adjacent to the home sites (Fig. 1).

A few individuals in both populations utilized large areas, whereas most individuals were characterized by small activity spaces (Fig. 3, G-H). The MCP estimates of the total activity space were 145,837 m^2 for 14 gray snapper and 46,565 m^2 for 15 schoolmaster snapper. Eleven gray and 12 schoolmaster snapper used less than 10% of the total activity space for each population, while three gray and three schoolmaster snapper used between 40-60% and 20-35%, respectively. Importantly, activity spaces differed among individuals by their spatial orientation and location in the creek (e.g., Fig. 4). These data suggest that movements and habitat use among individuals varied substantially.

The WIC/TNW of gray snapper and schoolmaster snapper equaled 0.34 and 0.47, respectively, with BIC larger than WIC in both cases. The WIC/TNW index for both populations was significantly different from the null model ($p < 0.001$), which provides evidence for individual specialization in habitat use (Bolnick et al. 2002). Specialization is evident when looking more closely at the differential habitat use of individual fish. For instance, four gray snapper and five schoolmaster snapper only utilized one home site area during the entire study period and were never observed outside the home site areas. The seven gray snapper and three schoolmaster snapper that utilized other zones of the creek tended to move to the same areas repeatedly, with areas differing among individuals (Table 3). Four gray snapper and two schoolmaster snapper moved to only one zone in addition to the home sites.

The $\delta^{13}C$ values of schoolmaster snapper were significantly related to size of activity space ($R^2 = 0.31$, $p = 0.03$) with individuals with small activity spaces having more depleted $\delta^{13}C$ values (Fig. 5B). The $\delta^{13}C$ values of gray snapper became more enriched with increased activity space utilization, but this positive relationship was not statistically significant ($R^2 = 0.15$, $p = 0.19$; Fig. 5A). These patterns are consistent with the $\delta^{13}C$ values of prey in upper and lower portions of the creek. Individual snapper that moved further (i.e., had large activity spaces extending toward the ocean) tended to have enriched $\delta^{13}C$ values similar to prey collected at the mouths of creeks (i.e., marine influences). This finding likely reflects that individuals that moved further were feeding at a food web module originating from seagrass or seagrass epiphytes (that tend to be relatively enriched in $\delta^{13}C$). Snapper individuals that moved less had more depleted $\delta^{13}C$ values. These values were similar to prey collected in portions of creeks adjacent to the home sites, likely reflecting feeding pathways originating from micro- and macroalgae that are abundant in these areas (Kieckbusch et al. 2004).

Discussion

Populations usually are considered to be homogeneous entities with variation among individuals often not incorporated into ecological studies. My data suggest that there may be substantial small-scale intrapopulation variability in movement patterns in gray and schoolmaster snapper. In both populations, some individuals moved repeatedly outside of the home sites, while others remained in or near the deep pools for the entire study period. The activity space of individual fish also differed by spatial orientation and location. Such intrapopulation variation has been shown to be important in several freshwater fish taxa (Bourke et al. 1997, Morbey et al. 2006, Kobler et al. 2009), and I provide one of the first extensions of this research framework to marine fishes (see also Egli & Babcock 2004).

Intrapopulation variation in movement patterns and habitat use was generally not explained by body size even though the body size range in this study included juvenile and adult individuals. While body size is widely accepted as driver of intrapopulation variation in fish habitat utilization (e.g., Minns 1995), my results support recent research findings that body size had no effect on intraspecific patterns of home range/activity space (Lowry & Suthers 1998, Weller & Winter 2001, Sakaris et al. 2003, Morbey et al. 2006) and movement patterns (Bourke et al. 1997, Egli & Babcock 2004, Ng et al. 2007, Childs et al. 2008, Koster & Crook 2008). Only the mean and maximum distances moved in schoolmaster snapper were marginally significant ($0.1 > p > 0.05$; Table 2) likely because three of the larger individuals moved outside the home site zones (Fig. 1). These findings could be affected by the inherently small sample size that is common in telemetry studies as a result of costs associated with tagging technology (Luo et al. 2009). Yet, despite this limitation, I demonstrated that intrapopulation differences in movement patterns of marine fishes may be greater than has previously been recognized and that factors other than body size may drive much of this variation.

In back reef systems, seascape attributes have been shown to be a primary determinant of habitat use of fishes (Pittman et al. 2007). Many coastal fishes, including snapper, generally prefer mangroves surrounded by dense seagrass (Pittman et al. 2007) since mangrove prop roots provide shelter (Hammerschlag et al. 2010) and seagrass beds contain high densities of prey items for coastal fishes (Orth et al. 1984). In the present study system, potential resource pools, such as seagrass, were patchily distributed across the creek system. Such a heterogeneous matrix of resources provides a large scope for individuals to develop specialized movement patterns. Such systems contrast with places where resources are concentrated in a single location. For example, schoolmaster snapper in Spanish Water Bay, Curaçao, typically move less than 5m during the day (Verweij et al. 2007), perhaps because dense seagrass beds are found immediately adjacent to fringing mangroves. In this context, distinct movement patterns among individuals may be less likely to develop because of the concentration of food resources. Alternatively, the relatively short movement distances of schoolmaster snapper in Spanish Water Bay could also be because they feed and seek shelter in mangroves during the day, while feeding in adjacent seagrass beds at night (Nagelkerken & van der Velde 2004, Verweij et al. 2006), probably to minimize predation risk (e.g., Laedsgaard & Johnson 1995). Predation pressure could be higher in Spanish Water Bay than in my study system (I did not quantify this variable), and is another factor that must be considered when analyzing movement distances of individual fish.

Several contexts could be used to elucidate the intrapopulation variation in habitat use. The simplest explanation is that individuals moved randomly, thereby creating habitat use variation among individuals. However, repeated use of certain zones by the same individuals does not seem to support this explanation. Alternatively, movement patterns of individuals may relate to optimal foraging at an individual level (MacArthur & Pianka 1966) in conjunction with differential learning among individuals (Brown & Laland 2003). In this context, it could be more beneficial for certain individuals to forage in proximity of the home sites, while others maximize their intake by foraging in other areas of the creek. Differential habitat use patterns among individuals also are consistent with the "boldness versus shyness" dichotomy of behavioral traits (Gosling & John 1999, Gosling 2001), a pattern found in many fish species (Sih et al. 2004a, Sih et al. 2004b). Bold individuals would be those that frequently explore other habitats or zones, while shy individuals largely remain in the proximity of their home sites (Russell 1983, Wilson et al. 1993).

An underlying driver for the above-mentioned contexts of intrapopulation habitat variation could be differential responses of individuals to competition. Specialization in movement patterns and habitat use is most likely when intraspecific competition is high (Svanbäck et al. 2008), and my empirical data may provide such an example in a marine system. Because all individuals are forced into the home sites at low tide, competition for food resources is likely high (Whitham 1978). Fishes that move further may be able to access underutilized food resources in patchily distributed seagrass beds outside the home site zones, with a trade-off of increased risk of predation (i.e., less shelter away from home sites) and energy expenditure (MacArthur & Pianka 1966).

Snapper $\delta^{13}C$ values tended to be more enriched in individuals that had large activity spaces (Fig. 5). For both species, individuals that used large activity spaces (i.e., moved further toward the ocean) had similar $\delta^{13}C$ values to prey collected from creek mouths, while individuals with small activity spaces tended to have more depleted $\delta^{13}C$ values. These findings suggest that individuals with large activity spaces were feeding from a marine-derived food web module, likely originating in seagrass beds ($\delta^{13}C = -10.5 \pm 2.5$; Kieckbusch et al. 2004). In contrast, individuals with small activity spaces seem to feed on prey in the upstream portion of the creek (in and around the home sites), likely on the basis of diverse macro- and microalgae assemblages ($\delta^{13}C = -18.0 \pm 5.4$, Kieckbusch et al. 2004). Patterns in tissue $\delta^{13}C$ provides strong evidence that the movement patterns observed over the course of the four-week study period were reflective of longer term feeding trends (Hesslein et al. 1993, Suring & Wing 2009).

Fisheries management strategies often have ignored intrapopulation variation in marine systems. Simply concentrating on the “typical” habitats of a fish population may inherently ignore those individuals that use alternative habitats or food sources (Durell 2000, Bolnick et al. 2003). For instance, in a New Zealand marine protected area ~50% of New Zealand Snapper, *Pagrus auratus*, remained within the area during the research period. However, the remaining individuals spent most of their time outside the reserve (Egli & Babcock 2004). This marine protected area would only provide protection for those individuals that moved less through time. Such cases and the present study suggest that a shift in perspective – from a population to an individual level –may be warranted in the management of some marine fisheries. Such an approach may help preserve species' ecological, phenotypic and genetic diversity, and thus their ability to adapt to environmental change and to human impacts in marine ecosystems (Moritz 1994, Coates 2000, Smith et al. 2001, Bolnick et al. 2003).

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Institutional Animal Care and Use Committee (IACUC; Permit Numbers: 09-009, 08-008).

Table 1 Characteristics of 20 gray snapper (GS) and 20 schoolmaster snapper (SM) implanted with acoustic tags in April 2009. Individuals that were tagged at the south-west margin (SW mar) were not included in the analysis since these individuals had <10 observation points (see text for details). Number of detections from mobile receiver (MR) and stationary receiver (SR) and number of total distance moved per tidal cycle (D) are included (see text for details)

#	ID	Species	SL (mm)	Tagging Date	Caught at	MR	SR	D
1	57223	GS	161	4/22/2009	HS B	12	49	10
2	57224	GS	184	4/22/2009	HS B	8	56	4
3	57225	GS	126	4/23/2009	HS B	15	26	15
4	57228	GS	147	4/28/2009	HS B	0	7	0
5	57229	GS	143	4/23/2009	HS B	11	53	10
6	57230	GS	111	4/23/2009	HS B	11	46	14
7	57237	GS	185	4/26/2009	SW Mar	1	0	1
8	57238	GS	134	4/23/2009	HS B	26	36	30
9	57241	GS	150	4/23/2009	HS B	4	14	9
10	57242	GS	139	4/28/2009	SW Mar	3	4	0
11	57245	GS	158	4/22/2009	HS A	19	45	23
12	57249	GS	153	4/28/2009	SW Mar	1	0	0
13	57250	GS	276	4/28/2009	SW Mar	7	0	0
14	58468	GS	162	4/22/2009	HS A	25	42	28
15	58470	GS	187	4/21/2009	HS A	5	91	4
16	58471	GS	194	4/21/2009	HS A	2	62	1
17	58472	GS	166	4/21/2009	HS A	0	18	0
18	58473	GS	118	4/20/2009	HS A	0	0	0
19	58474	GS	212	4/20/2009	HS A	22	26	28
20	58475	GS	264	4/20/2009	HS A	3	80	10
1	57221	SM	162	4/23/2009	HS B	12	48	11
2	57222	SM	160	4/23/2009	HS B	7	48	9
3	57226	SM	131	4/22/2009	HS A	4	102	17
4	57227	SM	126	4/22/2009	HS A	4	110	7
5	57231	SM	140	4/23/2009	HS B	2	53	0
6	57232	SM	110	4/26/2009	HS B	0	0	0

Table 1 continued

#	ID	Species	SL (mm)	Tagging Date	Caught at	MR	SR	D
7	57233	SM	129	4/23/2009	HS B	2	52	0
8	57234	SM	141	4/23/2009	HS B	10	11	10
9	57235	SM	139	4/28/2009	HS B	22	0	0
10	57236	SM	158	4/28/2009	HS B	2	15	3
11	57239	SM	134	4/23/2009	HS B	30	9	31
12	57240	SM	128	4/23/2009	HS B	0	0	0
13	57243	SM	136	4/28/2009	HS B	2	0	0
14	57244	SM	120	4/26/2009	SW Mar	2	2	0
15	57246	SM	146	4/22/2009	HS A	5	29	1
16	57247	SM	140	4/22/2009	HS A	9	64	23
17	57248	SM	166	4/22/2009	HS A	3	27	9
18	58466	SM	147	4/22/2009	HS A	8	100	9
19	58467	SM	180	4/22/2009	HS A	2	32	5
20	58469	SM	272	4/22/2009	HS B	8	161	46

Table 2 Influence of body size on habitat use measures for *Lutjanus griseus* (gray snapper, GS) and *L. apodus* (schoolmaster snapper, SM), on the basis of linear regressions

Measure	**Species**	**R^2**	**Slope**	**p-value**
Mean distance moved	GS	0.03	-0.25	0.64
	SM	0.4	1.03	0.07
Max distance moved	GS	0.03	-0.67	0.68
	SM	0.36	2.17	0.09
Furthest distance from HS	GS	0.06	-0.84	0.55
	SM	0.07	0.48	0.49
Minimum convex polygon	GS	0.04	-0.01	0.5
	SM	0.15	0.02	0.15

Table 3 Total number of days that *Lutjanus griseus* (gray snapper, GS) and *L. apodus* (schoolmaster snapper, SM) moved outside the home sites and the proportion of trips that each individual visited the different creek zones (see text and Fig. 1 for more details). Total number of days is smaller than the actual number of observation points per individual because observations in home site areas are excluded here (see Table 1 for more details)

ID	Species	Total # of days	South West Margin	West Margin	South Margin	Middle	Mouth
57223	GS	9	0	100	0	0	0
57224	GS	1	0	100	0	0	0
57229	GS	10	0	100	0	0	0
57230	GS	3	0	0	33	67	0
57245	GS	3	0	0	0	100	0
58468	GS	7	29	0	0	57	14
58474	GS	17	88	0	0	12	0
57221	SM	9	0	100	0	0	0
57222	SM	2	0	50	0	50	0
58469	SM	1	0	0	0	100	0

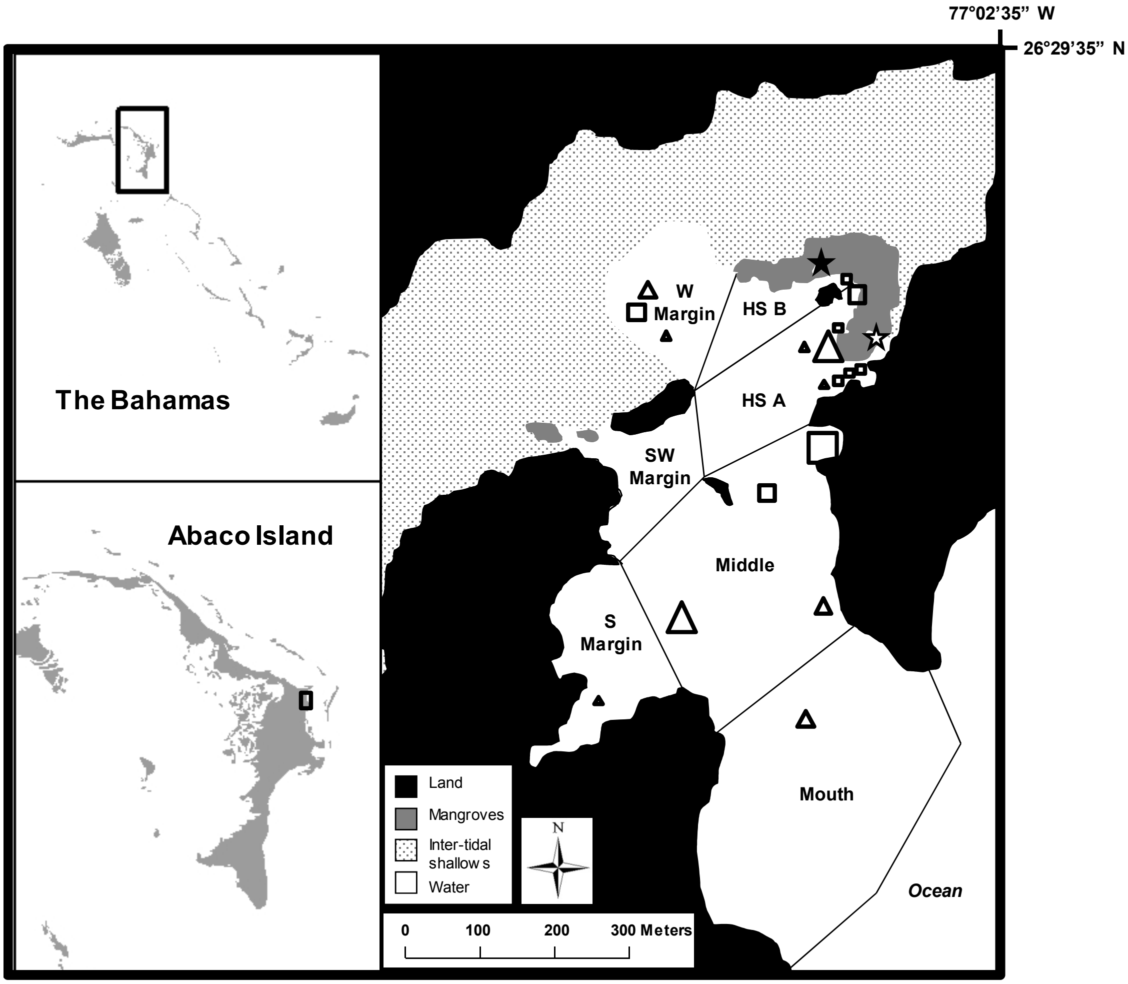

Fig. 1 Broad Creek system coded by land/seascape type. (Δ, □) Furthest distance away from home sites by gray snapper, *Lutjanus griseus* and schoolmaster snapper, *L. apodus* , respectively, during the study period. Size of triangles and squares reflects size of the fish (small: 110-150 mm standard length (SL), medium: 151-200 mm SL, big: > 200 mm SL). The open star represents home site A (HS A) and the closed home site B (HS B). Panels on the left are maps of The Bahamas (top left) and Abaco Island (bottom left) with the rectangle representing the location of Broad Creek

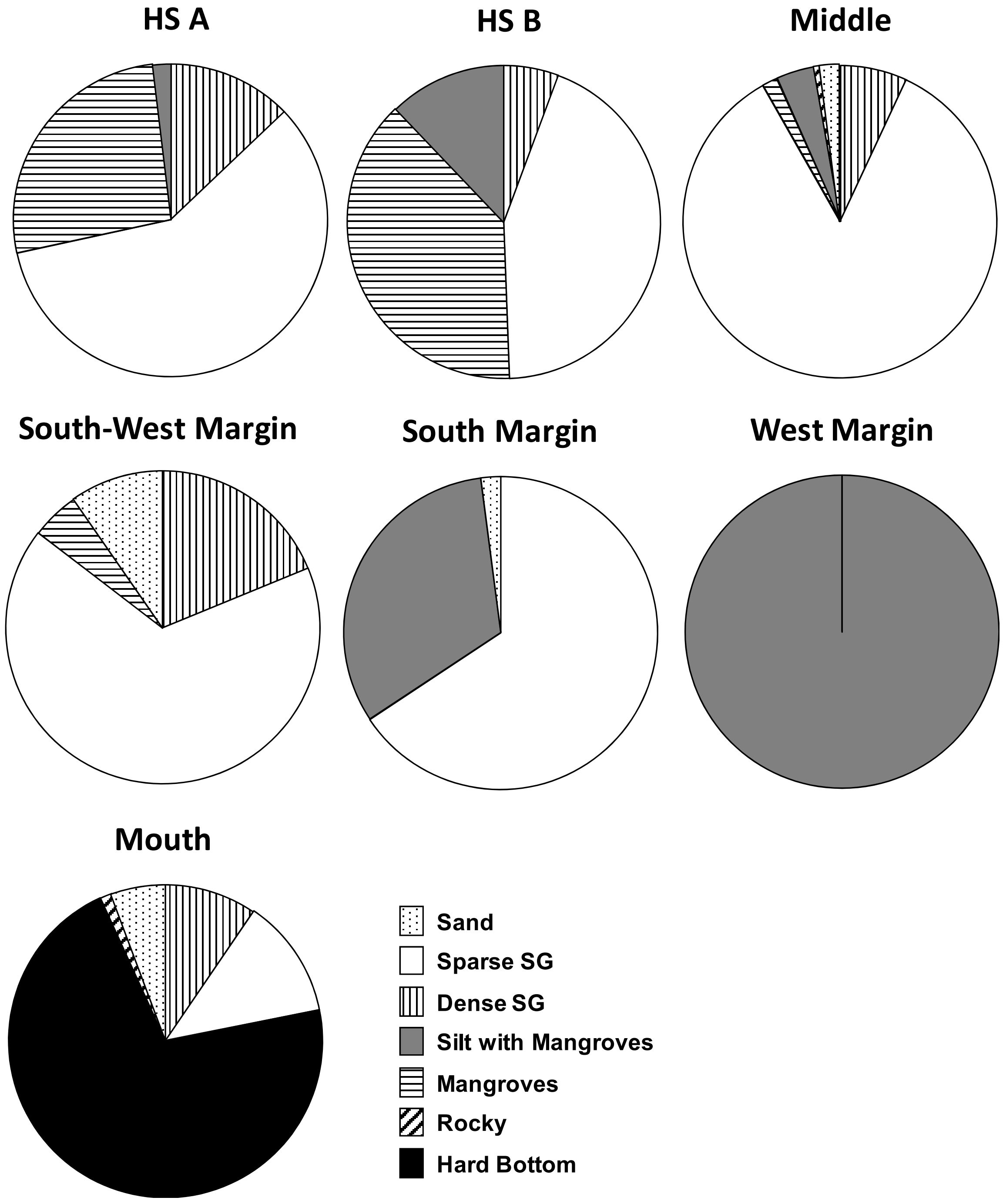

Fig. 2 Proportion of habitat types in each zone. HS: home site; SG: seagrass; Silt: mangrove-derived, rich sediment

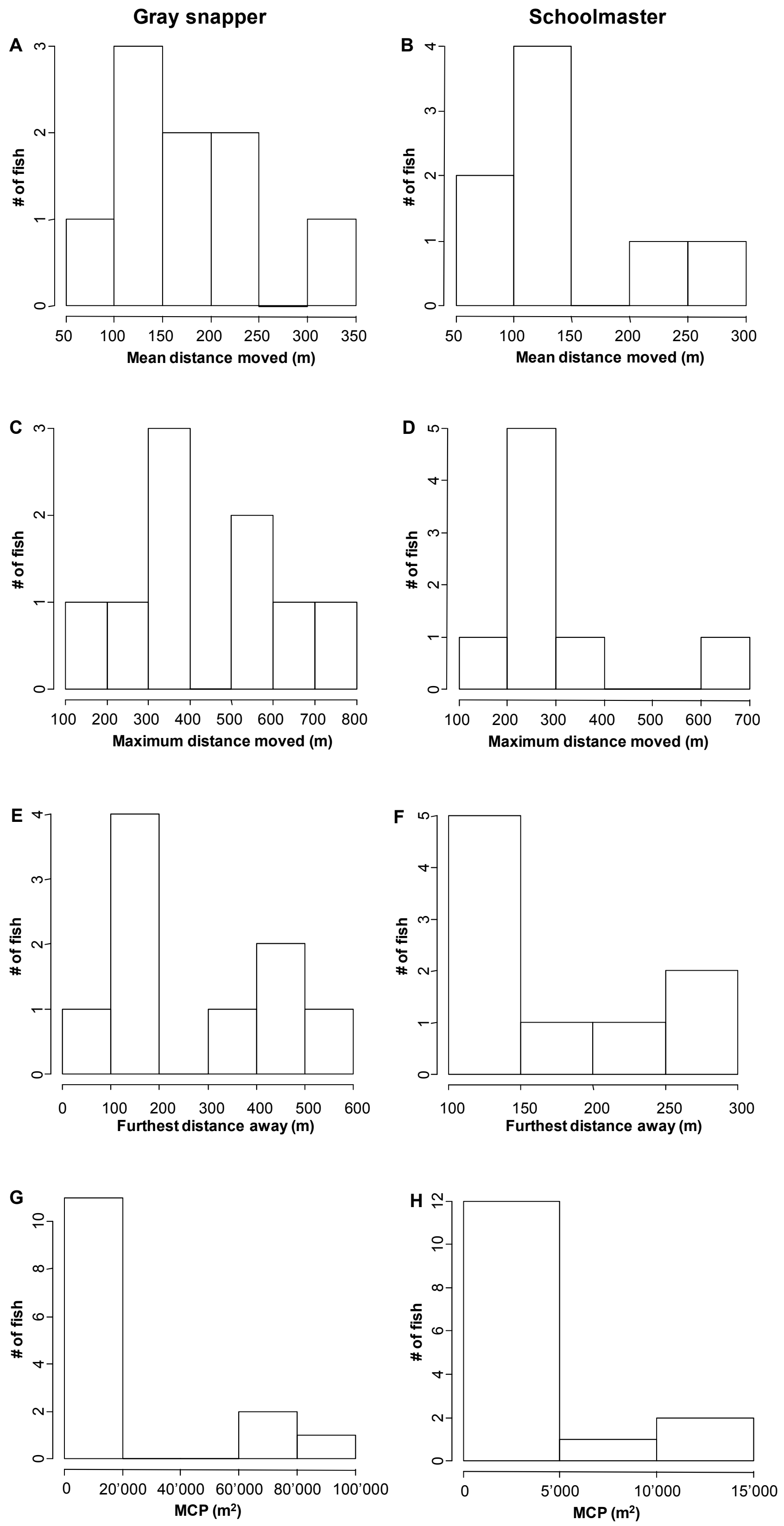Gray snapper
Schoolmaster
A
# of fish
0
1
2
3
50
100
150
200
250
300
350
Mean distance moved (m)
B
# of fish
0
1
2
3
4
50
100
150
200
250
300
Mean distance moved (m)
C
# of fish
0
1
2
3
100
200
300
400
500
600
700
800
Maximum distance moved (m)
D
# of fish
0
1
2
3
4
5
100
200
300
400
500
600
700
Maximum distance moved (m)
E
# of fish
0
1
2
3
4
0
100
200
300
400
500
600
Furthest distance away (m)
F
# of fish
0
1
2
3
4
5
100
150
200
250
300
Furthest distance away (m)
G
# of fish
0
2
4
6
8
10
0
20'000
40'000
60'000
80'000
100'000
MCP (m^2)
H
# of fish
0
2
4
6
8
10
12
0
5'000
10'000
15'000
MCP (m^2)

Fig. 3 *Lutjanus griseus* (left panels) and *L. apodus* (right panels). Frequency histograms of: 1) mean distance moved (average of daily movement distances, April 26 – May 24 2009) (A-B); 2) maximum distance moved (C-D); 3) furthest distance away from home sites (HS; E-F); 4) activity space on the basis of minimum convex polygon (MCP) estimates (G-H)

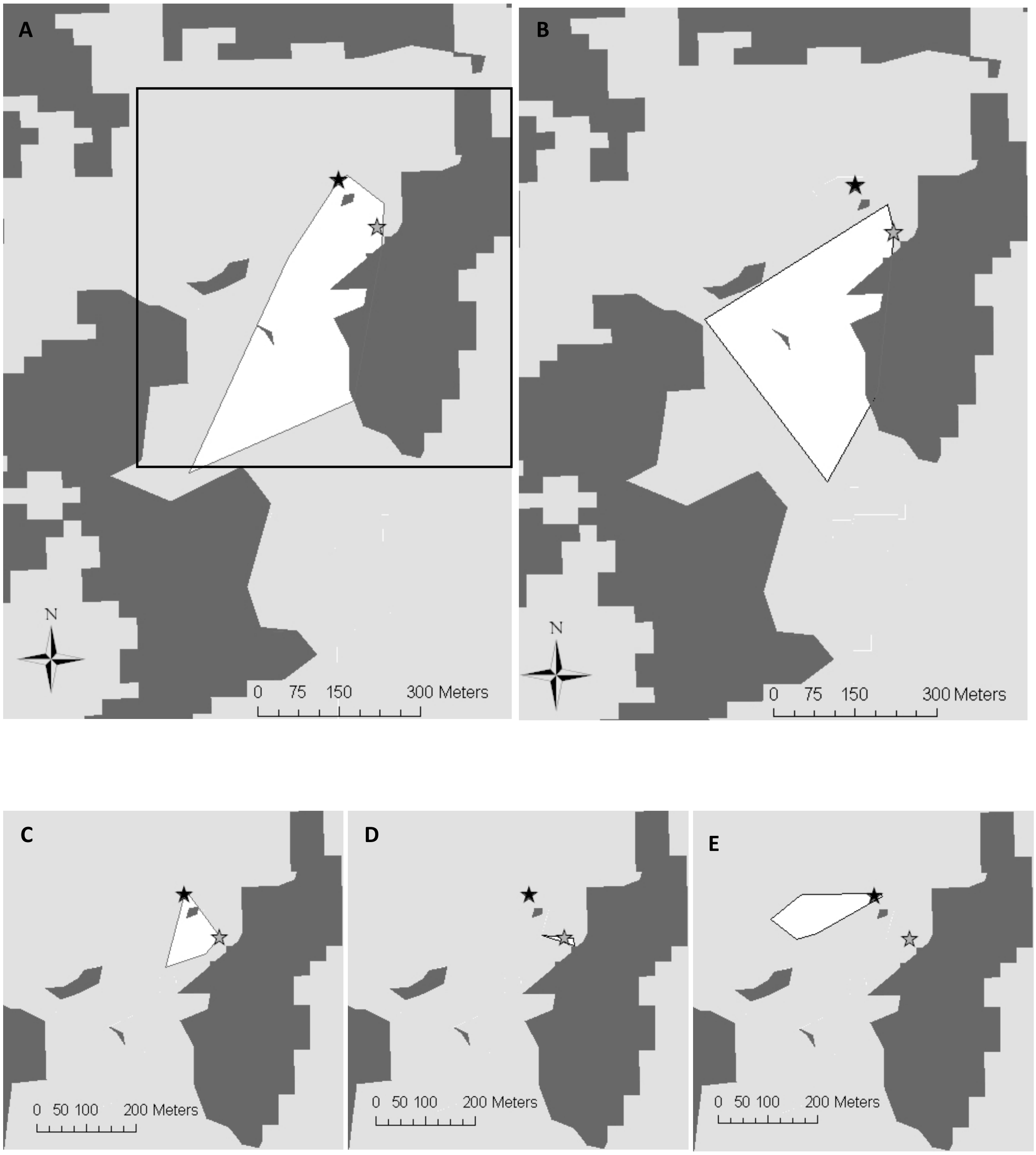

Fig. 4 Examples of the activity space for 5 individuals (gray snapper: A-C; schoolmaster snapper: D and E) in the study area (dark gray: land, light gray: aquatic habitat) from April 26 to May 24 2009. The black frame in A corresponds to the area represented in the smaller maps (C-E)

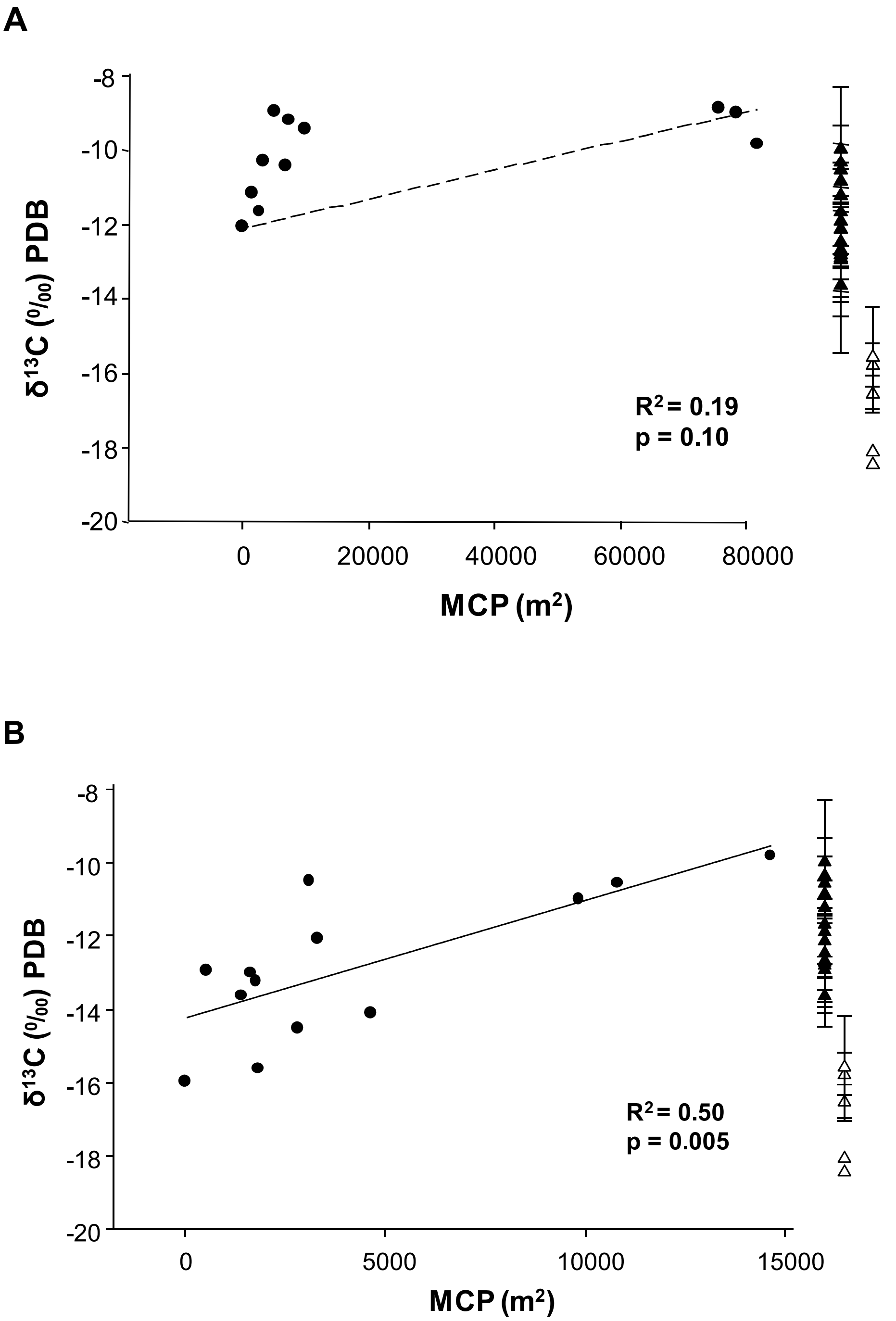

Fig. 5 Linear regression between δ^{13}C and activity space (minimum convex polygon, MCP) for A) gray snapper and B) schoolmaster snapper. (●) Data for an individual snapper, while each triangle represents a mean δ^{13}C value for individual taxa known to be

snapper prey (error bars: SD). The δ^{13}C values of prey items vary between creek mouth (▲) and upstream (Δ) areas. PDB: PeeDee belemnite, global standard of δ^{13}C. The δ^{13}C values of prey items were corrected for trophic discrimination ($1^{0}/_{00}$, according to Post 2002)

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CHAPTER III

FACTORS AFFECTING RESOURCE USE VARIATION FOR AN ABUNDANT COASTAL FISH PREDATOR, *LUTJANUS APODUS,* IN A BAHAMIAN WETLAND SYSTEM

Abstract

Studies of resource use by fishes reflect important ecological interactions, and provide insight into the structure of aquatic food webs. To this end, fish stocks are often viewed as homogeneous units despite increasing evidence that among-individual variation in resource use within populations is common. Such intraspecific variation in resource use can be a result of ontogenetic-based diet shifts, differences in individual feeding behavior within age groups (i.e., individual specialization), and temporal variation in resource pools. I examined trophic interactions in schoolmaster snapper *Lutjanus apodus* (Walbaum, 1972), over multiple seasons and across size classes, in a Bahamian wetland system. Using combined stable isotope and stomach content analyses, I found that, as with many other fishes, sub-adults fed at higher trophic levels than juveniles, likely because of a shift from feeding predominantly on smaller prey taxa (e.g., shrimps) to larger prey taxa (e.g., crabs and teleosts). Sub-adults seem to extend their foraging range to adjacent seagrass beds, whereas juveniles predominantly feed within mangrove prop root habitats. Niche width and degree of individual dietary specialization varied among years, suggesting important levels of temporal variation. In sum, I show that individual snapper did not use resources homogeneously, and outline some of the factors that underlie this variation.

Introduction

Overfishing and habitat degradation have driven drastic declines in many coastal fish stocks (Jackson et al. 2001, Myers et al. 2007, Worm et al. 2009). These declines are of great concern given fishes' economic and ecological importance in coastal ecosystems (Jackson et al. 2001, Hilborn et al. 2003). Understanding resource use of focal species can aid in documenting the wide ranging impacts that population declines may have on ecosystem function. For instance, severe declines of top predators on the east coast of the United States ultimately led to the widespread collapse of scallop populations (Myers et al. 2007). An understanding of such cascading impacts can be gleaned from the study of the underlying trophic relationships and resource use patterns of the focal organisms.

Fish populations are often treated as homogeneous units, despite increasing evidence that fishes exhibit great among individual variation in resource use (Bolnick et al. 2003, Chassot et al. 2008, Adams et al. 2009). Intrapopulation variation in resource use can be related to ontogenetic diet shifts (Polis 1984, Werner & Gilliam 1984), but also to differences in feeding behavior within certain life history stages (Bolnick et al. 2003, Bolnick et al. 2011, Araujo et al. 2011). For example, individual specialization, defined as a significantly smaller dietary niche of an individual than the population niche for reasons not attributable to its sex, body size, or age classes, has been identified in a number of diverse taxa (Ringler 1983, Magurran 1986, Schindler et al. 1997, Bolnick et al. 2003, Araujo et al. 2011). In addition, individuals may experience temporal differences in resource availability that may drive variation in resource use (Weliange & Amarasinghe 2003, Swanson et al. 2008, Hammerschlag et al. 2010). Such resource variation can influence community dynamics and ecosystem function, with important evolutionary, ecological and conservation implications (Van Valen 1965, Roughgarden 1972, 1974, Schindler et al. 1997, Bolnick et al. 2003, Filin & Ovadia 2007, Okuyama 2008, Byron & Link 2010).

In the present study, I investigated diet and feeding behavior of the schoolmaster snapper *Lutjanus apodus* (Walbaum, 1972) within a Bahamian wetland system, and examined various factors that may affect resource use within this population. Specifically, I investigated whether (1) diet changed through ontogeny, (2) diet specialization was present within ontogenetic groups, and (3) season and year affected diet within and between ontogenetic groups. To address these questions, I employed stable isotope and stomach content analyses, two complimentary methods used to characterize trophic relationships (Layman & Post 2008). Combined, these approaches revealed extensive insight into schoolmaster feeding patterns, and suggested the multiple levels at which diet variation can occur.

Materials and Methods

Study Site and Species

Jungle Creek (26°21'36"N, 77°00'59"W) is a mangrove dominated tidal wetland, locally called a "tidal creek", situated on the east side of Abaco Island, Bahamas. Jungle Creek is ~40 hectares in size with a maximum low tide depth of ~1 m. The system has semi-diurnal tidal regime and mean daily tidal amplitude of ~0.8 m. There is little freshwater input to this system and thus it is marine-dominated throughout its extent. The most prevalent benthic habitat types are seagrass beds (primarily *Thalassia testudinum*, Banks ex. König, 1805), submerged mangrove prop roots (predominantly *Rhizophora mangle*, Linnaeus) and sand flats.

Schoolmaster snapper *L. apodus* is a generalist fish predator in many nearshore ecosystems in the tropics and subtropics of the Atlantic (Allen 1985), and are locally abundant throughout Caribbean coastal ecosystems, likely playing an important ecological role (Nagelkerken et al. 2000, Valentine-Rose et al. 2007). Reproductively immature individuals mainly use mangroves and seagrass beds as nursery habitats, while adults often migrate to patch and coral reefs (Allen 1985). Immature individuals are highly abundant fishes in Bahamian tidal creeks, likely playing an important role in estuarine food webs (Valentine-Rose et al. 2007, Hammerschlag-Peyer & Layman 2010, Valentine-Rose et al. In Press) and potentially providing new individuals to the adult populations on nearby patch and coral reefs as they mature (Nagelkerken et al. 2000, Adams et al. 2006). Since the size range of schoolmaster snapper in Jungle Creek does not include reproductively mature adults (>250 mm fork length; Munro 1983), I *a priori* divided individuals into juveniles (<125 mm standard length, SL; including age class 1 and 2) and sub-adults (≥125 mm SL; including age classes 3 to 7 years) on the basis of schoolmaster otolith readings (A. Rypel, University of Alabama, unpublished data). Ideally, size categories for comparisons would be on the basis of ecologically relevant divisions, e.g., on the basis of year classes of individuals or on the basis of *a priori* sizes at which Gestalt diet shifts occur (Werner & Gilliam 1984). Such clear divisions were not available in my case, so I chose a size division that would best balance sample sizes among groups. In using such an approach, I increased my power to identify overall differences among larger and smaller individuals, providing the foundation for more detailed size-based analyses.

Data Collection

Schoolmaster snapper were caught using baited hooks, fish traps, and cast nets during two consecutive wet (May – August) and dry seasons (December – February) from 2007 to 2009 (i.e., Wet 2007, Dry 2008, Wet 2008, Dry 2009). Sizes of individuals sampled in this study were representative of the size structure of schoolmaster in these systems (Hammerschlag-Peyer & Layman 2010). Upon capture, each fish was anesthetized in a mixture of fresh seawater and clove oil (active ingredient: eugenol), a commonly used fish anesthetic (Cotter & Rodruck 2006). After measuring standard length, non-lethal stomach regurgitation was performed on each individual for gut content analysis following methods modified from Layman and Winemiller (2004). During stomach regurgitation, the entire stomach was inverted to ensure collection of all contents. After the procedure, each fish was immediately transferred to a cooler with fresh seawater for recovery and a small sample of the dorsal fin tissue (~1 cm^2) was removed for stable isotope analysis. After ~15min, individual fish were released at their capture location. Fifty individuals were sacrificed to verify the effectiveness of the regurgitation method; only 2% (n=1) of the sacrificed individuals had additional stomach contents remaining after regurgitation. Stomach contents were identified to the lowest taxonomic level possible, and the volume of each prey item was measured via displacement with a graduated cylinder. Fin clips were transported on ice to a field station, stored in a freezer, and later processed at Florida International University.

All stable isotope values are reported in the δ notation where $\delta^{13}C$ or $\delta^{15}N$ = $[(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$, and R is the $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratio. I focused on ratios of $\delta^{15}N$ and $\delta^{13}C$ because each reveals a distinct aspect of the consumer's long-term (for fin: week to months) trophic niche. The $\delta^{15}N$ values exhibit stepwise enrichment with trophic transfers, and can thus be used to estimate an organism's trophic position relative to that of others in a food web (DeNiro & Epstein 1981, Minagawa & Wada 1984, Peterson & Fry 1987). The $\delta^{13}C$ values vary substantially among primary producers with different photosynthetic pathways (e.g., C3 vs. C4 plants) and are subject to diverse environmental conditions (e.g., productivity), but change little with trophic transfers, and can thus be used to infer sources of dietary carbon (Rounick & Winterbourn 1986, Peterson & Fry 1987, France & Peters 1997, Layman 2007).

Prey taxa (identified in stomach content analysis) were collected in Jungle Creek using dip and cast nets during 2008 and 2009. At least three individuals of each prey item were sampled. Each prey organism was dried at 60° Celsius for a minimum of 48 hours and subsequently dry weight was measured. For stable isotope analysis, the whole organism for prey taxa and the fin tissue of schoolmaster snapper were used. The $\delta^{13}C$ and $\delta^{15}N$ of schoolmaster snapper fin and muscle tissue are highly correlated within individuals ($\delta^{13}C$ fin = 1.06 * $\delta^{13}C$ muscle + 2.84, $R^2 = 0.97$; and $\delta^{15}N$ fin = 1.13 * $\delta^{15}N$ muscle – 1.8, $R^2 = 0.82$, N = 23 individuals). For shrimps and crabs, separate analyses were performed for $\delta^{13}C$ and $\delta^{15}N$, with samples for $\delta^{13}C$ first acidified to remove inorganic carbon following Kolasinski et al. (2008). Stable isotope preparation of prey and fin tissues followed Post et al. (2007) and the analysis was conducted at the Yale

Earth System Center for Stable Isotopic Studies (ESCSIS). Internal standards used were trout muscle with a precision (SD) of 0.14‰ for δ^{13}C and 0.22‰ for δ^{15}N values.

Data Analysis

I first applied stable isotope analysis to examine shifts in niche width and isotopic position between sample years, seasons and ontogenetic groups. I then investigated stomach content data for differences in diet between years, seasons and size classes. Finally, I used the combination of stable isotope and stomach content data to measure the degree of individual specialization for each group and potential changes of their degree with time. Details for these analyses are outlined herein.

For stable isotope data, univariate analysis was applied to examine potential differences in δ^{13}C and δ^{15}N values between years (2007-08 and 2008-09), seasons (wet and dry) and size classes (juveniles and sub-adults). The δ^{13}C and δ^{15}N values were tested for normality and homogeneity of variance in R version 2.11.1 (R Development Core Team 2008). The δ^{13}C values met the model assumptions, thus stepwise one-way analysis of variance (ANOVA) was used to assess the influence of each factor (year, season, size class) separately (Ley & Halliday 2007, Hammerschlag & Serafy 2009). The δ^{15}N values did not meet model assumptions, so stepwise one-way Kruskal-Wallis analysis was employed. Analyses were performed in SYSTAT version 10.2 (SYSTAT 2002) and statistical significance was declared at $\alpha < 0.05$.

One representation of niche width of a given group is the *total area* of a subset of individuals of that group within a bivariate isotope space (here within a δ^{13}C-δ^{15}N biplot). It can be calculated as the minimum convex polygon (MCP; Anderson 1982), i.e., the area of the smallest convex polygon that contains all individuals of the sample group (Layman et al. 2007). I measured MCP of each size class in ArcMap GIS version 9.3.1 (ERSI 2008) and verified that the sample size of each group was sufficient to adequately represent the niche width of that particular group on the basis of performed bootstraps (1000 replicates) in Animal Movements extension (Hooge & Eichenlaub 1997) for ArcView GIS version 3.2 (ERSI 1999). If the curve of the relationship between sample size and niche width reaches an asymptote, it can be assumed that enough individuals were sampled (Hurturbia 1973, Cailliet 1977, Ferry & Cailliet 1996).

The MCP approach offers some advantages for characterizing niche width when compared to alternative analyses. The MCP approach is powerful because it incorporates each individual of the population’s sub-sample, and thus includes information about the niche width of the population including every sampled individual. Conversely, other approaches are targeted at identifying the “core” niche of the population, a niche metric which could exclude particular individual niches from the characterization of the population niche (Jackson et al. 2011). Either of these approaches may be more relevant with respect to a particular question of interest and/or the nature of the underlying data set. Herein, I chose to examine niche width of juvenile and sub-adult schoolmaster snapper using the MCP approach, as the importance of individual level niche variation is increasingly recognized as an important component of ecological dynamics and evolutionary trajectories (Bolnick et al. 2003, Bolnick et al. 2011).

To identify any changes in resource use between the two size classes, I performed a multivariate test for differences in central tendency and dispersion following Turner et al. (2010) in R version 2.11.1 (R Development Core Team 2008). In the context of this study, differences in central tendency represent a shift in isotopic niche position, and differences in dispersion represent a change in niche width between the two size classes. Difference in central tendency was measured by computing Euclidean distance between the centroids (bivariate means) of the two groups and was considered to be different between the two groups if the Euclidean distance between them was significantly greater than zero (Turner et al. 2010). Similarly, the mean distance to centroid was computed to test for differences in dispersion (for more details, see Turner et al. 2010).

Gut contents of schoolmaster snapper were analyzed on the basis of the volume of prey items from various taxonomic groups. For analysis, I omitted all empty stomachs, as well as prey items that were classified as unidentifiable crustacean, crab, or shrimp. Although the proportion of unidentifiable crustacean and shrimp were relatively low (<3.3%, see below), the proportion of unidentifiable crab was relatively high (11%). Despite the omission of this group, identifiable crabs (i.e., *Panopeus* sp., *Aratus* sp. and Xanthoidea) still constituted a large percentage of the schoolmaster diet and thus, their importance was well represented (see Results, Fig. 3). The external features of teleost fishes disintegrate rather quickly once ingested (Randall 1967, Brulé & Canché 1993), and are thus difficult to identify to species. Consequently, I grouped all consumed fishes into a teleost category. Several other prey taxa constituted a relatively small volume in the schoolmaster diets. Since small volumes of prey taxa can bias stomach content analysis (Clarke & Warwick 1994), I used a quantitative criterion following Araujo et al. (2007b) to determine which prey categories to include in the analysis. This criterion consists of calculating the reciprocal of the number k of prey categories consumed ($1/k$), and using this value as a cutoff for inclusion of prey categories in further analyses. A category *j* is included if its proportion in the population diet $q_j \geq 1/k$. The cut-off value for schoolmaster snapper was 0.033, so that categories representing less than 3.3% of diet items in each species were eliminated. Prey categories included were teleosts (fishes), *Panopeus* sp. (mud crabs), *Aratus* sp. (mangrove tree crab), Xanthoidae (superfamily of mud crabs, excluding *Panopeus* sp.), *Alpheus* spp. (snapping shrimp), *Palaemonetes* sp. (grass shrimp), and *Farfantepenaeus* sp. (pink shrimp).

As with stable isotope data, univariate analysis was applied to examine potential differences in diet among years, seasons and size classes using stomach content data. Stepwise one-way χ^2 analysis was performed on volumes of prey taxa to assess the influence of each factor (year, season, size class) separately (Ley & Halliday 2007, Hammerschlag & Serafy 2009). Average dissimilarity between groups was measured when necessary using similarity percentages (SIMPER) in PRIMER 5.2.9 (Clarke & Warwick 1994).

When used together, stable isotope and stomach content analysis are powerful tools to quantify the degree of individual specialization (Votier et al. 2003, Matthews & Mazumder 2004, Araujo et al. 2007a). To this end, I employed the model of Araujo et al. (2007a) separately for δ^{13}C and δ^{15}N values on both juvenile and sub-adult schoolmaster snapper. This model uses the variance in individual stable isotope values (i.e., δ^{13}C or δ^{15}N) of a size class, the stable isotope values (i.e., δ^{13}C or δ^{15}N) of each prey taxa, and the dietary proportion for each prey taxa to estimate the index of individual specialization (i.e., WIC/TNW, WIC = within-individual component, TNW = total niche width; Bolnick et al. 2002). In this approach, null populations with varying degrees of individual specialization are generated, for which both isotope variances and indices of individual specialization are calculated. A curve relating the expected isotopic variances and indices of individual specialization is built, and is then used to interpolate a measure of individual specialization given an empirical variance in isotopes (i.e., given the actual estimated variance in $\delta^{13}C$ or $\delta^{15}N$ for a selected sample of individual consumers). The calculations were performed in the program "VarIso" (http://www2.fiu.edu/~marine/araujo/software.html) using 100 simulations following Araújo et al (2007a). Output data were applied to calculate the expected index of individual specialization for schoolmaster snapper (WIC/TNW). Indices of WIC/TNW close to zero imply strong individual specialization within a size class, while WIC/TNW indices close to 1 suggest homogeneous resource use among individuals of a size class.

Results

I performed stomach regurgitation on 842 individual schoolmaster snapper during the study period (May 2007-February 2009) with mean SL of 122.6 ± 29.6 mm (mean ± SD; range 45–245 mm) and used a subsample of 150 individuals for my stable isotope analysis (Table 1) with mean SL of 135.4 ± 34.5 mm (mean ± SD; range 63–245 mm). Stepwise one-way analysis of variance revealed that $\delta^{13}C$ values were not significantly affected by year or season, but were affected by size class (Table 2). The $\delta^{15}N$ values did not vary between seasons, yet differed significantly between sampling years and between size classes (Table 3). Linear regression revealed a significant increase in $\delta^{13}C$ values with body size (i.e., standard length; $R^2 = 0.16$, $P < 0.0001$, n = 150, Fig. 1A). Similarly, $\delta^{15}N$ values increased significantly with body size in 2007-08 ($R^2 = 0.22$, $P < 0.0001$, n = 90) and in 2008-09 ($R^2 = 0.32$, $P < 0.0001$, n = 60, Fig. 1B).

The MCP of all juveniles (pooled across years and seasons) was 20.7, and the MCP of all sub-adults 17.9 (Fig. 2A). There was a significant difference in isotopic niche position (central tendency) between juveniles ($\delta^{13}C$ = -13.8‰, $\delta^{15}N$ = 7.3‰) and sub-adults ($\delta^{13}C$ = -12.4‰, $\delta^{15}N$ = 8‰; Euclidean distance = 1.52, *P* = 0.001), but no change in niche width (dispersion; centroid distance = 0.09, *P* = 0.63; Fig. 2A) for both years combined. When niche widths of size classes were separated into the two sampling years, the niche width of juveniles and sub-adults was 7.0 and 9.5, respectively, for 2007-2008 (Fig. 2B). There was a significant difference in isotopic niche position between juveniles ($\delta^{13}C$ = -13.8‰, $\delta^{15}N$ = 7.9‰) and sub-adults in 2007-08 ($\delta^{13}C$ = -12.4‰, $\delta^{15}N$ = 8.2‰; Euclidean distance = 1.47, *P* = 0.001), but no significant shift in niche width (centroid distance = 0.01, *P* = 0.95; Fig. 2B). In contrast, juveniles in 2008-09 did not only have a different isotopic niche position ($\delta^{13}C$ = -13.8‰, $\delta^{15}N$ = 6.6‰) as the sub-adults ($\delta^{13}C$ = -12.6‰, $\delta^{15}N$ = 7.5‰; Euclidean distance = 1.51, *P* = 0.008), but also their niche width was significantly smaller than that of sub-adults (11.9 vs. 13.6; centroid distance = 0.69, *P* = 0.012; Fig. 2C).

From the 842 sampled individuals, 261 individuals (31%) with mean SL of 120.7 ± 30.6 mm (mean ± SD; range 63–245 mm) had identifiable prey items in their stomachs (Table 4). The stepwise one-way χ^2 analysis revealed that there was only a statistically significant difference in diet composition between juveniles and sub-adults in 2008-09 (χ^2 = 17.7, df = 6, *P* = 0.007; Table 5). Prey taxa that were primarily responsible for the observed difference in dietary composition between juveniles and sub-adults in 2008-09 were *Aratus* sp. (30.1%) and teleosts (26.3%, percent contribution to the overall dissimilarity from SIMPER). Diet comparison between juveniles and sub-adults (pooled across years) revealed that juveniles mostly consumed *Aratus* sp. crabs (35%), *Alpheus* spp. shrimps (27%), and teleosts (20%), while sub-adults' diets were dominated by teleosts (29%) and *Aratus* sp. (24%) (Fig. 3A). The diets of the two groups were significantly different (χ^2 = 18.7, df = 6, *P* = 0.005; Fig. 3A, Table 5). When their diet was compared within each year, juveniles in 2007-08 mostly consumed teleosts (36%) and *Aratus* sp. (26%), and sub-adults teleosts (48%) and *Alpheus* spp. (14%), but the diets between the two groups did not differ significantly (χ^2 = 5.6, df = 6, *P* = 0.47; Fig. 3B, Table 5). In 2008-09, juveniles mainly fed on *Aratus* sp. (39%) and *Alpheus* spp. (31%), and sub-adults *Aratus* sp. (33%), *Panopeus* sp. (19%) and teleosts (18%). The diet of both groups in 2008-09 differed significantly (χ^2 = 17.7, df = 6, *P* = 0.007; Fig. 3C, Table 5). Regardless of year, the proportion of teleosts, *Panopeus* sp., Xanthoidea, and *Farfantepenaeus* sp. was higher, and the proportion of *Aratus* sp., *Alpheus* spp., and *Palaemonetes* sp. was lower in sub-adult schoolmaster snapper (Fig. 3).

The estimated degree of individual specialization (WIC/TNW) for juvenile and sub-adult schoolmaster snapper (pooled across years and seasons) on the basis of δ^{13}C values were relatively low (i.e., relatively high WIC/TNW; 0.71 and 0.67, respectively). Likewise, the magnitude of individual specialization on the basis of δ^{15}N values was relatively low for juveniles and sub-adults in 2007-08 (0.88 and 0.71, respectively), whereas it was relatively higher for the two size classes in 2008-09 (0.71 and 0.50, respectively), suggesting some temporal variation in degree of dietary specialization. For comparison, natural populations across broad taxonomic groups have been found to have an average WIC/TNW index of 0.66 ± 0.209 (mean ± s.d.; N = 78; Araujo et al. 2011).

Discussion

Variation in resource use affects population dynamics, community structure and ecosystem functions (Werner & Hall 1988, Polis & Strong 1996, Claessen et al. 2002, Subalusky et al. 2009). For example, many fishes change their diet through ontogeny, which can decrease intrapopulation resource competition (Werner & Gilliam 1984). An increasing number of studies also have revealed the occurrence of individual-level variation within size classes (Bolnick et al. 2003, Araujo et al. 2011). In this context, I examined patterns in resource use in one of the most abundant wetland fishes in The Bahamas. In doing so, I provide a framework for incorporating such intrapopulation variation into the study of coastal organisms' resource usage.

As $\delta^{13}C$ can differ considerably among primary producers with different photosynthetic pathways (e.g., C3 vs. C4 plants) or with diverse environmental conditions (e.g., productivity), but changes little with trophic transfers (DeNiro & Epstein 1981, Peterson & Fry 1987, Post 2002), $\delta^{13}C$ can be useful in help determining primary habitats or source pools utilized by consumers. The $\delta^{13}C$ value is especially useful in coastal ecosystems because some of the most prominent habitat types, i.e., mangroves and seagrass beds, have distinct $\delta^{13}C$ signatures, with mangroves (and mangrove-associated algae) being more depleted in $\delta^{13}C$ than seagrass habitats (and seagrass-associated algae; Kieckbusch et al. 2004). Snappers (Lutjanidae) are known to reside in mangrove areas, but may either feed within this habitat or in others (Hammerschlag-Peyer & Layman 2010). In my study, juvenile schoolmaster snapper were characterized by values similar to mangrove-based food webs, whereas sub-adult schoolmaster snapper had more enriched $\delta^{13}C$ values than juveniles, likely reflecting greater reliance on seagrass-based food sources (Kieckbusch et al. 2004, Figs. 1, 2 and 4). Dietary information supported this interpretation. For example, sub-adults fed more on sp. that are common in seagrass beds (Fig. 4), than juveniles. *Aratus* sp., the primary diet item of juveniles (Fig. 3), is only found on mangrove prop roots where they feed on mangrove-associated epiphytic communities (and thus have a depleted $\delta^{13}C$, Fig. 4). As such, my data suggest that sub-adults could have expanded their foraging range to adjacent seagrass beds, whereas juveniles remained closer to the mangrove fringe of the creeks feeding on local food sources in their protective nursery habitat.

Such an increase in foraging range with ontogeny is common in fishes (for a review: Minns 1995), often because of a decrease in predation risk (Werner & Hall 1988) or change in resource requirements (Carfagno & Weatherhead 2008) with increasing body size. In a previous study, I found that differences in foraging range of schoolmaster snapper (*L. apodus*) and a closely related species gray snapper (*L. griseus*), were not explained by body size (Hammerschlag-Peyer & Layman 2010). Yet, I used larger individuals in that study (schoolmaster snapper: SL 110-272mm, gray snapper: SL 111-276mm) than in this focal study. Since the smallest individuals are the most susceptible to predators, juveniles used in this study (SL 45–124 mm) may be expected to have the most constrained foraging range to minimize predation risk. Once a certain size threshold is reached, individual-level foraging differences may override the apparent restricted foraging range of the juveniles (Hammerschlag-Peyer & Layman 2010). These data again suggest how a combination of stable isotope, diet and movement data can be a powerful suite of tools to study resource use of coastal organisms (Hammerschlag-Peyer & Layman 2010, Matich et al. 2010, Rosenblatt & Heithaus 2011).

Body size and trophic position are often correlated, such that larger animals feed at higher trophic levels (Sholtodouglas et al. 1991, Cohen et al. 1993, Fry & Quinones 1994, France et al. 1998, Jennings et al. 2001). In my study, sub-adult schoolmaster snapper had more enriched $\delta^{15}N$ values than juveniles, suggesting a higher trophic position (Figs. 1, 2, 4). This higher trophic level of sub-adults could have been the result of their consumption of larger prey items and/or increased proportion of teleosts in their diet. On the basis of $\delta^{15}N$ values (and an assumed fractionation of ~3‰) teleosts were approximately a trophic level higher than most other prey taxa (Fig. 3, Table 6). Studies on gray snapper (*L. griseus*) have shown that piscivory increases through ontogeny (Starck & Schroeder 1971), and I would expect this trend to be even more pronounced in schoolmaster snapper if I would have included larger size classes in the diet analysis.

Temporal differences can be used to explore mechanisms driving ontogenetic niche shifts and individual specialization (Link & Garrison 2002, Herrera et al. 2008). In the present study, niche width and degree of individual specialization differed between years. The data were consistent with the "niche variation hypothesis" (Van Valen 1965) which suggests that populations (or size/age groups) with broader niches are more variable in resource use (i.e., higher among-individual variation) than populations with narrower niches (Soule & Stewart 1970). A wider niche width can be attained in one of two ways: (1) all individuals of that population/group utilize more resources (all individuals have large niche widths; low among individual variation) or (2) the entire population/group utilizes more resources, yet each individual maintains a narrow niche that overlaps little among conspecifics (high among individual variation; Bolnick et al. 2007, Araujo et al. 2011). In this study, juvenile and sub-adult schoolmaster snapper had a larger niche width and relatively higher degree of individual specialization in 2008-09, suggesting the occurrence of the latter scenario (#2 above). These niche differences were mostly driven by juveniles and sub-adults presumably feeding on prey at different trophic levels, as suggested by the more variable $\delta^{15}N$ range of juvenile and sub-adult snappers in 2008-09.

Underlying factors driving changes in niche width and degree of individual specialization between years could have been related to temporal changes in the relative degree of intraspecific competition and/or resource abundance. For instance, several empirical studies found that niche width and magnitude of individual specialization increased with population density (a proxy for intraspecific competition; Svanbäck and Persson 2004, Svanbäck et al. 2008, Svanbäck and Persson 2009, Frederich et al. 2010). In the present example, varying recruitment rates of schoolmaster snapper between years may have driven different population densities. In addition, seagrass productivity might have fluctuated between years (Fourqurean et al. 2001), which could have affected prey abundance. Additional research is needed to explore mechanisms which drive niche variation in these systems.

Some other factors might have affected the findings of my study. For example, variation in stable isotope ratios between juvenile and sub-adult schoolmaster snapper could also have been driven by differences in isotopic turnover rates (i.e., renewal process of molecules in a given tissue commonly measured when half of the tissue composition has changed; Martinez del Rio et al. 2009) between the two size classes, rather than a shift in resource use. Some studies have shown that turnover rates of $\delta^{13}C$ and $\delta^{15}N$ can change with body size in fishes, with smaller individuals having faster turnover rates as a result of higher growth rates or increased metabolic rates (Hesslein et al. 1993, Suring & Wing 2009). Yet, my stomach content data corroborate the isotope pattern of a shift in resource use between juvenile and sub-adult schoolmaster snapper, especially in 2008-09 (Table 5, Fig. 3). Another potential study limitation could have been the low resolution of the taxonomic identification level of teleosts in the stomach content analysis, especially because teleosts were an important component of the schoolmaster diet (Fig. 3). My stable isotope analysis, however, supports the stomach content findings that schoolmaster snapper increasingly were relaying on teleosts in their diet (Figs. 2 and 4). Lastly, potential spatial and temporal variability in isotopic values of primary producers could also have affected my isotopic findings (Fourqurean et al. 2005, Fourqurean et al. 2007). Yet, patterns found on the basis of stable isotope analysis were greatly confirmed by stomach content analysis. Consequently, although my findings might have been affected by the limitations of stable isotope and stomach content analyses (Votier et al. 2003, Newsome et al. 2007, Layman & Post 2008), my results of these two methods are largely consistent and thus suggest real ecological patterns.

I show that schoolmaster snapper do not use resources homogeneously, and offer a framework that illustrates how to investigate several levels of intrapopulation resource variation. Specifically, my study demonstrates that the combined use of stable isotope and gut content analysis can be very powerful in providing in-depth insights on resource use (Layman & Post 2008). My study also provides additional evidence of the need to change the common management perspective that populations consist of homogeneous individuals (Hammerschlag-Peyer & Layman 2010). The incorporation of intrapopulation resource variability in population models has the potential to help generate and improve management strategies.

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Table 1: Sample size of stable isotope analysis of fin tissue of individual schoolmaster snapper (*Lutjanus apodus*)

Season	Juveniles	Sub-adults	Total
Wet 07	16	41	57
Dry 08	15	18	33
Wet 08	10	17	27
Dry 09	20	13	33
Total	61	89	150

Table 2 Results of stepwise one-way ANOVA on $\delta^{13}C$. Bold *P*-values indicate statistically significant findings ($P < 0.05$). For each test, df = 1

Step	Grouping factor	Factor analyzed	F	*P*
1	none	Year	1.0	0.32
1	none	Season	3.3	0.07
1	none	Size Group	18.0	**< 0.001**

Table 3 Results of stepwise one-way Kruskal-Wallis analysis on $\delta^{15}N$. Bold *P*-values indicate statistically significant findings ($P < 0.05$). For each test, df = 1

Step	Grouping factor	Factor analyzed	U	*P*
1	none	Year	4558	**< 0.001**
1	none	Season	1978	**0.003**
1	none	Size Group	1538	**< 0.001**
2	Year (07-08)	Season	742	0.10
2	Year (07-08)	Size Group	620	**0.01**
2	Year (08-09)	Season	330	0.12
2	Year (08-09)	Size Group	156	**< 0.001**

Table 4: Sample size of gut contents in schoolmaster snapper (*Lutjanus apodus*)

Season	Juveniles	Sub-adults	Total
Wet 07	20	45	65
Dry 08	39	14	53
Wet 08	40	27	67
Dry 09	66	10	76
Total	165	96	261

Table 5 Results of stepwise one-way χ^2 analysis on gut content data. Bold *P*-values indicate statistically significant findings ($P < 0.05$). For each test, df = 6

Step	Grouping factor	Factor analyzed	χ^2	*P*
1	none	Year	12.9	**0.04**
1	none	Season	11.3	0.08
1	none	Size Group	18.7	**0.005**
2	Year (07-08)	Size Group	5.6	0.47
2	Year (08-09)	Size Group	17.7	**0.007**

Table 6: $\delta^{13}C$ values, $\delta^{15}N$ values and sample size (n) for prey items used in the individual specialization model (see text for more detail)

Prey Category	Mean $\delta^{13}C$	Mean $\delta^{15}N$	n
Teleost	-13.25	6.09	32
Panopeus	-14.33	3.52	12
Aratus	-20.40	2.90	6
Xanthoidea	-13.62	2.58	5
Alpheus	-12.70	3.65	5
Palaemonetes	-13.36	5.38	8
Farfantepenaeus	-10.27	4.49	3
Total			71

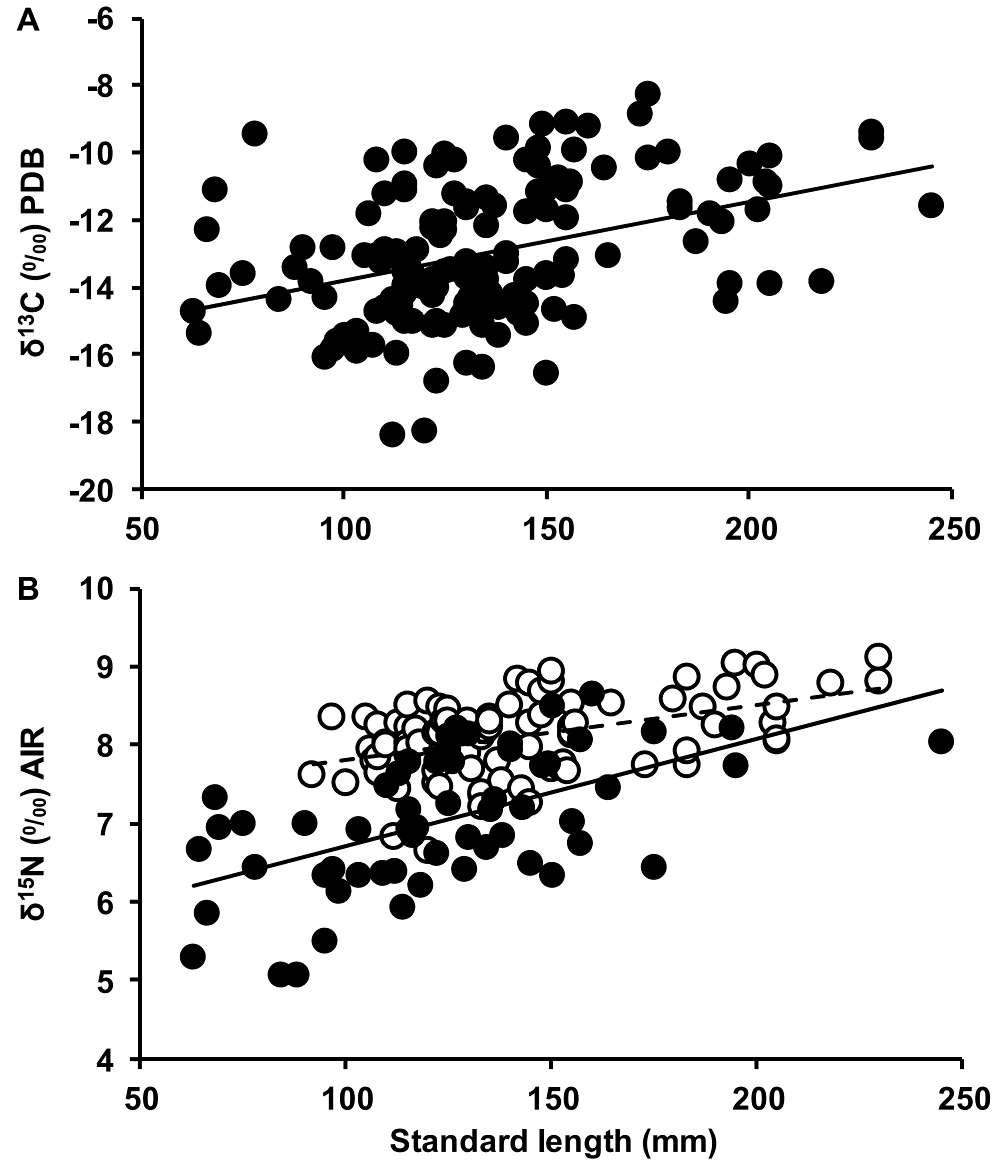

Fig. 1: Significant linear regression between body size (i.e., standard length) and A) δ^{13}C ($R^2 = 0.16$, $P < 0.0001$, n = 150) and B) δ^{15}N values. In panel B, open circles represent δ^{15}N of individual schoolmaster snapper for 2007-08 ($R^2 = 0.22$, $P < 0.0001$, n = 90; dashed trendline), and closed circles indicate snapper in the year 2008-09 ($R^2 = 0.32$, $P < 0.0001$, n = 60; solid trendline). PDB (PeeDee belemnite) and AIR (atmospheric nitrogen) are the global standards of δ^{13}C and δ^{15}N, respectively

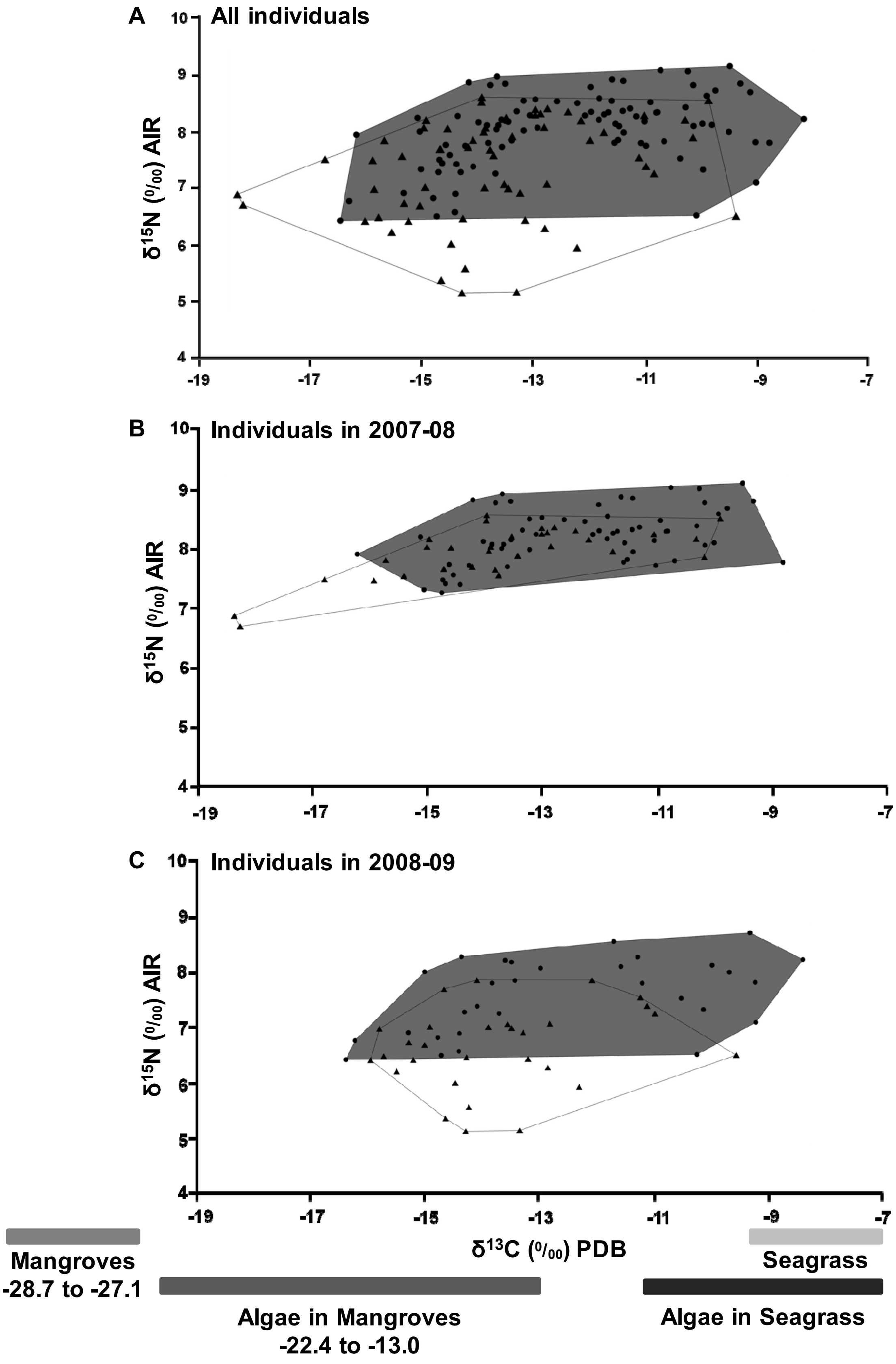
A
All individuals
B
Individuals in 2007-08
C
Individuals in 2008-09
δ15N (0/00) AIR
10
9
8
7
6
5
4
-19
-17
-15
-13
-11
-9
-7
δ13C (0/00) PDB
Mangroves
-28.7 to -27.1
Algae in Mangroves
-22.4 to -13.0
Seagrass
Algae in Seagrass

Fig. 2 Niche width (estimated using minimum convex polygon, MCP) of juveniles (white) and sub-adults (gray) of schoolmaster snapper *Lutjanus apodus* represented in a δ^{13}C-δ^{15}N niche space. Triangles represent isotope data of individual juveniles and circles individual sub-adults. A) includes all individuals from both sampling years, B) from 2007-08, and C) from 2008-09. The δ^{13}C ranges of primary producers are represented by gray bars below the x–axis in Panel C and are on the basis of stable isotope data from Bahamian primary producers in similar study systems (Kieckbusch et al. 2004). PDB (PeeDee belemnite) and AIR (atmospheric nitrogen) are the global standards of δ^{13}C and δ^{15}N, respectively

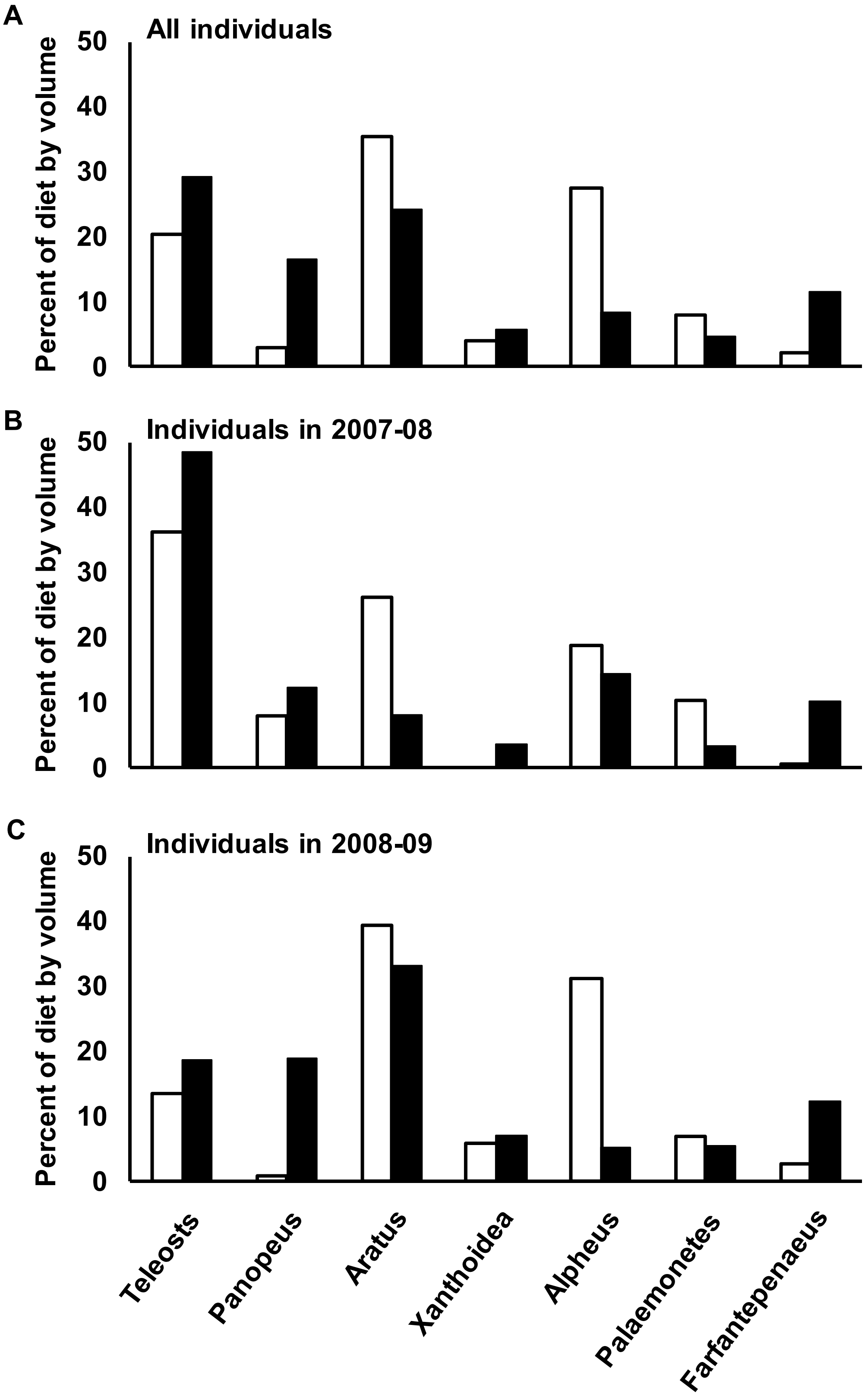
A
All individuals
B
Individuals in 2007-08
C
Individuals in 2008-09
Percent of diet by volume
0
10
20
30
40
50
Teleosts
Panopeus
Aratus
Xanthoidea
Alpheus
Palaemonetes
Farfantepenaeus

Fig. 3 Percent of diet by volume in individual stomachs of A) all schoolmaster snapper (pooled across years), B) schoolmaster snapper in 2007-08, and C) in 2008-09. White bars represent stomach contents of juveniles and gray bars of sub-adults. *Panopeus* and *Aratus* are a crab genera, Xanthidoidae a crab superfamily, while *Alpheus*, *Palaemonetes* and *Farfantepenaeus* are shrimp genera

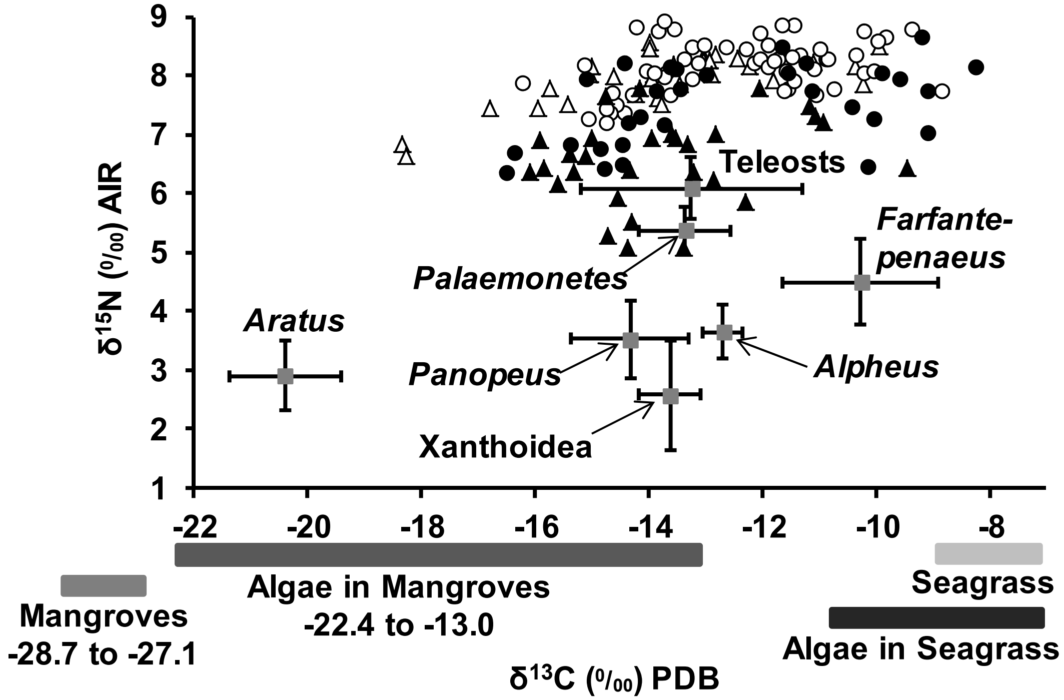

Fig. 4 Stable isotope data of prey taxa (mean value; gray squares), as well as individual juvenile (triangles) and sub-adult (circles) schoolmaster snapper sampled during the sampling year of 2007-08 (white symbols) and of 2008-09 (black symbols) represented in a δ^{13}C-δ^{15}N niche space. For the teleost group, I used frillfin goby (n=8), crested goby (n=3), banded goby (n=1), and rosy blenny (n=1). Error bars represent standard deviation of prey taxa stable isotope values. The δ^{13}C ranges of primary producers are represented by gray bars below the x–axis according to stable isotope data from Bahamian primary producers (Kieckbusch et al. 2004). PDB (PeeDee belemnite) and AIR (atmospheric nitrogen) are the global standards of δ^{13}C and δ^{15}N, respectively

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CHAPTER IV

A HYPOTHESIS-TESTING FRAMEWORK FOR STUDIES INVESTIGATING ONTOGENETIC NICHE SHIFTS USING STABLE ISOTOPE RATIOS

Abstract

Ontogenetic niche shifts occur across diverse taxonomic groups, and can have critical implications for population dynamics, community structure and ecosystem function. Most studies that have used stable isotope ratios to examine ontogenetic niche shifts applied qualitative methods, or quantitative approaches that analyzed isotope elements separately. Yet, multivariate analyses are beneficial in identifying the nature of dietary shifts through ontogeny because they can provide an enhanced understanding of changes in niche width, niche position and niche overlap, which are important factors in investigating changes in resource use. Herein, I provide a hypothesis-testing framework combining univariate and multivariate analyses to examine ontogenetic niche shifts using stable isotope ratios. The framework is founded on three main ontogenetic niche shift scenarios. For identifying each ontogenetic niche shift scenario, I developed specific criteria, as well as provided an empirical example for illustration purposes. The present framework provides a foundation for future studies on ontogenetic niche shifts and can also be applied to examine resource variability among other population groupings (e.g., by sex or phenotype).

Introduction

Changes in resource use with body size or age, i.e., ontogenetic niche shifts, may occur in 80% of animal taxa (Werner & Hall 1988) and have been shown to affect the structure and dynamics of populations, communities and ecosystems (Werner & Hall 1988, Polis & Strong 1996, Claessen et al. 2002). For instance, species often feed at higher trophic levels as they mature (Stein et al. 1988, Polis et al. 1989) and thus, interactions with other species may shift from competition to predation through ontogeny (Persson 1988, Olson et al. 1995). Many organisms increase their foraging range with ontogeny (Minns 1995), thereby changing the nature of nutrient and energy flow through different habitats or ecosystems (Subalusky et al. 2009). Finally, ontogenetic niche shifts may render life stages as functionally distinct groups that should be considered as distinct nodes in food web models (Olson 1996). Hence, the study of ontogenetic niche shifts is of core interest in the ecological sciences.

In a classic paper, Werner and Gilliam (1984) proposed three possible scenarios for how organism's resource use (e.g., diet, habitat use) may (or may not) change through ontogeny. First, a consumer may have no substantial ontogenetic changes in resource use (Fig. 1A, 1D). Second, the niche of a smaller size class may be a subset of the niche of a larger size class, e.g., because larger individuals expand their foraging range and incorporate prey items that smaller individuals do not encounter (Fig. 1B, 1E). Finally, consumers may switch to a different resource pool during ontogenetic development (Fig. 1C, 1F). Ontogenetic differences in resource use therefore will translate into changes in niche width, niche position and/or niche overlap between size groups. As such, measures of niche width, niche position and niche overlap can be used to distinguish among these different ontogenetic niche shift scenarios.

Stable isotope analysis often is applied to investigate ontogenetic niche shifts because they provide a time- and space-integrated representation of diet and/or are useful for those organisms whose diets are difficult to characterize directly (Hentschel 1998). The majority of diet studies have employed stable isotope ratios of carbon (i.e., $\delta^{13}C$) and nitrogen (i.e., $\delta^{15}N$), as they provide information related to a consumer's basal resource pool and trophic position, respectively (Peterson & Fry 1987, Newsome et al. 2007). Most studies using stable isotopes to examine ontogenetic changes in diet rely on qualitative observations or analyze $\delta^{13}C$ and $\delta^{15}N$ separately, either against a continuous body size gradient (e.g., regression analysis; Rolff 2000, Cocheret de la Morinière 2003, Post 2003) or among size/age groups (e.g., t-test, analysis of variance; Quevedo & Olsson 2006, Zimmerman et al. 2009, Young et al. 2010; Fig. 1A-C). Yet, recent food web studies have shown the power of simultaneously analyzing $\delta^{13}C$ and $\delta^{15}N$ to better characterize overall patterns in niche variation (Layman et al. 2007b, Semmens et al. 2009, Turner et al. 2010, Jackson et al. 2011).

My aim was to provide a single hypothesis-testing framework to examine the ontogenetic niche shift scenarios outlined by Werner and Gilliam (1984) using stable isotopes. My proposed framework incorporates both univariate and multivariate analyses to investigate shifts in niche width, niche position and niche overlap through ontogeny. I developed specific criteria characterizing each ontogenetic niche shift category and provide empirical examples to illustrate each of them.

Materials and Methods

I evaluated three aspects of the niches of size classes through ontogeny, including (1) niche width (variety in resources consumed), (2) niche position (i.e., types of resources consumed), and (3) niche overlap (similarity in resource use among individuals). I examined changes in niche width and niche position through ontogeny using multivariate analyses (see below). If niche width and/or niche position were found to differ through ontogeny, conventional univariate tests were performed to elucidate which niche axis (e.g., $\delta^{13}C$, $\delta^{15}N$) drove the observed niche shift (Fig. 1). For example, ontogenetic shifts in $\delta^{13}C$ values could indicate dissimilar use of habitats or source pools by different size groups (Rounick & Winterbourn 1986, Peterson & Fry 1987, France & Peters 1997, Layman 2007), whereas changes in $\delta^{15}N$ values typically imply a shift in trophic position (DeNiro & Epstein 1981, Minagawa & Wada 1984, Peterson & Fry 1987). I then measured niche overlap between size groups in a two-dimensional niche space (i.e., $\delta^{13}C$-$\delta^{15}N$-biplot space) using a % overlap measure (Vaudo & Heithaus 2011). Niche width, niche position and niche overlap are important aspects to identify ontogenetic niche shifts and can be used to classify an organism into one of the three categories proposed in the classic paper of Werner and Gilliam (1984).

The criteria for the first ontogenetic niche shift scenario, involving no change in diet through ontogeny are: no significant difference in (1) niche width and (2) niche position, imparting (3) high degree of overlap in individuals' isotope values (Figs. 1A, 1D, 2). For the second scenario, resource use (i.e., diet or habitat use) is larger in one group than in the other, resulting in (1) significant difference in niche width and (2) potentially a change in mean niche position. More specifically, the isotopic niche width of one group is statistically larger than that of the other and the niche of the latter group is largely encompassed by the former, leading to (3) an asymmetry in niche overlap (Figs. 1B, 2). Niche position may or may not differ between groups, depending on whether resource expansion takes place from the center of the isotopic niche space (no niche shift) or is directed away from that center (Figs. 1B, 1E, 2). For the third scenario, involving a discrete ontogenetic diet shift, (1) niche width of one group can either be the same, smaller or larger than the other (Fig. 1C, 1F), and (2) there is a significant shift in niche position, resulting in (3) little or no overlap in isotopic niche (Figs. 1C, 1F, 2).

I used empirical data to illustrate these different niche shift scenarios. I chose these examples specifically to illustrate the methodological framework discussed herein, and not as independent tests of the nature of niche shifts in these particular taxa. For these taxa, direct diet data (or in one case, published diet information) were collected to further help me characterize and understand niche variation. Post-metamorphic *Eupemphix nattereri* frogs (i.e., no tadpoles), gray snapper (*Lutjanus griseus*) and hardhead silversides (*Atherinomorus stipes*) constituted the model species.

Post-metamorphic *Eupemphix nattereri* specimens were collected from an area of Brazilian savannahs locally known as Cerrado in the municipality of Uberlândia (18º55' S, 48º17' W) in southeastern Brazil, a region characterized by shrubby grassland areas surrounding wet areas such as *veredas* (marshes with buriti-palms *Mauritia flexuosa*) or temporal and permanent ponds. Frogs were collected from October 1999 to October 2001 and immediately killed upon collection, preserved in 5% formalin and later transferred to 70% ethanol. Since all individuals were preserved in the same manner, differences in isotope values among individuals should have not been affected by preservatives (Araujo et al. 2009). Gut content analysis was performed via dissection and prey items were counted and identified to the lowest taxonomic level. Upon dissection, individuals were sexed by examination of gonads and classified as adults if the gonads were fully developed (reproductive) or as juveniles if gonads were underdeveloped (non-reproductive). After preservation, a piece of muscle was used from the thigh to measure $\delta^{13}C$ and $\delta^{15}N$ (Araujo et al. 2009).

Gray snapper (*Lutjanus griseus*) were collected in the Loxahatchee River (26°57' N, 80°06' W) located on the southeast Atlantic coast of Florida, USA. Snappers were caught during the summers of 2007 – 2009 by angling and electrofishing in the mesohaline areas of the river. Fish were anesthetized using eugenol (i.e., clove oil in sea water; Cotter & Rodruck 2006) and their standard length was measured. Each individual was forced to regurgitate their stomach contents by pressing on the abdomen while using a metal spatula to help invert the stomach. A small sample (~1cm^2) of dorsal fin tissue was taken from each fish for stable isotope analysis. After sampling their stomach contents, fish were returned to cool, fresh, ambient water and allowed to recover before being released. Since the size range of *L. griseus* in the Loxahatchee River does not include reproductively mature adults, I *a priori* divided the individuals into juveniles (<100 mm SL) and sub-adults (≥100 mm SL) according to observed differences in habitat use between these two life-history stages (Hammerschlag & Serafy 2009).

Hardhead silversides (*Atherinomorus stipes*) were collected with cast-nets in a tidal creek (26°21'36.58"N, 77°00'58.91"W) on Abaco Island, Bahamas on November 15th 2009. This creek is lined by mangroves (primarily red mangrove, *Rhizophora mangle*) and supports extensive seagrass beds predominantly consisting of turtle grass, *Thalassia testudinum*. The creek is dominated by marine waters with relatively little topographic relief, a small watershed, and little freshwater input (Layman et al. 2007b). All captured individuals were immediately put on ice and later frozen. The whole organism was used for stable isotope analysis. Diet information of *A. stipes* was obtained by Boveri and Quiros (2002). On the basis of gonad inspections, *A. stipes* was divided into juveniles (underdeveloped gonads) and adults (fully developed gonads).

I focused on ratios of $\delta^{15}N$ and $\delta^{13}C$ because each reveals a distinct aspect of the consumer's long-term trophic niche (see above). Stable isotope values are reported in the δ notation where $\delta^{13}C = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$, and where R is $^{13}C/^{12}C$ and $^{15}N/^{14}N$, respectively. Isotope sample preparation and analysis followed Post et al. (Post et al. 2007) and was conducted at the Yale Earth System Center for Stable Isotopic Studies using a ThermoFinnigan DeltaPlus mass spectrometer (for *Lutjanus griseus* and *Atherinomorus stipes*) and at the Centro de Energia Nuclear na Agricultura of the Universidade de São Paulo using a Micromass 602E mass spectrometer (for *Eupemphix nattereri*).

To evaluate which model species met the criteria for one of the ontogenetic niche shift scenarios, I performed multivariate analyses, using $\delta^{13}C$ and $\delta^{15}N$ simultaneously, and "post-hoc" univariate analyses, separately on $\delta^{13}C$ and $\delta^{15}N$. For the multivariate analyses, I first examined significant differences in (1) niche width and (2) niche position between the two groups, and then (3) niche overlap (Fig. 2). To do so, I performed a test for differences in dispersion and central tendency, respectively, following Turner et al. (2010) in R version 2.12.2. In the context of this study, difference in dispersion represents a change in niche width because this metric measures the average trophic variability within size groups. More precisely, using analysis of nested linear models and residual permutation procedure, the mean distance to centroid (bivariate mean) was computed for each size group separately, and then the absolute value of the difference was evaluated between size groups. An absolute value greater than zero indicates a difference in niche width between size groups (Turner et al. 2010). Similarly, the difference in central tendency represents a shift in isotopic niche position and was measured by computing the Euclidean distance between the centroids of the two groups (Turner et al. 2010). The isotopic niche position was considered to be different if the Euclidean distance between the two groups was significantly greater than zero (R codes for the test of dispersion and central tendency are provided in the Appendix of Turner et al. 2010). The test statistics for dispersion and central tendency are herein referred to as “mean distance to centroid” and “Euclidean distance”, respectively.

Conventional univariate analysis was applied after significant results from multivariate analysis to provide additional detail. To this end, I first tested all data for normality (Shapiro-Wilk test) and square-root transformed them when applicable. Then, I examined shifts in niche width and niche position for each stable isotope element by measuring (1) homogeneity of variance between size groups using Bartlett test and (2) by comparing mean isotopic values between size groups using t-test for independent samples (for normally distributed data) or Wilcox test (for non-normally distributed data). All tests were performed in R version 2.12.2. Significance was declared at $\alpha \leq 0.05$.

I measured niche overlap between groups by quantifying, for each group, the percentage of individuals that were encompassed by the other group’s convex hull

(Vaudo & Heithaus 2011), which is the area of the smallest convex polygon that contains all individuals of a group in a $\delta^{13}C$-$\delta^{15}N$-biplot (Figs. 1, 3) (Layman et al. 2007a).

Since for many organisms body size is more important in determining life history characteristics than age per se (Kirkpatrick 1984), I used body size as a proxy for ontogenetic stage. More specifically, I used categorical size groups instead of continuous body size data (Fig. 1). Yet, for the univariate analyses, my framework could easily be applied to a continuous body size gradient using linear regression (to test for non-zero slope, instead of comparing means between groups) when examining shifts in niche position and testing for changes in niche width with body size (instead of between groups). When categorical size groups are used, biologically meaningful size classes should be chosen (as in this study), or a break point analysis (Gomez & Gomez 1984) could be performed, to determine the size at which change in resource use occur.

Finally, the convex hull approach offers some advantages for characterizing niche width when compared to alternative analyses. The convex hull approach is powerful because it incorporates each individual of the population’s sub-sample, and thus includes information about the niche width of the population including every sampled individual. Conversely, other approaches are targeted at identifying the “core” niche of the population, a niche metric which could exclude particular individual niches from the characterization of the population niche (Jackson et al. 2011). Either of these approaches may be more relevant with respect to a particular question of interest and/or the nature of the underlying data set. Herein, I chose to measure niche overlap on the basis of the convex hull approach, as the importance of individual level niche variation is increasingly recognized as an important component of ecological dynamics and evolutionary trajectories (Bolnick et al. 2003, Bolnick et al. 2011).

Results

For the illustration of the first ontogenetic niche shift scenario, I used 25 post-metamorphic juveniles (size range: 13-33mm Snout-Vent Length (SVL)) and 26 adults (size range: 34-47mm SVL) of *E. nattereri.* Juvenile and adult *E. nattereri* did not statistically differ in their (1) niche widths (mean distance to centroid = 0.08, *P* = 0.87), and (2) isotopic niche position (Euclidean distance = 0.41, *P* = 0.58; Fig. 3A). Thus, (3) individuals of both groups overlapped substantially with each other (juveniles = 92% overlap with adults, adults = 85% overlap with juveniles, Fig. 3A).

For the illustration of the second ontogenetic niche shift scenario, juvenile (n = 31, size range: 40-96mm Standard Length (SL)) and sub-adult (n = 89, size range: 101-204mm SL) *L. griseus* differed significantly in their (1) niche width (mean distance to centroid = 1.22, *P* = 0.006, Fig. 3A), which was driven by a difference in variance of δ^{13}C values (Bartlett: K^2 = 10.37, df = 1, *P* = 0.001), not δ^{15}N (Bartlett: K^2 = 1.07, df = 1, *P* = 0.3). There was no shift in (2) isotopic niche position (Euclidean distance = 0.94, *P* = 0.13; Fig. 3B) and (3) most juvenile *L. griseus* overlapped with the niche width of sub-adults (97% of individuals), whereas only 35% of sub-adults were encompassed by the convex hull of the juveniles (Fig. 3B).

For illustration of the third ontogenetic niche shift scenario, juveniles (n = 16, size range: 23-35mm SL) and adults (n = 14, size range: 40-61mm SL) of *A. stipes* differed significantly in (1) niche width (mean distance to centroid = 0.51, *P* = 0.01; Fig. 3C), which was mainly caused by differences in variance of $\delta^{15}N$ (Bartlett: $K^2 = 10.6$, df = 1, $P = 0.001$), but also by $\delta^{13}C$ (Bartlett: $K^2 = 3.85$, df = 1, $P = 0.05$). In addition, the (2) isotopic niche position changed significantly between juvenile and adult *A. stipes* (Euclidean distance = 1.5, $P < 0.0001$; Fig. 3C), which was driven by a change in their mean $\delta^{15}N$ values (Wilcox: W = 224, $P < 0.001$), but not mean $\delta^{13}C$ values (t-test: t = 0.29, df = 20.3, $P = 0.77$). Consequently, (3) no individuals were encompassed by the convex hull of the other group (Fig. 3C).

Discussion

Because of the significant effects ontogenetic niche shifts can have on the structure and dynamics of populations, communities and ecosystems, it is important to identify the nature of these dietary shifts using quantitative techniques (Werner & Hall 1988, Polis & Strong 1996, Claessen et al. 2002). Stable isotope analysis is especially useful for this purpose because of its time- and space-integrated representation of diet. Yet, most studies using stable isotope ratios have examined ontogenetic niche shifts either qualitatively or by analyzing stable isotope elements separately (Landman et al. 1983, Mueller-Lupp et al. 2003, Post 2003, Lukeneder et al. 2010, Taylor & Mazumder 2010). My study provides a hypothesis-testing framework to investigate ontogenetic niche shifts in organisms by applying univariate and multivariate analyses simultaneously on stable isotope elements. In doing so, I provide a foundation for exploring the three major categories of ontogenetic niche shifts originally outlined by Werner and Gilliam (1984) in their review of ontogenetic niche shifts.

Post-metamorphic juveniles and adults of *E. nattereri* illustrate the first ontogenetic niche shift scenario: there were no differences in niche width, niche space or niche overlap between the two size groups (Fig. 3A). Since frogs grow substantially after metamorphosis to reach adult size, they could be expected to experience considerable diet shifts during the terrestrial phase of their life cycle, but this was not found to be the case here. Stomach content analysis supported the isotope findings by showing that both juvenile and adult *E. nattereri* tend to specialize on ants and termites (Araujo et al. 2009). Since stable isotope ratios of muscle tissue represent diet over a long time period (weeks to months, Sweeting et al. 2005), it can be inferred that the observed diet specialization was long-term, and not just driven by local prey availability at the time of sampling (an advantage of stable isotope analysis over stomach content analysis, Araujo et al. 2007).

Gray snapper illustrate the second ontogenetic niche shift scenario: sub-adult *L. griseus* expanded their isotopic niche to include diet items with more depleted $\delta^{13}C$ values (Fig. 3B). Direct diet analysis confirmed that the feeding of juvenile *L. griseus* was essentially confined to the oyster reef matrix of the Loxahatchee River, where their diet was composed almost entirely of oyster reef-associated prey items. Conversely, sub-adult *L. griseus* move to the adjacent mangrove habitats to feed on mangrove-associated prey (Yeager & Layman 2011). Prey items in oyster reef habitats are largely supported by microalgae- and phytoplankton-based trophic pathways that are more enriched in $\delta^{13}C$ values (~ -18 $^{0}/_{00}$), whereas prey from mangrove-based food web modules are more depleted ($\delta^{13}C$ ~ -27 $^{0}/_{00}$) (Kieckbusch et al. 2004, Yeager & Layman 2011). Sub-adults most likely increased their foraging area because of decreased predation pressure or increased mobility because of larger body size (Werner & Hall 1988). Such foraging and predation risk trade-offs and/or increase in mobility with body size can drive many ontogenetic niche shifts, and stable isotope ratios can be a prime tool to reflect such long-term feeding shifts when isotopic signatures of sources are distinct.

Juvenile and adult *A. stipes* displayed a distinct niche shift, mainly along the δ^{15}N axis (Fig. 3C). Since *A. stipes* is a visual feeder that actively selects zooplankton (Boveri & Quiros 2002), no major ontogenetic niche shifts would be expected for that species. Yet, my stable isotope data suggest that adults likely fed exclusively on larger-sized zooplankton prey, as larger zooplankton are often more enriched in δ^{15}N (Rolff 2000). Since adult and juvenile *A. stipes* share the same resources (i.e., habitat and diet), adults might shift to larger prey sizes as a means to reduce intrapopulation niche competition (Bolnick et al. 2003).

My empirical examples highlight the benefit of using both univariate and multivariate measures, as each was useful to identify different aspects of the niche differences. For example, in the case of gray snapper, multivariate approaches were useful in identifying degree of niche width and niche overlap, whereas univariate analysis was important to elucidate niche expansion in the larger size group primarily along the carbon axis. It would be difficult to differentiate among the three major niche shift scenarios by using univariate analyses alone (Fig. 1D-F).

When applying the proposed framework, it is important to consider that the three ontogenetic niche shift scenarios outlined in this study should be understood as endpoints of a continuum. Some organisms might fall between two of the proposed scenarios. Yet, my framework will allow for the identification of such “in-between scenarios” as well. In addition, the much discussed limitations of isotopes must be considered when interpreting their application to study ontogenetic diet shifts (Newsome et al. 2007, Layman & Post 2008). For instance, source pools need to have distinct isotopic signatures for stable isotopes to be useful, and δ values can be particularly sensitive to spatial and temporal variation in isotope values of source pools (Newsome et al. 2007). As such, scattering among consumers in a δ^{13}C-δ^{15}N biplot could be the result of a broad resource use among individuals, or because of high variation in isotope values of source pools (Matthews & Mazumder 2004). To avoid this problem, Newsome et al. (2007) proposed to convert the "δ-space" (e.g., δ^{13}C-δ^{15}N biplot space) into "p-space" according to dietary proportions of different isotopic sources using mixing models. However, in order for the mixing models to work, the study system can have only one more source pool than the number of isotopes used (Phillips & Gregg 2001). Since most study systems, such the ones from which my example taxa were collected, have many more than two or three source pools, this p-space approach is not applicable. Consequently, the use of a complimentary method such as stomach content analysis (as applied in this study), fecal analysis, or direct observations are useful to interpret and better understand patterns in isotope signatures. When stable isotope ratios are put in the proper context, they can be a very powerful tool (Layman & Post 2008) and provide insights that would not be possible with some conventional methods (Hentschel 1998).

Intrapopulation resource variation has critical ecological, evolutionary and conservation implications (Bolnick et al. 2003, Bolnick et al. 2011), and ontogenetic niche shifts are one primary driver of this variation (Bolnick et al. 2011). My approach provides a framework for exploring questions related to ontogenetic diet shifts, as well as other among-group (e.g., sex or phenotype) comparisons. Such studies are critical for understanding interactions among individuals at population, community and ecosystem levels.

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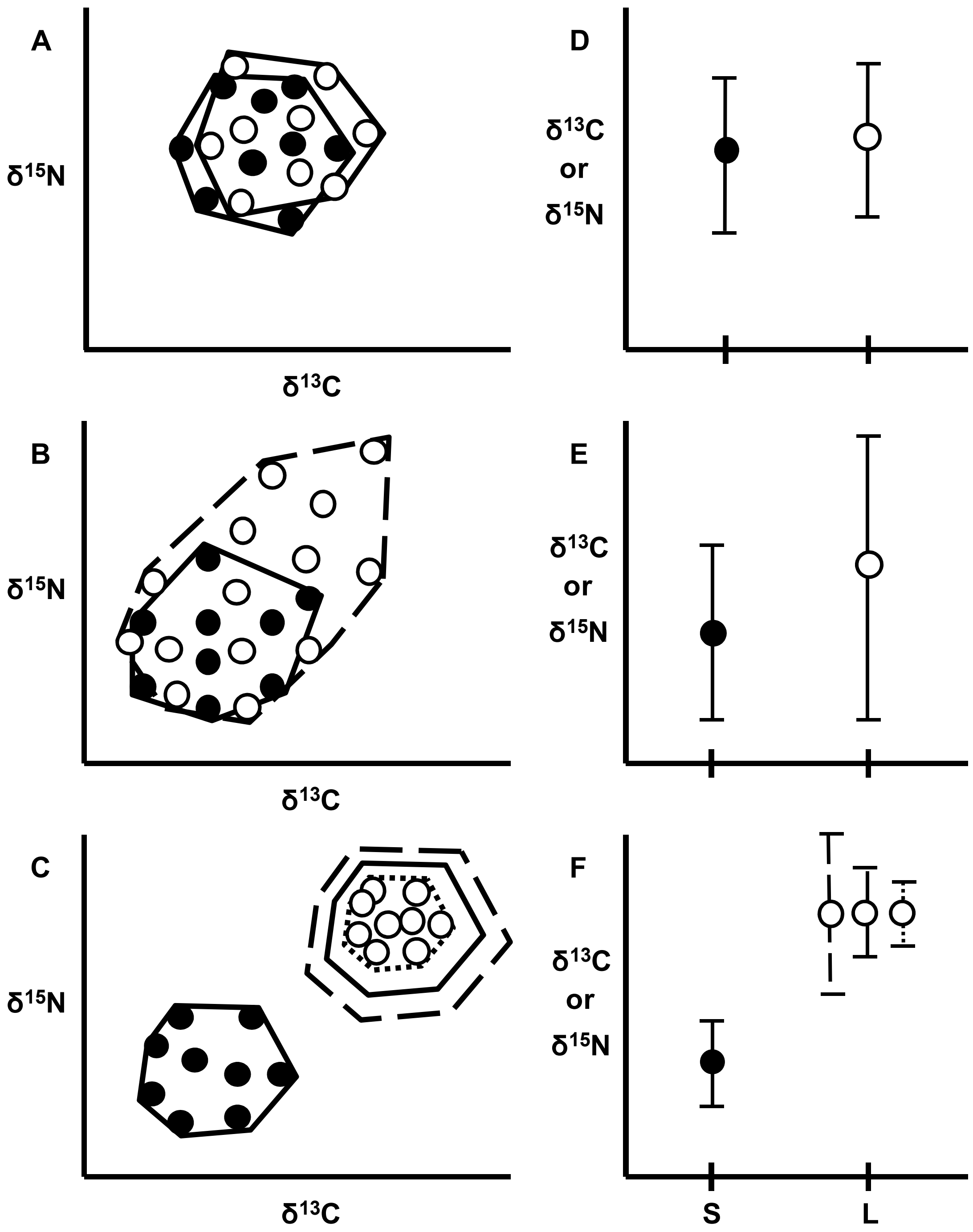


Fig. 1 Representation of three possible ontogenetic niche shift scenarios using stable isotope ratios. Horizontally adjacent panels represent the same ontogenetic niche shift

scenario. (A-C) Multivariate illustration of potential differences in niche width (represented by convex hull polygons), niche position and niche overlap (see text for more details) between two size groups in δ^{13}C-δ^{15}N niche space. (D-F) Univariate representation of niche width (variance of isotope values) and niche position (mean isotopic value) of either δ^{13}C or δ^{15}N between size groups. Closed circles represent isotope data of small individuals and open circles of large individuals. Solid line = constant niche width, dotted line = niche reduction, dashed line = niche expansion; S = small size group, L = large size group. In panel F, solid line = constant variance, dotted line = reduced variance, dashed line = increased variance

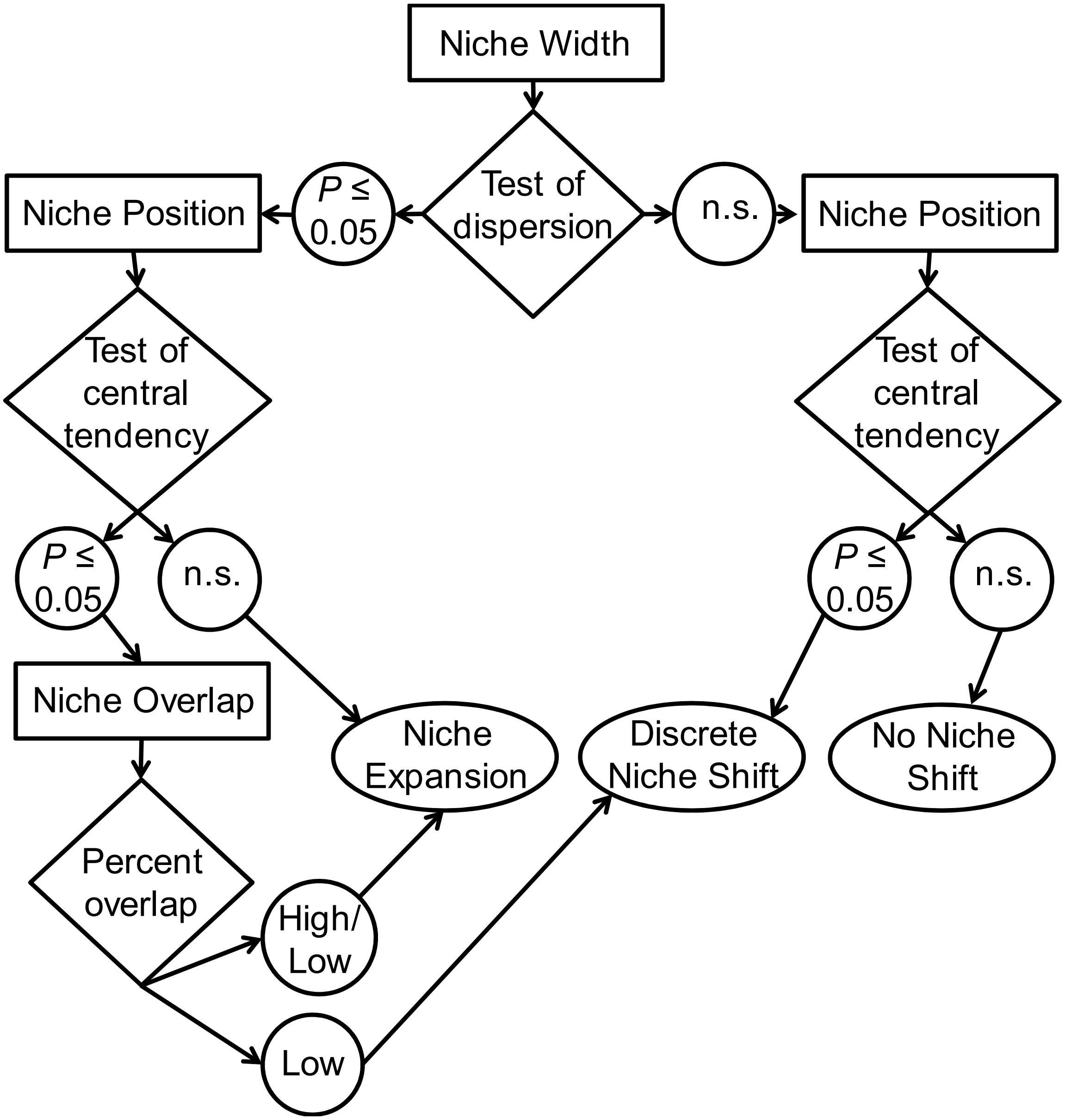
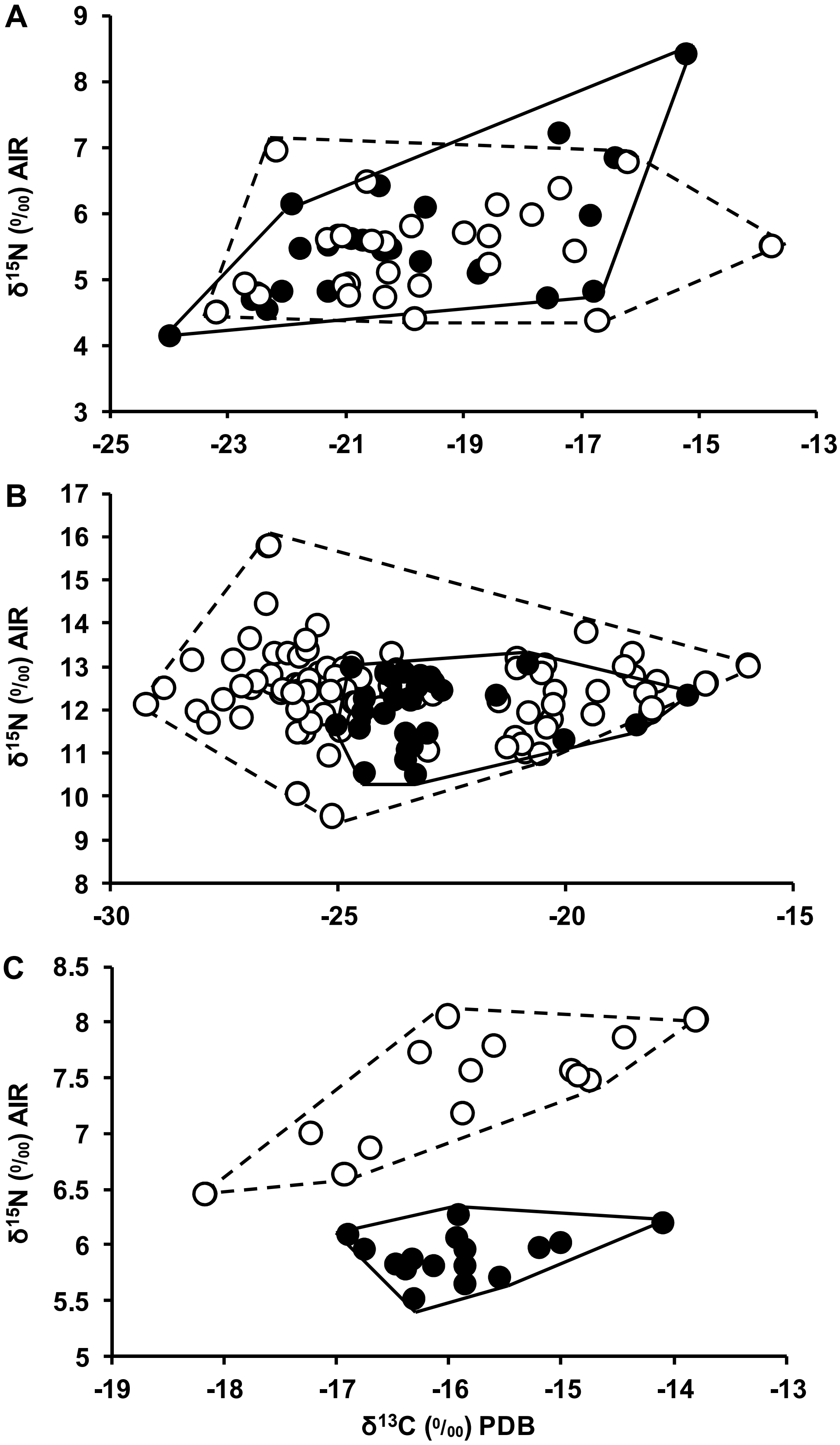


Fig. 2 Flow chart of the hypothesis-testing framework**.** Niche aspects (i.e., niche width, niche position, and niche overlap) are shown in rectangles, test types in diamonds, and possible test results in circles; n.s. = non-significant. The three possible scenarios are represented in ovals, with “No Niche Shift” = first scenario, “Niche Expansion” = second scenario, and “Discrete Niche Shift” = third scenario. Low = low niche overlap for both size groups; High/Low = asymmetric niche overlap between two size groups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δ13C (0/00) PDB

Fig. 3 Isotopic niche use of two ontogenetically distinct groups. Differences in niche width (for illustration purposes represented by convex hull polygons) of a small (solid line) and large (dashed line) size group of A) *Eupemphix nattereri,* B) *Lutjanus griseus,* and C) *Atherinomorus stipes* represented in a $\delta^{13}C$-$\delta^{15}N$ niche space. Closed circles represent isotope data of individual juveniles and open circles individual adults (or sub-adults in case of *L. griseus*). PDB (PeeDee belemnite) and AIR (atmospheric nitrogen) are the global standards of $\delta^{13}C$ and $\delta^{15}N$, respectively

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CHAPTER V

PREDATOR EFFECTS ON FAUNAL COMMUNITY COMPOSITION IN SHALLOW SEAGRASS BEDS OF THE BAHAMAS

Abstract

Over the past fifty years, much emphasis has been placed on predator effects that cascade through food webs. Such top-down effects are most common in systems with relatively simple food chains, and rather rare in species-rich systems where numerous interactions among species and high omnivory (feeding at >1 trophic level) typically buffer strong predator effects. Seagrass ecosystems are typically species-rich and are characterized by complex food webs, but evidence of top-down effects in these systems has been mixed. I examined the effect of predatory fishes on the species richness, total biomass, total density, and composition of the epifaunal community in a shallow seagrass system of The Bahamas. I used exclusion experiments at two different spatial scales, and applied mesh sizes that excluded different-sized predator individuals. My study found some evidence of species-level top-down effects (i.e., strong interactions within a subset of the community), driving higher biomass in some decapod mesopredators and overall lower species richness in the exclusion treatments than in the controls. In contrast, community-level predator effects were rather weak, with predator size and spatial scale of experiments displaying no detectable impact on the epifaunal community. Multiple factors may have contributed to these patterns such as species richness, omnivory, water depth, microhabitat features, as well as size range and abundance of predators. Because of the rapid global decline of seagrasses and their associated fauna, an increased knowledge of predator effects on faunal communities of seagrass beds are critical for conservation efforts.

Introduction

Over the past five decades, much emphasis has been placed on cascading effects of predators in food webs (Polis et al. 2000), and strong top-down effects have been observed in many aquatic ecosystems (Strong 1992). Often these systems are relatively simple, low-diversity food webs, with little omnivory or intraguild predation (Polis & Strong 1996, Chase 2000, Shurin et al. 2002, Bruno & O'Connor 2005, Finke & Denno 2005, Shurin et al. 2006, Fox 2007, Heck & Valentine 2007). Classic examples of strong top-down effects have been especially well studied in freshwater lentic and marine benthic systems, rocky intertidal zones and kelp forests (Paine 1966, Estes et al. 1998, Shurin et al. 2002). Species-rich ecosystems are less likely to have such strong top-down effects, largely because of the inherently reticulate food webs with many weak interaction links (Strong 1992, McCann et al. 1998).

Seagrass beds are species-rich ecosystems that provide food and shelter to numerous ecologically and economically important organisms (Orth et al. 1984, Beck et al. 2001). Evidence of predator effects in these ecosystems has been mixed, with some studies suggesting strong (Ambrose 1984, Heck et al. 2000, Hindell et al. 2000, Moksnes et al. 2008), and others weak to no top-down effects on faunal seagrass communities (Summerson & Peterson 1984, Leber 1985, Gacia et al. 1999, Hindell et al. 2001, Valentine et al. 2008, Moore & Hovel 2010). Predator effects in seagrass ecosystems have been suggested to be rather weak because other factors may play more important roles than predation, such as landscape context (i.e., the spatial position of a given patch within a larger mosaic of habitats or landscape features, Turner 1989) or structural complexity of seagrass beds (Orth et al. 1984, Summerson & Peterson 1984, Leber 1985, Rypel et al. 2007, Moore & Hovel 2010). In contrast, high local abundances of predatory fishes have been proposed to drive strong top-down effects in seagrass systems (Hindell et al. 2001).

In marine ecosystems, such as seagrass beds, predators can span broad ranges in body size (Costa 2009), which may be another factor determining the strength of top-down effects in these systems. In terrestrial, freshwater and temperate marine ecosystems, predator size has been shown to play an important role in regulating prey communities (Radloff & Du Toit 2004, Winkler & Greve 2004, Langlois et al. 2006, Rudolf 2006, Magnusson & Williams 2009, Perez et al. 2009). Consequently, the removal of different-sized predators would be expected to differently affect community structure and composition. For instance, in a marine food web, the removal of large-bodied predators has been shown to increase the abundance of mesopredators, which subsequently suppress the densities of their prey (Myers et al. 2007). As many seagrass-associated organisms are threatened by overexploitation and extinction (Hughes et al. 2009), it is critical to examine whether different-sized predators have divergent effects on seagrass communities.

I examined predator effects on the seagrass epifaunal community in a shallow Bahamian wetland system. I employed exclusion experiments at two different spatial scales, and utilized mesh sizes that excluded different-sized predator individuals. Specifically, I investigated how predatory fishes affected species richness, total biomass and density, and community composition of the epifaunal community. Given the high abundance of predatory fishes, especially schoolmaster (*Lutjanus apodus*) and gray snapper (*L. griseus*), in this study system, I hypothesized strong predator effects on epifaunal community. Furthermore, because these predators have been observed to shift their diet through ontogeny (Starck & Schroeder 1971, Hammerschlag et al. 2010, Hammerschlag-Peyer & Layman In Revision), I also hypothesized divergent responses between the two exclusion treatments that excluded different-sized predators.

Materials and Methods

I examined effects of predatory fishes using exclusion experiments at two spatial (and temporal) scales: 1) “small-scale” (i.e., 0.77 m^2 treatment area, 34 days), and 2) “medium-scale” (i.e., 19.6 m^2 treatment area, 77 days). On the basis of ecological theory, responses in the small-scale experiment would be expected to be driven predominantly by movements of epifaunal taxa (i.e., behavior mechanism) caused by indirect predator effects, while the medium-scale experiment more likely reflects changes in prey density because of direct predation (Englund 1997, Englund et al. 2001).

Both manipulations were conducted in the subtidal region of seagrass beds in Jungle Creek (26°21’36”N, 77°00’58”W, same area as descript in Stoner et al. 2011 as North Bight of Old Robinson), a seagrass- and mangrove-dominated tidal wetland, locally called “tidal creek”. This study site is located on the east side of Abaco Island, Bahamas and is ~40 hectares in size. Jungle Creek is lined by mangroves (predominantly *Rhizophora mangle*) and the most prevalent benthic habitat types are seagrass beds (primarily *Thalassia testudinum*), submerged mangrove prop roots and sand flats. The system has a semi-diurnal tidal regime and mean daily tidal amplitude of ~0.8 m; most of the area of the wetland has low tide depths <0.5 m. Consequently, fish predators were only able to access the seagrass beds twice daily for ~3-4 hours around high tide (depending on individual body size), and were restricted to deeper refuge areas, such as sink holes or mangrove-lined channels, during lower tidal levels (Hammerschlag-Peyer & Layman 2010).

The most abundant fish predators in Jungle Creek were schoolmaster (*Lutjanus apodus*) and gray snapper (*L. griseus*) (>90% of total predator biomass, Fig. 1) which are generalist species that have been observed to feed primarily on benthic invertebrates and small teleosts in these seagrass systems (Layman & Silliman 2002, Layman et al. 2007, Hammerschlag-Peyer & Layman In Revision). These species mostly consist of juveniles (schoolmaster: <12.5 cm standard length (SL); gray: <10 cm SL) and sub-adults (schoolmaster: 12.5-25 cm SL; gray: 10-20 cm SL; Hammerschlag et al. 2010, Yeager & Layman 2011, Hammerschlag et al. In Revision), likely because larger individuals move to deeper habitats, including coral reefs, as they grow (Nagelkerken et al. 2000, Sheridan & Hays 2003). Other epibenthic predators observed at the study site were cubera snapper (*L. cynopterus*), sergeant major (*Abudefduf saxatilis*), beaugregory (*Stegastes leucostictus),* blennies, slippery dick (*Halichoeres bivittatus*), mojarras (including *Gerres cinereus* and *Eucinostomus* spp.), and grunts (Haemulidae), all of which were far less abundant than schoolmaster and gray snapper. Jungle Creek is not adjacent to human settlements (Stoner et al. 2011) and thus, likely experiences little fishing pressure.

Four treatments were applied in both the small- and medium-scale experiment: unmanipulated control (UC), manipulated control (MC), small-predator exclusion (SPE) and large-predator exclusion (LPE). The SPE and LPE consisted of green plastic fence material (Landware$^{®}$) of 2 x 2 cm and 5 x 5 cm mesh size, respectively. Visual observations during the medium-scale experiment confirmed that SPE and LPE excluded different-sized fish predators (Fig. 1), yet allowed for free movement of most epibenthic fauna (e.g., small fishes, crabs, shrimps, snails, mussels). For example, schoolmaster snapper (*Lutjanus apodus*) ≤8 cm total length (TL) and gray snapper (*L. griseus*) ≤6 cm TL were observed feeding in the SPE treatment, whereas schoolmaster snapper ≤12 cm TL and gray snapper ≤16 cm TL were seen feeding in the LPE treatment (Fig. 1A,B). Individuals that were able to forage in the SPE treatment were considered to be too small to substantially affect the epifaunal community. Specifically, gray and schoolmaster snapper ≤8 cm and ≤6 cm TL, respectively, mostly feed on very small (<4 mm) epifaunal organisms (e.g., copepods, small caridean shrimps; Starck & Schroeder 1971) that were not sampled in this study (see below). MC treatments included approximately the same amount of fencing material with both mesh sizes, but had gaps on the sides (more details for each experiment below) allowing fish predators of all sizes to move freely in and out of the experimental area (Fig. 1C). UC treatments consisted of no "cage" material (i.e., no fencing or rebar stakes), but were comparable to the other treatments in terms of percent seagrass cover, distance to seagrass edge and water depth.

Small-scale experiment – I employed a randomized block design, with each block (n = 4) located ~50 m apart. The blocks were set up June 20th – 23rd 2008 (one block per day). Within each block, the four treatments (SPE, LPE, MC, and UC) were randomly assigned to four *a priori* identified sub-sites. The exact treatment locations specifically were selected in an attempt to minimize differences in water depth, distance to seagrass edge and percent cover of *Thalassia testudinum* (≥80%) since these factors have previously been shown to affect faunal seagrass communities and predation rates (Orth et al. 1984, Rypel et al. 2007, Moore & Hovel 2010).

The SPE, LPE and MC treatments were constructed as oval "cages" (1.16 x 0.85 x 0.3 m, length x width x height) using plastic fencing material, rebar stakes and plastic ties. Sixteen 0.6 m-long and 1 cm-thick rebar stakes were spaced in equal intervals and the fencing material of the entire oval was pushed ~5 cm into the substrate. Compared to SPE and LPE, MC had one large gap on each side of the simulated exclosure to allow the free movement of all organisms in and out of the experimental area. Since the fencing height was ~0.3 m (i.e., lower than the water depth at high tide), the top of each cage was covered using two crossing 1.2 m-long rebar stakes and fencing material.

After 34 days, an oval throw trap (1.16 x 0.85 x 1 m, length x width x height) was placed over each treatment area during low tide. After removal of the fencing material and rebar stakes, I recorded percent cover of *Thalassia testudinum* within the throw trap. The area enclosed in the throw trap was sampled with two dip nets (4 mm and 10 mm mesh) until three consecutive dips yielded no organisms. Since the smallest dip net had a mesh size of 4 mm, I collected epibenthic organisms that were retained by this mesh size. All sampled organisms were immediately put on ice and later frozen. In the laboratory, organisms were sorted and identified to the lowest taxonomic level possible. I then measured, dried (60°C), and weighed each organism to obtain dry biomass (g m^{-2}). For all mollusks, only the soft tissue was measured for dry biomass.

Medium-scale experiment – A randomized block design also was employed (distances between blocks varied from 130 to 530 m). Treatments (SPE, LPE, MC, and UC) were constructed from February 13th to 16th 2009 (one block per day). The treatment "cages" were constructed as 5 m-diameter circles with 1.8-m rebar stakes spaced in 0.5-m intervals. The same fencing material was applied as in the small-scale experiment and was pushed ~5 cm into the substrate after cage construction. The height of the fencing (~1.2 m) exceeded the height of the highest spring tides, and thus tops were not necessary. In addition, no birds were observed in any experimental area during the study period. The "cage" of the MC treatment had a 1-m opening every ~2 m to allow the free movement of organisms of all sizes in and out the experimental area. Using the same throw trap as in the small-scale experiment, I collected three subsamples per treatment after 77 days of deployment (3 subsamples x 4 treatments x 4 blocks = 48 subsamples). Data collection and sample processing were performed as in the small-scale experiment.

Data Analyses – For both experiments, I examined the effect of treatment and block on 1) species richness, 2) total biomass and density (summed across all taxa), and 3) community composition of epifaunal community. For the medium-scale experiment, the three sub-samples of each treatment were averaged to obtain a mean value for each response variable. Hence, the total sample size was n = 16 (4 blocks x 4 treatments) for both exclusion experiments. I omitted sea cucumbers (*Holothuria* sp., n = 27, 250 g), sponges (Porifera, 1026 g), and one large spider crab (Majidae, 23 g) from the analyses because these taxa were unlikely prey of the excluded predators. All data were tested for normality and homogeneity of variance in R version 2.12.2.

Effects of block and treatment on species richness (# of species m^{-2}), total biomass (g m^{-2}), and total density (# of individuals m^{-2}) were analyzed using randomized-block ANOVA and pairwise comparisons of Least Significant Difference (LSD; on the basis of *a priori* decisions). For community structure analysis, rare taxa (<3% of total biomass and density, respectively) were omitted (Clarke & Warwick 1994). Taxa used for the community structure analysis are shown in Table 1. Biomass and density of taxa were ln(x+1)- and sqrt(x+1)-transformed, respectively, and subsequently similarity matrices on biomass and density data were constructed using standardization and the Bray-Curtis similarity coefficient. Treatment and block effects were separately tested on biomass and density data of the epifaunal taxa using ANOSIM without replication (i.e., Spearman rank correlation method, with test statistic = ρ) in PRIMER 5.2.9 (Clarke & Warwick 1994). Statistical significance was tested at $\alpha = 0.05$.

Results

I identified 60 species from 49 families in the small-scale experiment, and 68 species from 57 families in the medium-scale experiment. In total, I collected 951 (357 g) and 4,927 (1025.6 g) individuals in the small- and medium-scale experiments, respectively. In the small-scale experiment, the most dominant organisms in terms of biomass averaged across all treatments and blocks were 1) *Panopeus* sp. (mud crab, 6.2 g m^{-2}, 44% of overall biomass), 2) *Pitho* sp. (urn crab, 3 g m^{-2}, 21% of biomass), 3) Gobiidae (gobies, 2 g m^{-2}, 14% of biomass), and 4) *Alpheus* sp. (snapping shrimp, 1 g m^{-2}, 7% of biomass). In the medium-scale experiment, the highest biomass was 1) *Panopeus* sp. (4.2 g m^{-2}, 41% of biomass), 2) *Phascolion* sp. (hermit sipunculid, 1 g m^{-2}, 10% of biomass), 3) Portunidae (swimming crabs, 0.99 g m^{-2}, 9% of biomass), and 4) *Cerithium* spp. (ceriths, 0.8 g m^{-2}, 8% of biomass). In terms of density, the most common epifaunal taxa were 1) *Alpheus* sp. (18 individuals m^{-2}, 25% of overall density), 2) *Palaemonetes* sp. (grass shrimp, 14 individuals m^{-2}, 20% of density), 3) *Phascolion* sp. (11 individuals m^{-2}, 15% of density), and 4) *Cerithium* spp. (5 individuals m^{-2}, 7% of density) in the small-scale experiment, and 1) *Phascolion* sp. (85 individuals m^{-2}, 60% of overall density), 2) *Cerithium* spp. (18 individuals m^{-2}, 12% of density) and 3) *Alpheus* sp. (9 individuals m^{-2}, 7% of density) in the medium-scale experiment.

Small-scale experiment – Species richness varied among treatments, and block had a marginally significant effect (Table 2, Fig. 2A). Pairwise comparisons demonstrated that there was a difference in species richness between LPE and MC (LSD: mean treatment difference = 7.5, *P* = 0.007), as well as between LPE and SPE treatments (LSD: mean treatment difference = 5.5, *P* = 0.032; Fig. 2A). Total biomass had a marginally significant treatment effect and no block effect (Table 2, Fig. 2B). Yet, pairwise comparisons indicated that total biomass differed between the SPE and UC treatments (LSD: mean treatment difference = 17.2, *P* = 0.026; Fig. 2B). Total density did not vary among treatments, but did among blocks (Table 2, Fig. 2C). Finally, there were no treatment or block effects in community structure for biomass (ANOSIM, treatment: ρ = -0.048, *P* = 0.57; block: ρ = -0.105, *P* = 0.67) or density data (ANOSIM, treatment: ρ = -0.105, *P* = 0.65; block: ρ = 0.01, *P* = 0.41).

Medium-scale experiment – Treatment and block had marginally significant effects on species richness (Table 2, Fig. 2D). Pairwise comparisons demonstrated that there was a difference in species richness between SPE and UC treatments (LSD: mean treatment difference = 5.3, *P* = 0.019; Fig. 2D). In terms of total biomass, the treatment effect was marginally significant, whereas there was no block effect (Table 2, Fig. 2E). Pairwise comparisons indicate that total biomass was different between the LPE and UC (LDS: mean treatment difference = 5.17, *P* = 0.039), as well as between SPE and UC treatments (LDS: mean treatment difference = 4.97, *P* = 0.046; Fig. 2E). For total density, there was no treatment effect, but a block effect (Table 2, Fig. 2F). Finally, there were no treatment or block effects in community structure for biomass (ANOSIM, treatment: $\rho = -0.095$, $P = 0.65$; block: $\rho = -0.095$, $P = 0.63$) or density data (ANOSIM, treatment: $\rho = -0.029$, $P = 0.52$; block: $\rho = 0.114$, $P = 0.27$).

Discussion

Predators may play fundamental roles in regulating population dynamics and community structure (Sih et al. 1985). Strong top-down effects, including community-level cascades (Polis 1999), typically garner the most attention, yet may be limited to ecosystems with low species diversity, little omnivory, and/or strong, concurrent interactions between trophic levels (Strong 1992, Polis & Strong 1996, Estes et al. 1998, Shurin et al. 2002, Heck & Valentine 2007, Ferretti et al. 2010). Although seagrass beds are species-rich systems, strong predator effects have sometimes been identified (Ambrose 1984, Heck et al. 2000, Hindell et al. 2000, Moksnes et al. 2008). I extended the assessment of predator effects on food web structure in seagrass ecosystems, focusing especially on potential effects of different-sized predators. Contrary to my hypotheses, my findings suggest (1) weak predator effects in these shallow seagrass ecosystems, supporting the notion that the complex nature of species-diverse ecosystems disables strong predator control on food web structure, and (2) no predator size impact on faunal community structure and composition. I discuss several factors that might underlie my findings.

Two of the characteristics that often define systems with weak top-down effects are high species richness and high incidence of omnivory (Strong 1992, Fox 2007), both of which are apparent in the shallow Bahamian seagrass systems. For example, I collected at least 60 species in my benthic throw traps alone, not including the diverse assemblage of meiofauna that is also present (<4 mm; Yeager et al. In Review). In similar Bahamian seagrass ecosystems, species richness of macroinvertebrates and fishes were also high (Layman & Silliman 2002, Layman et al. 2004, Valentine-Rose et al. 2007), contrasting sharply to systems where strong predator effects are often observed (e.g., Paine 1966). Furthermore, omnivory is expected to be high in seagrass ecosystems (Livingston 1982, Marguillier et al. 1997, Jaschinski et al. 2008). For example, the two most common fish mesopredators in my study site (gray snapper and schoolmaster snapper) are well-known generalists that feed on a variety of prey items from different trophic levels (Starck & Schroeder 1971, Hammerschlag et al. 2010, Yeager & Layman 2011, Hammerschlag-Peyer & Layman In Revision). Likewise, typical prey items of snappers, such as many of the crabs and small teleosts, are omnivorous as well (Silliman et al. 2004, Yeager & Layman 2011). Consequently, it is possible that predator effects in my study system were dampened (at least to a certain degree) by myriad weak and reticulated interactions among species.

Other factors may also have driven weak predator effects in this system. For example, in Bahamian wetlands, predation risk has been shown to increase with water depth, suggesting that predation is limited to higher water periods of the tidal cycle (Rypel et al. 2007). During lower tidal levels, predators in shallow Bahamian systems are restricted to deeper refuge areas, i.e., mangrove-lined channels (Hammerschlag-Peyer & Layman 2010). Most other studies examining predator effects on seagrass faunal communities have been in deeper systems where predators have continuous access to prey (Leber 1985, Gacia et al. 1999, Heck et al. 2000, Hindell et al. 2000, Moore &

Hovel 2010). Consequently, in my study, the predation window was limited, perhaps diminishing predator effects on the epifaunal community.

Furthermore, heterogeneity in community structure and composition seemed to be generally high in this study, as suggested by the significant block effects in both experiments (Table 2). The heterogeneity was likely driven by microhabitat features of the selected sites and sub-sites. For instance, macroinvertebrates have been found to use sponges for shelter and sometimes food (Rützler 1976, Klitgaard 1995, Tsurumi & Reiswig 1997, Magnino & Gaino 1998, Turon et al. 2000, Saito et al. 2001, Gaino et al. 2004), and their abundance to increase with sponge biomass (Gaino et al. 2004). In this study, sponge biomass potentially may have driven the significant block effects on total densities (Table 2), as total density of epifaunal taxa tended to increase with sponge biomass, and differed mostly among blocks (Fig. 4). Other microhabitat features, such as epiphytes and macroalgae, may also have affected the epifaunal community structure (Sala 1997, Bologna & Heck 1999, Gacia et al. 1999, Tomas et al. 2005). For example, Bologna and Heck (1999) showed that seagrass epiphytes increased epifaunal richness and density because they augmented the spatial complexity of seagrass beds, and were an important food source for several taxa. Consequently, my findings may suggest that microhabitat features, such as sponge biomass, epiphytes and macroalgae, could play critical roles in shaping faunal community structure.

Within complex food webs that have overall weak community-level predator effects, it is also possible that particular interactions are especially strong, with predators controlling the abundance of a subset of the available prey taxa (Berlow et al. 1999, Neutel et al. 2002, Berlow et al. 2004). Such patterns have been labeled species-level cascades (Polis 1999). My experimental results were consistent with this framework, because, in both experiments, the biomass of the decapod mesopredators, *Panopeus* sp., *Pitho* sp. and Portunidae, which are common prey of gray and schoolmaster snappers (Starck & Schroeder 1971, Hammerschlag-Peyer & Layman In Revision), were higher in the predator exclusions (i.e., either SPE or LPE) than in the control treatments (i.e., either MC or UC; with the exception of *Panopeus* sp. in the small-scale exclusion; Fig. 3). I also found that species richness was lower in the exclusion treatments than in the controls (Fig. 2), possibly because these decapod mesopredators had strong effects on some of their prey/competitors through competitive exclusion and/or direct predation (Ambrose 1984, Leber 1985). Hence, these findings suggest that species-level top-down controls may exist within my overall community, although my experimental design did not allow me to examine this further.

In contrast to my hypothesis, one of the most consistent patterns in my findings was the lack of differences in the responses to the two treatments, SPE and LPE. It is possible that the predator size range (e.g., schoolmaster snapper: 3-20 cm TL, gray snapper: 3-22 cm TL, Fig.1) might have been too narrow in my study to show significant differences between SPE and LPE treatments. In Bahamian tidal creeks, top predators are rare and the most abundant mesopredators (i.e., Lutjanidae) are typically composed of juvenile and sub-adult individuals (Fig. 1A,B), because larger individuals often move to nearby reefs as they grow (Nagelkerken et al. 2000, Sheridan & Hays 2003). Furthermore, juvenile schoolmaster (<12.5 cm SL) and gray (<10 cm SL) snapper seemed to be more abundant than sub-adult individuals (schoolmaster: 12.5-25 cm SL; gray: 10-20 cm SL; Fig. 1). Consequently, because local abundance of predators can potentially affect the strength of top-down effects (Hindell et al. 2001), I would expect that higher abundances of sub-adult and adult snappers (or other larger-sized predatory fishes) would have driven significant differences between the different-sized predator exclusions.

According to ecological theory, results of the small-scale experiment would be expected to be mostly driven by behavioral mechanisms of the epifaunal seagrass taxa responding to the presence of predators (i.e., anti-predator behavior), while results of the medium-scale experiment were expected to additionally be driven by some density-based mechanisms as a result of direct predation (Englund 1997, Englund et al. 2001). In general, I did not observe differences in outcome between the small- and medium-scale exclusion. These findings suggest that either (1) there was no overall difference between the indirect (i.e., behavioral mechanisms) and direct (i.e., density-based mechanisms) predator effects on the community, or (2) the medium-scale exclusion was not large enough to display direct predator effects. I suggest the latter is a more likely explanation. For example, a recent empirical experiment demonstrated that effects of a small benthic fish (*Cottus gobio*) on densities of invertebrates did not differ between instream channels of different lengths in a Swedish stream (Englund 2005), and suggested that even large-scale experimental units (~8 m in length) are not sufficient to allow direct predation effects to be manifested (Englund 2005). Consequently, although system specific, it has been suggested that experiments performed in the time period of weeks to months and that use experimental units that are smaller than 10 m belong to the small-scale domain, and are thus behavior controlled (Englund 2005). My results seem to be consistent with these observations.

Although much ecological emphasis has been placed on the role of predation on food web structure, the lack of consistency in how food webs respond to predators in seagrass ecosystems, and generally across ecosystem types, encourages further exploration (Borer et al. 2005, Fox 2007). Moreover, in light of the rapid global decline of seagrasses and their associated fauna (Orth et al. 2006, Hughes et al. 2009), a better understanding of predator effects on faunal communities of seagrass beds are critical for conservation efforts. My study contributes to these endeavors and suggests that shallow, species-rich, seagrass communities may have rather weak community-level predator effects. Increased knowledge of predator effects in seagrass ecosystems may help to enhance the understanding of possible consequences of large-scale seagrass declines on community structure and ecosystem function.

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Table 1 Taxa that contributed ≥3% to the overall biomass and density and were included in the community analysis (relative biomass and density for the small-scale and medium-scale exclusion experiment). Taxa are organized in phylogenetic order

Scientific Name	**Common Name**	**Small-scale**		**Medium-scale**	
		Biomass	Density	Biomass	Density
Cerithium spp.	Sea snail		x	x	x
Gastropoda [1]	Sea snails other than *Cerithium* spp.		x	x	x
Codakia spp.	Marine mussel	x	x		x
Lucina spp.	Marine mussel				x
Bivalvia [2]	Marine mussels other than *Codakia* spp. and *Lucina* spp.			x	x
Phascolion sp. [3]	Hermit sipunculid		x	x	x
Oligochaeta	Annelids				x
Amphipoda	Amphipods		x		
Alpheus sp.	Snapping shrimp	x	x	x	x
Palaemonetes sp.	Grass shrimp		x		x
Squilla sp.	Mantis shrimp			x	
Panopeus sp.	Mud crab	x	x	x	x
Xanthidoidae	Mud crabs other than *Panopeus* sp.			x	x
Portunidae	Swimming crabs			x	
Pitho sp.	Urn crab	x	x	x	
Dromidia sp.	Decorator crab			x	
Majidae [4]	Spider crabs				x
Ophiurida	Brittle stars		x	x	x
Anguilliformes	Eels			x	
Gobiidae/Blenniidae	Gobies and Blennies	x	x	x	x
Pomacentridae	Damselfish	x			

[1] *Modulus* sp., *Tegula* sp., *Bulla* sp. and *Cerodrillia* sp.; [2] Galeommatidae, Tellinidae, and *Glycymeris* spp.; [3] unsegmented worm that inhabits abandoned shells, in this study mostly in *Cerithium* spp. shells; [4] *Pitho* sp., *Dromidia* sp., and *Mithrax* sp.

Table 2 Results of analysis of variance (ANOVA) for the small- and medium-scale exclusion experiment. Treatments consisted of small- and large-predator exclusion, manipulated and unmanipulated control, and in each experiment, four blocks were used. Bold *P*-values indicate statistically significant findings ($P < 0.05$), and italic *P*-values represent marginally significant results ($0.05 < P \leq 0.1$)

		Small-scale		**Medium-scale**	
		F	*P*	F	*P*
Species Richness	Treatment	4.29	**0.04**	2.81	*0.1*
	Block	3.46	*0.06*	3.4	*0.06*
Total Biomass	Treatment	2.77	*0.1*	2.98	*0.09*
	Block	0.17	0.92	1.11	0.39
Total Density	Treatment	1.18	0.37	0.49	0.7
	Block	6.14	**0.015**	7.45	**0.008**

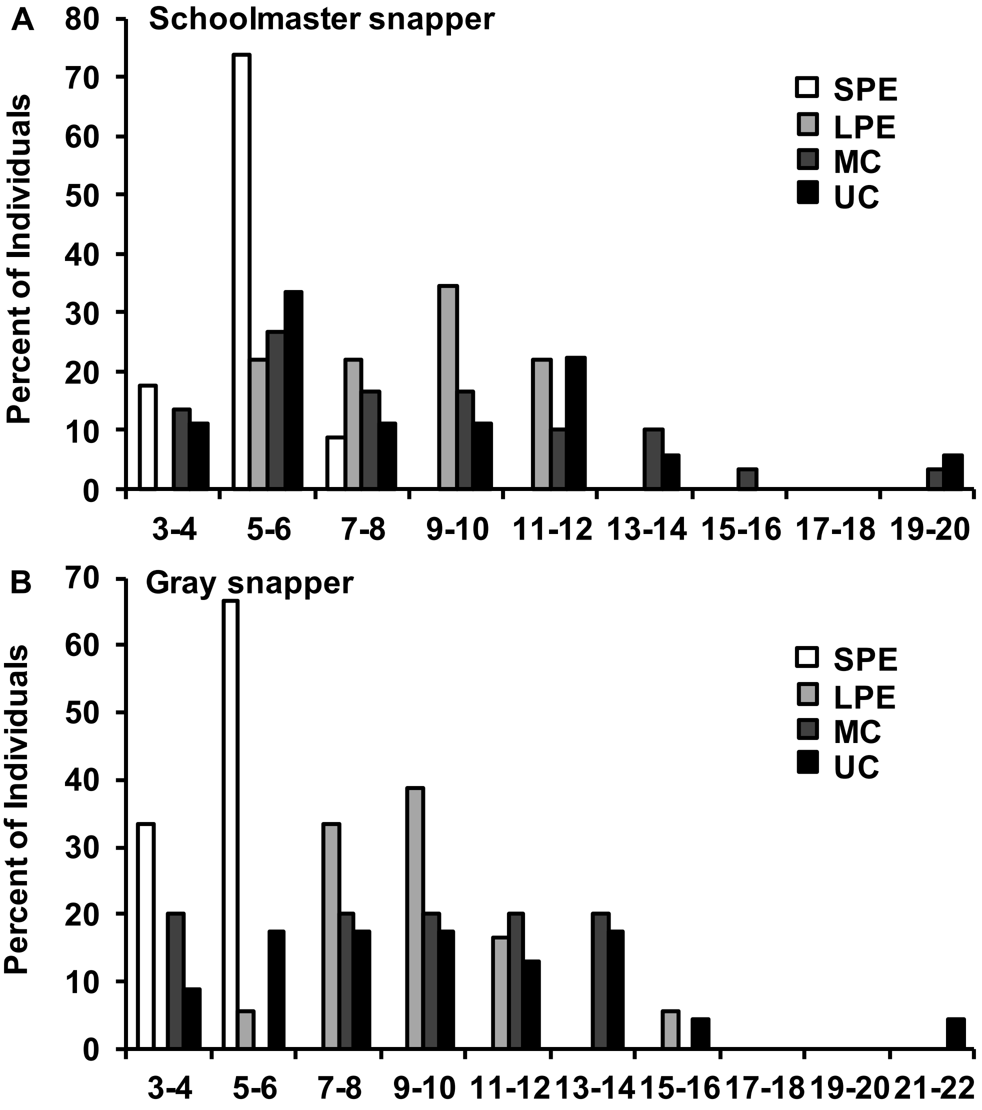

Fig. 1 Size-frequency distribution of A) schoolmaster snapper (*Lutjanus apodus*) and B) gray snapper (*L. griseus*) observed in the four different treatments: SPE = small-predator exclusion, LPE = large-predator exclusion, MC = manipulated control, and UC = unmanipulated control. Bins included 2 cm total length (TL) starting at 3 cm TL

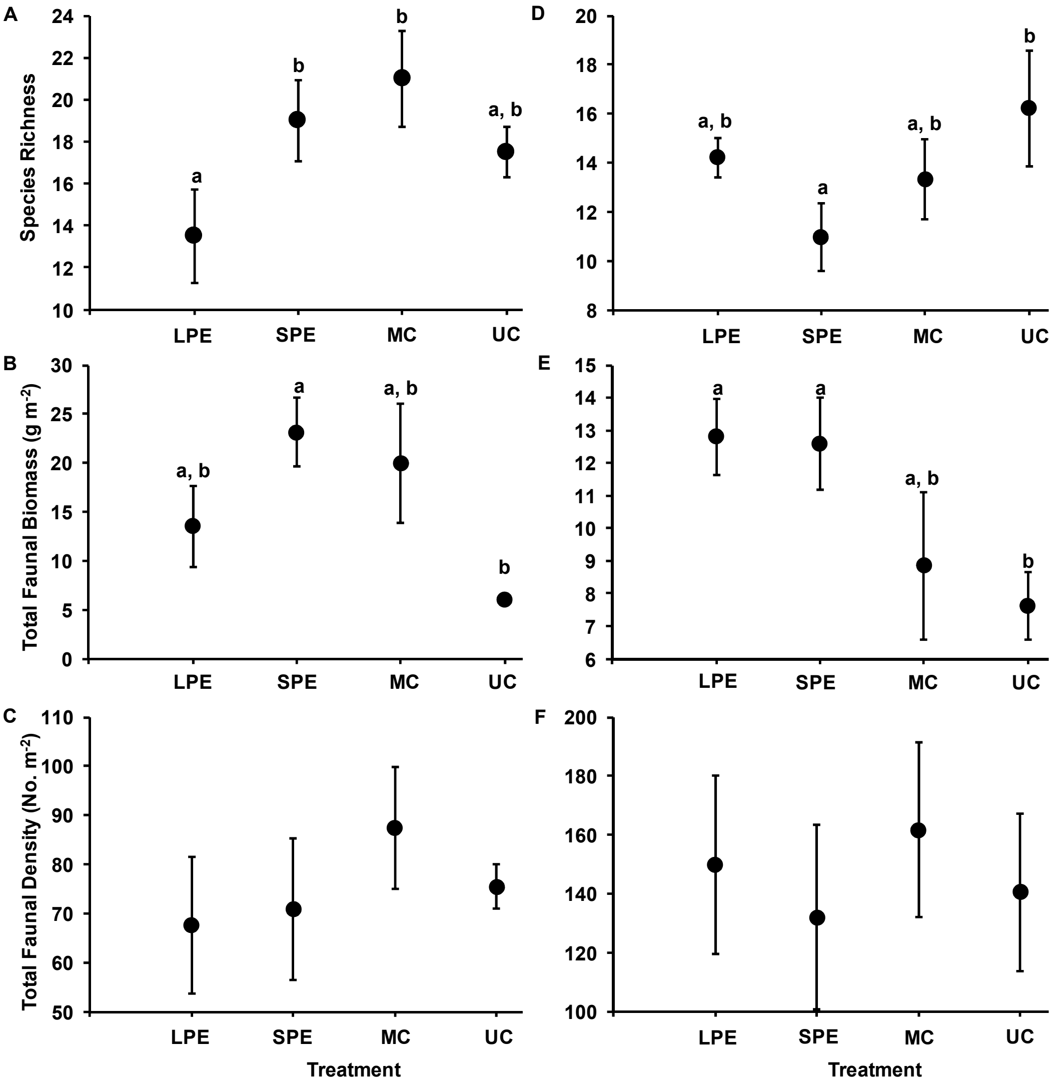

Fig. 2 Species Richness (A and D), Total Biomass (B and E), and Total Density (C and F) of the small-scale (A-C) and medium-scale (D-F) experiments. LPE = large-predator exclusion, SPE = small-predator exclusion, MC = manipulated control, UC = unmanipulated control (see text for more details). Error bars represent standard error. Standard error for total biomass (small-scale exclusion) was low in the unmanipulated control and thus not visible in panel B. (a, b) indicate statistically significant ($P < 0.05$) differences between treatments (on the basis of Least Significant Difference

comparisons) and are not present for Total Density (C and F) because all pairwise comparisons were $P \geq 0.05$

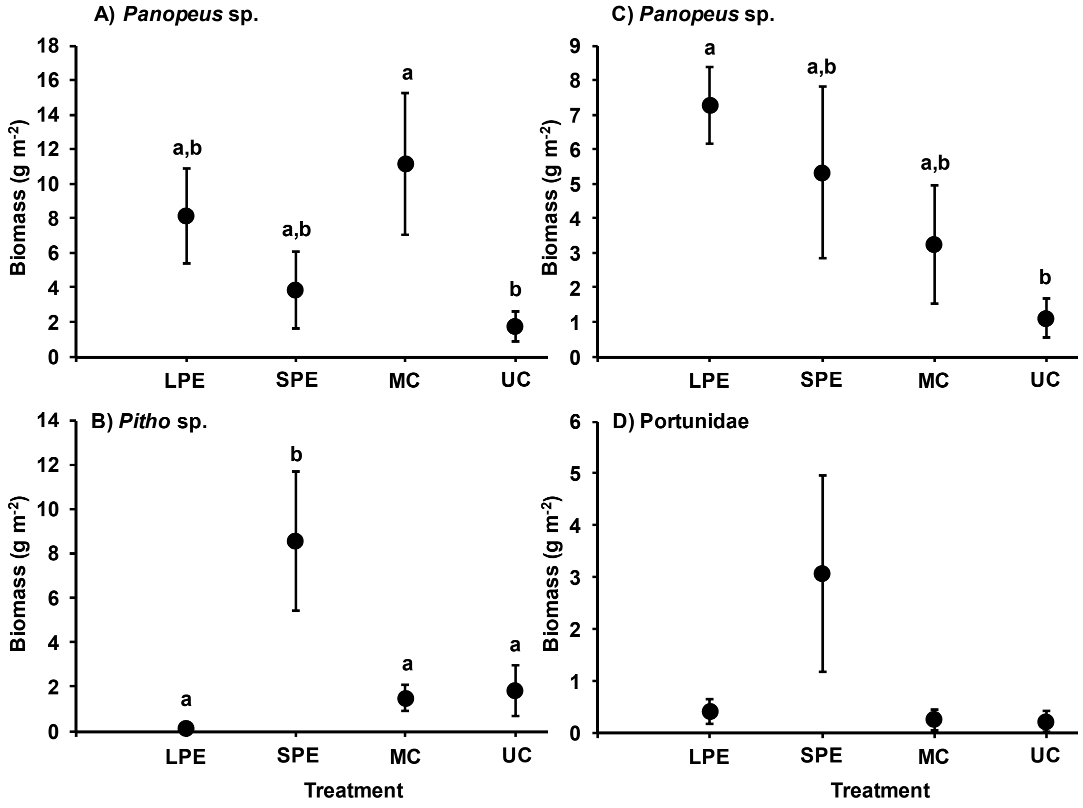

Fig. 3 Total Biomass of A) *Panopeus* sp. (mud crab), B) *Pitho* sp. (urn crab), C) *Panopeus* sp. and D) Portunidae (family of swimming crabs) in the small-scale (A-B) and medium-scale (C-D) exclusion. LPE = large-predator exclusion, SPE = small-predator exclusion, MC = manipulated control, UC = unmanipulated control (see text for more details). Error bars represent standard error. Standard error of *Pitho* sp. (small-scale exclusion) was low in the large-predator exclusion and thus not visible in panel B. (a, b) indicate statistically significant ($P < 0.05$) differences between treatments (on the basis of Least Significant Difference comparisons), and are not present for Portunidae (D) because all pairwise comparisons were $P \geq 0.05$ (i.e., SPE-LPE: $P = 0.08$, SPE-MC: $P = 0.06$, SPE-UC: $P = 0.06$)

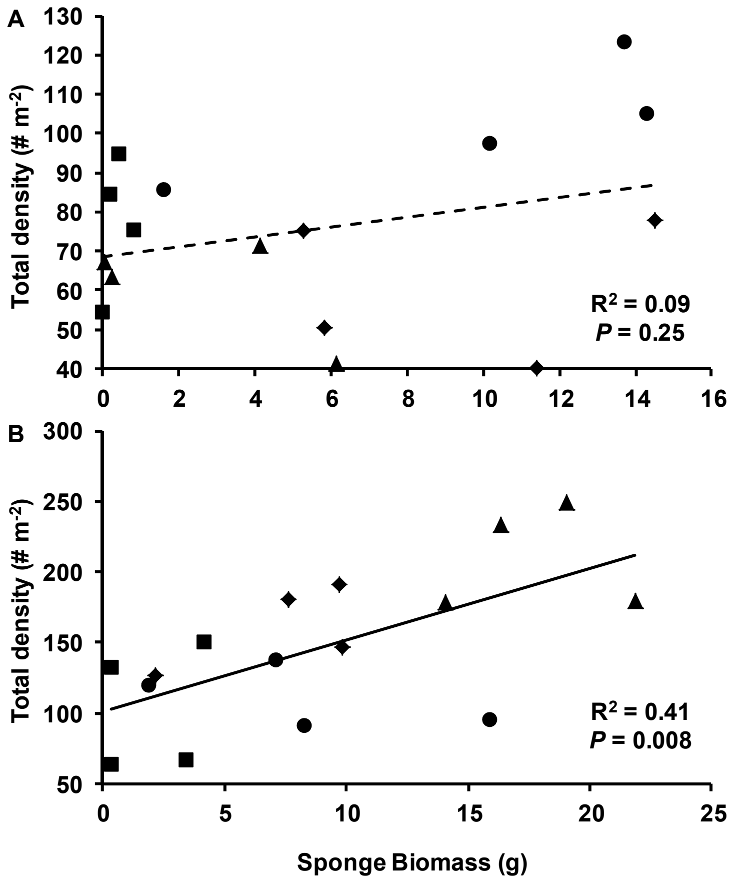

Fig. 4 Linear regression between total density and sponge biomass in the A) small-scale and B) medium-scale exclusion experiment. Block 1 = squares, block 2 = triangles, block 3 = diamonds, block 4 = circles. Linear regression across the four blocks result in a R^2 = 0.09 and *P* = 0.25 in the small-scale exclusion (A), and R^2 = 0.09 and *P* = 0.008 in the medium-scale exclusion (B). Dashed regression line represents a non-significant trend ($P \geq 0.05$), and solid line statistically significant relationship ($P < 0.05$)

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CHAPTER VI

CONCLUSIONS AND FUTURE DIRECTIONS

Body size is a fundamental characteristic of organisms, determining various important life history and physiological traits (Peters 1983, Werner & Gilliam 1984, Persson 1988, Brown et al. 2004). Body size also mediates the occurrence and consequences of the interactions among organisms, thus affecting population dynamics, predator-prey interactions, community structure, and ecosystem function (Brooks & Dodson 1965, Marquet et al. 1990, Brown et al. 1993, Greenwood et al. 1996, Jennings et al. 2002, Cohen et al. 2003, Dalerum & Angerbjorn 2005, Rudolf 2006, Hildrew et al. 2007, Akin & Winemiller 2008). My dissertation research focused primarily on the effect of body size on the resource use (i.e., diet and habitat use) of economically and ecologically important coastal fish predators, as well as the influence of body size of these predators on their prey communities. Herein, I summarize the major conclusions of my dissertation, and suggest some future directions that could build on this research.

One major finding of my dissertation research was high variation in resource use among individuals of a population (Chapter II and III). Consistent with other recent reviews, it may be likely that intraspecific variation is more common and pronounced than has previously been acknowledged (Bolnick et al. 2003, Araujo et al. 2011). In the snapper species studied herein, some of this intrapopulation variation in resource use was explained by body size (Chapter III), and some by individual behavior (Chapter II and III), being further influenced by temporal variability (Chapter III). Such intrapopulation variation has important ecological, evolutionary and conservation implications (Bolnick et al. 2003, Bolnick et al. 2011, Araujo et al. 2011). For example, population models that integrate intrapopulation variation can cause extremely different dynamical behavior because of the added capacity for frequency-dependent effects (Bolnick et al. 2003).

Consequently, such population models can more precisely simulate and predict population and community dynamics and ecosystem function.

Furthermore, intrapopulation variation in resource use has been typically ignored from a fisheries management perspective. Simply focusing on the “average” habitat or prey of a fish population may inherently ignore those individuals that use alternative habitats or food sources, rendering such management efforts ineffective (Durell 2000, Bolnick et al. 2003, Egli & Babcock 2004). In contrast, fisheries management and conservation measures that take intrapopulation resource variation into account may help preserve species’ ecological, phenotypic and genetic diversity, and thus their ability to adapt to environmental change and to respond to human impacts in marine ecosystems (Moritz 1994, Coates 2000, Bolnick et al. 2003).

Another core finding of my research was that effects of these predators were generally weak in a shallow, species-rich, Bahamian seagrass system, with predator size and experimental spatial scale having no major impact on the epifaunal community (Chapter V). These findings were likely the result of high species richness, high incidence of omnivory, and numerous weak and reticulate interactions among species. These findings may be critical for conservation efforts, especially because of drastic declines of seagrasses and their associated fauna worldwide (Orth et al. 2006, Hughes et al. 2009). Decrease in faunal diversity as a result of seagrass die-offs could lead to stronger predator effects in seagrass communities, subsequently driving such seagrass food webs to be less stable (McCann 2000), and to be more prone to effects of predator removal (e.g. because of overfishing) than species-rich seagrass systems.

I also developed a hypothesis-testing framework (Chapter IV) that extends beyond my focal study systems. This approach can help guide future research focused on categorizing taxonomic or functional classes into specific niche shift scenarios, as well as to help elucidate underlying mechanisms causing particular niche shifts. Future studies should also try to expand the application of this framework to other methods (e.g., stomach content analysis), or make it applicable for the use of combined methodologies (e.g., stable isotope and stomach content analyses), so that the framework can be widely used in the field of ecological studies.

Another future direction building on my research findings would be to attempt to tease apart which mechanisms may drive the high intrapopulation niche variation that I observed. For instance, predation risk may be one major factor affecting habitat use and ontogenetic diet shifts in Lutjanidae (Werner & Hall 1988). Smaller snappers likely have higher predation risks than larger ones, and thus probably experience a trade-off between feeding opportunities and predation risk. In addition, intraspecific competition has been shown to play an important role in driving intrapopulation resource variation (Svanbäck & Persson 2004, Svanbäck et al. 2008, Kobler et al. 2009, Svanbäck & Persson 2009, Frederich et al. 2010). For example, when resources are scarce due to intraspecific competition, some individuals may be driven to forage on less optimal prey items and/or to expand their foraging area (Chapter II). In the shallow systems used for my dissertation research, densities of snappers were especially high because individuals were forced to few deeper areas at low tide (Chapters II, III, and V).

Lastly, future research could examine predator exclusions at even larger spatial scales than employed in my dissertation research. Although the exclusion experiments in my medium-scale experiment were relatively large (treatment cages ~20 m^2) compared to many field experiments, it is still relatively small compared to the spatial scales at which important ecological processes may operate. Although large-scale experiments have obvious limitations in funding and logistical constraints (Carpenter 1990), they may reveal effects that may not be manifested at smaller spatial scales (Werner et al. 2009).

Bahamian wetland systems are increasingly threatened by human activities, such as direct removal through development activities, fragmentation and other forms of habitat alteration and pollution (National Wetlands Committee 2007). Yet, these systems are crucial for coastline protection, recreation and ecotourism, as well as provide critical habitats to numerous ecologically and economically important species (Adams et al. 2006). Consequently, an increased understanding of the ecology of the organisms inhabiting these systems is necessary to properly protect and manage them. My dissertation research contributed to this endeavor by providing insights about dynamics within important fish predator populations, their interactions with prey, as well as their effects on faunal community structure in Bahamian wetland systems.

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