

# Seasonal diet and feeding habits of juvenile fishes foraging along a subtropical marine ecotone

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**ABSTRACT:** Few studies have examined seasonal diet variation and trophic relationships among fishes in shallow subtropical waters. We sampled consecutive wet and dry seasons within Biscayne Bay, Florida, USA, to examine seasonal diet and feeding habit variation in juvenile gray snapper *Lutjanus griseus* (GS), bluestriped grunt *Haemulon sciurus* (BSG), seabream *Archosargus rhomboidalis* (SB) and great barracuda *Sphyraena barracuda* (GB). We found significantly lower feeding intensity during the dry season compared to the wet, which is likely related to lower water temperatures during the former season. GS fed on a variety of fishes and crustaceans, while BSG fed primarily on caridean shrimps. SB fed on vegetation and GB was piscivorous. Seasonal shifts in major food resources generally did not correspond with changes in relative abundance of food supply. Seasonal population niche breadth differences were evident for GS, GB and BSG, but for SB niche breadth was similar between seasons. Based on seasonal food supply, population niche breadth values did not match basic foraging theory predictions, which state that niche breadth should expand as preferred food items become scarce. In GS, BSG and GB, individuals fed on a narrow subset of prey consumed by the population, revealing the existence of individual specialization. For these species, seasonal expansion in population niche breadth did not correspond to increased individual specialization, but rather via increased within-individual variation in resource use. Given the seasonal differences in feeding habits, it is important to incorporate seasonal variation when modeling trophodynamics of shallow subtropical systems or characterizing them as essential fish habitats.

**KEY WORDS:** Diet · Niche breadth · Resource use · Habitat use · Snapper · Grunt · Barracuda · Food availability · Feeding intensity · Individual specialization

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## INTRODUCTION

Studies of diets and feeding patterns can contribute to an understanding of ecological interactions and community structure (e.g. Winemiller 1989, Krebs 1998, Nagelkerken et al. 2006, Layman et al. 2007). Dietary ecology and feeding habits can be explored by quantifying variation in resource use, feeding intensity and trophic niche breadth. Individuals are predicted to shift resource

use in response to food availability in the environment (Stephens & Krebs 1986). Trophic niche breadth is influenced by a variety of factors, including food diversity (Layman et al. 2007) and intraspecific competition (Svanback & Bolnick 2005). In fishes, feeding intensity is thought to decrease at lower temperatures (Tyler 1971) due to lower metabolic demands.

Although a number of studies have investigated fish feeding patterns and trophic dynamics in tropical and

subtropical marine environments (e.g. Randall 1967, Harrigan et al. 1989, Layman & Silliman 2002), most quantitative trophic studies involving fishes in these systems grouped diet data across seasons or did not investigate whether seasonal diet patterns existed (e.g. Lugendo et al. 2006, Cocheret de la Morinière et al. 2003, Nagelkerken & van der Velde 2004, Nagelkerken et al. 2006, Snodgrass et al. 2008). However, studies from mostly temperate marine and tropical freshwater systems have shown that seasonal changes in resource availability and environmental conditions influence fish feeding patterns (Winemiller 1989, Jepsen et al. 1997, Peterson & Winemiller 1997, Laidre & Heide-Jørgensen 2005, Tanimata et al. 2008).

Despite the few studies examining seasonal variation in the diets of fish populations inhabiting subtropical marine systems, little is known about between-individual variation in resource use within populations (Bolnick et al. 2003). This individual level variation is called individual specialization and refers to individuals whose dietary niche is significantly narrower than that of the population (see Bolnick et al. 2002, 2003). Basic optimal foraging theory predicts that dietary niche breadth of a population should expand as preferred food resources become scarce (Emlen 1966, Schoener 1971, Stephens & Krebs 1986, Rodel et al. 2004). However, recent advances in niche theory predict that the dietary niche breadth of a population can expand in 2 differing ways: every individual in the population may use a broader array of resources (i.e. consume a greater diversity of prey) or there can be greater individual specialization (i.e. increased inter-individual variation in resource use) (Bolnick et al. 2002). Recent studies on a variety of taxa have found inter-individual diet variation, which has been shown in some cases to comprise the majority of the population's niche width (e.g. Bolnick et al. 2003, Araújo & Gonzaga 2007, Araújo et al. 2007). However, seasonal variation in individual diet specialization has not yet been reported for fishes.

The present study focused on seasonal diet and feeding patterns of late-stage juvenile gray snapper *Lutjanus griseus*, bluestriped grunt *Haemulon sciurus*, seabream *Archosargus rhomboidalis* and great barracuda *Sphyraena barracuda* within subtropical Biscayne Bay, Florida (USA). These fishes were selected because they are among the most abundant species in the bay (Serafy et al. 2003, Faunce & Serafy 2008) and are economically important to the region's recreational fishery and dive tourism industry (great barracuda and gray snapper). Biscayne Bay's wet season is characterized by relatively warm water temperatures (~30°C) and high salinity variation, and its dry season by cooler temperatures and low salinity variation (Serafy et al. 2003). Given predictable seasonal variation in envi-

ronmental conditions, our specific objectives were to examine for seasonal differences in feeding intensity, diet composition, population trophic niche breadth and degree of individual dietary specialization. With these data, we addressed the following questions for juveniles of the 4 species: (1) Is feeding intensity lower in the cool, dry season? (2) Does trophic resource use shift with seasonal food abundance? (3) Does population trophic niche breadth vary inversely with seasonal food abundance? (4) Does seasonal expansion of population niche breadth correspond with higher degree of individual specialization?

## MATERIALS AND METHODS

**Study site and physical habitat measurements.** The present study was conducted along the eastern boundary of southern Biscayne Bay, Florida, USA, along the leeward side of Elliott Key, between latitudes 25.4271° and 25.4064° N (Fig. 1). Sampling was conducted during 2 consecutive seasons (wet season: July–October 2007; dry season: January–April 2008) by seine netting along three 120 m long transects that extended perpendicularly from shore (Fig. 1C). Water temperature and salinity were measured along the 3 transects using YSI® multi-probe instruments (600XL and 650 MDS). Water depth was measured using a PVC pole with 1 cm markings.

**Fish species.** We focused on late-stage juvenile gray snapper, bluestriped grunt, seabream and great barracuda, since this age class makes diel movements between mangrove and seagrass habitats. Fish length information and published size–age relationships (de Sylva 1963, Billings & Munro 1974, Manooch & Matheison 1981, Stoner & Livingston 1984, Domeier et al. 1996) were used to identify late-stage individuals. Individuals measuring larger than reported Age-1 size, but smaller than reported size at maturity, were designated as late-stage juveniles.

**Fish and food collection.** Center-bag seine nets (21.3 m long, 1.8 m high, 3 mm mesh) were used to collect fishes and to quantify their potential prey items along the 3 transects (Hammerschlag & Serafy 2010). Seine nets were hauled parallel to shore, against the current (or wind, if stronger) and pursed such that a standardized area of 142 m<sup>2</sup> was sampled with each haul. Although no gear is without bias, previous work at this site (Hammerschlag 2009) demonstrated that our seines and technique were effective for collecting the fishes and their potential prey (including caridean shrimp). Sampling was conducted in complete darkness, from 0.5 to 2.0 h after sunset and within 2.5 h of low tide. All collected fishes and invertebrates were identified to species and measured to the nearest mm

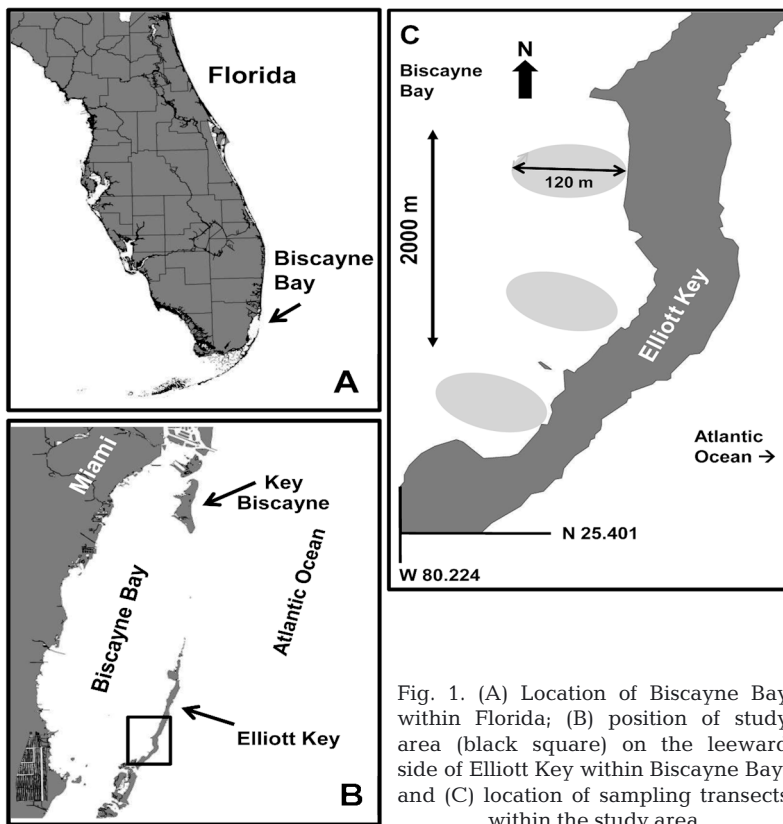


Fig. 1. (A) Location of Biscayne Bay within Florida; (B) position of study area (black square) on the leeward side of Elliott Key within Biscayne Bay; and (C) location of sampling transects within the study area

total length. To permit stomach content analysis, fishes were removed from seines immediately after capture and preserved to reduce post-capture digestion that could result in loss of dietary information (Bowen 1996). To halt digestive processes and preserve stomach contents for laboratory analyses, fishes were placed in a container of ethanol (80 to 90%), a slit was made in the animal's body cavity to accelerate preservation and containers were then refrigerated. Because seagrass and macroalgae have been previously reported as the primary food items for seabream (Vega-Cendejas & Arreguín-Sánchez, 2001), we quantified vegetation cover every 20 m along the 3 transects. This was achieved by estimating the areal percentage of seagrass and algae within  $50 \times 50$  cm quadrats (60 quadrats per transect in each season). This method was chosen to be consistent with existing aquatic vegetation monitoring programs in the region (Fourqurean et al. 2001, Browder et al. 2009).

**Fish diet.** Stomachs were removed from each individual by severing the esophagus, the first few millimeters of the intestine and the mesentery at its dorsal point of attachment (Bowen 1996). Stomachs were carefully opened by slitting them lengthwise with fine scissors. The presence or absence of food items within individuals was recorded, since the percentage of fish

with empty stomachs in each season can be used as a metric to compare seasonal feeding intensity (e.g. Laidre & Heide-Jørgensen 2005). Contents of individual stomachs were then sorted and identified to the lowest possible taxonomic level with the aid of compound and dissection microscopes. Volumes of individual food items were quantified by measuring water displacement of food items in graduated cylinders following Winemiller (1990).

**Data analysis.** To determine the adequacy of the number of collected fishes for diet description, cumulative food resource curves were created for each species-season combination following Maia et al. (2006).

Uses of specific statistical tests were based on whether the data conformed to assumptions of normality and homogeneity of variance (Sokal & Rohlf 1987). Seasonal differences in fish feeding intensity (i.e. the percentage of fishes with empty stomachs, sensu Laidre & Heide-Jørgensen 2005) were compared statistically using  $\chi^2$  analysis. To quantify the relative importance of different food items seasonally in the diets of the

focal fishes, we calculated the percent by volume (%V) of different food items in fish stomachs (following Bowen 1996, Cortes 1997). Percent volume (or weight) of different food items, compared to percent numbers or occurrence, is the better metric for quantifying the relative importance of different food items towards a fish's nutrition, since it is the only one of the widely used metrics which quantifies food types in directly comparable units (Bowen 1996). Seasonal differences in use of major food resources were compared statistically using Kruskal-Wallis tests. To adjust for multiple comparisons, experiment-wise error rate was held at the  $p = 0.10$  level using the Bonferroni method (Sokal & Rohlf 1987).

Seasonal differences in population dietary niche breadth ( $w$ ) were calculated for each species following Krebs (1998) using Levins' index (Levins 1968) where:  $w = 1/\sum (p_j)^2$ , where  $p_j$  is the proportion of individuals found using resource  $j$ . Population niche breadth values were compared for all species in both seasons.

To examine seasonal differences in food abundance for each of the fish species, we compared mean densities of their predominant food items individually between season using  $t$ -tests. To account for multiple comparisons, experiment-wise error rate was held at the  $p = 0.10$  level using the Bonferroni method (Sokal

& Rohlf 1987). Where appropriate, the same seasonal comparison was conducted on each fish's aggregate food abundance (i.e. all consumed food types combined for a particular species). As seabream consumed seagrass and macroalgae, we also compared mean vegetation cover along transects between seasons. All statistical analyses were conducted using SAS statistical software.

Here we define an individual specialist (sensu Bolnick et al. 2003) as an individual whose niche is substantially narrower than its population's niche for reasons not attributable to its sex, age or morphological group. Our fishes were all of the same age class (late-stage juvenile), which does not exhibit sexual dimorphism or possess different morphological types (e.g. benthic or pelagic morphologies). To examine the degree of individual dietary specialization within each season, we used an approach following Araújo & Gonzaga (2007). To this end, we used a proportional similarity index (*PS*) which calculates the overlap between individual *i*'s diet and the population's diet (following Bolnick et al. 2002):

$$PS_i = 1 - 0.5 \sum_j |p_{ij} - q_j| \tag{1}$$

where  $p_{ij}$  is the proportion of the prey category  $j$  in individual  $i$ 's diet, and  $q_j$  is the proportion of the  $j$ th prey category in the population niche.  $q_j$  is calculated as

$$q_j = \sum_i n_{ij} / \sum_i \sum_j n_{ij} \tag{2}$$

where  $n_{ij}$  is the number of items in individual  $i$ 's diet which is within category  $j$ . The average of the *PS*<sub>*i*</sub> values provides a population-wide measure of individual specialization, *IS*. The *IS* index ranges from 0 (maximum individual specialization) to 1 (no individual specialization). *IS* calculations were performed using IndSpec1 (Bolnick et al. 2002).

**Trophic diagrams.** To further explore seasonal trophic relationships, we synthesized all feeding data into preliminary simple trophic models. Linkages between fishes and their prey were constructed by incorporating the contribution by

volume of different food items to the diets of the fishes. To further explore seasonal feeding dynamics, fishes were arranged in order of increasing population niche breadth.

## RESULTS

### Abiotic variables

Table 1 presents seasonal summaries of abiotic data collected. Water temperature ranges during fish sampling were distinct between seasons (wet season: 29.4 to 34.0°C; dry season: 20.0 to 27.1°C), whereas seasonal ranges for the other environmental variables overlapped substantially.

### Fish diets

A total of 134 nocturnal seine samples were collected, 62 during the wet season and 72 during the dry season (20 to 24 seine samples per transect per season). Collections yielded 229 specimens (dry season: 74; wet season: 155) of late-stage juvenile gray snapper, bluestriped grunt, seabream and great barracuda for stomach content analysis (Table 2). Cumulative food resource curves (Fig. 2) for each species–season combination showed a trend toward an asymptote, suggesting that the number of stomachs analyzed in the present study was adequate for accurately describing the diet of each species in both seasons. Across all 4 species, there were significantly more individuals with

Table 1. Abiotic environmental variables (mean ± SE; range in parentheses) on the leeward side of Elliott Key, Florida, USA

	Dry season		Wet season	
Temperature (°C)	23.9 ± 0.3	(20.0–27.1)	32.2 ± 0.3	(29.4–34.0)
Salinity	37.8 ± 0.1	(36.4–38.9)	36.5 ± 0.3	(34.2–38.8)
Depth (m)	0.81 ± 0.02	(0.49–1.16)	0.94 ± 0.03	(0.55–1.20)

Table 2. *Lutjanus griseus*, *Haemulon sciurus*, *Archosargus rhomboidalis* and *Sphyraena barracuda*. Number and size range of late-stage juveniles collected at night for stomach content analysis. Empty: percentage with empty stomachs. p: seasonal difference in proportion of fish with empty stomachs (i.e. feeding intensity), based on  $\chi^2$  analysis. TL: total length; n: no. of fish; diet items: mean number of prey consumed per fish across seasons; na: not available (in seabream it was impossible to numerically quantify vegetation in a manner comparable to prey items in the other fishes)

	TL (cm)	Dry season		Wet season		Total		p	Diet items (no. fish <sup>-1</sup> )
		n	Empty (%)	n	Empty (%)	n	Empty (%)		
Gray snapper	10.4–31.0	25	48	49	8	74	22	<0.001	3.0
Bluestriped grunt	9.1–23.6	18	67	20	30	38	47	<0.05	1.5
Seabream	10.1–23.2	22	27	56	0	78	7	<0.001	na
Great barracuda	11.2–33.0	9	33	30	3	39	10	<0.01	2.6

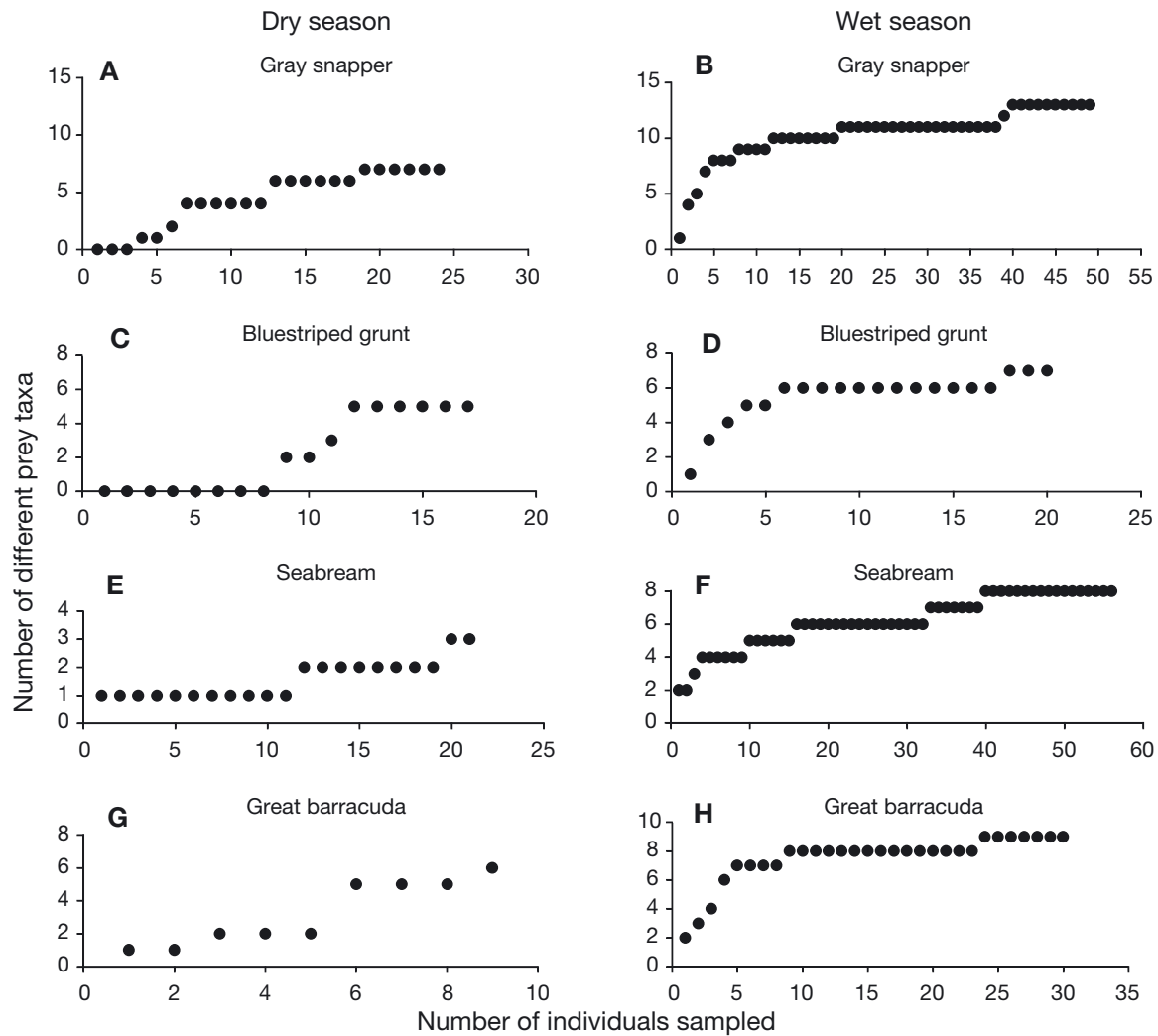


Fig. 2. *Lutjanus griseus*, *Haemulon sciurus*, *Archosargus rhomboidalis* and *Sphyraena barracuda*. Cumulative food resource curves for stomach contents

empty stomachs in the dry season compared to the wet season ( $\chi^2$ ,  $p < 0.05$ , Table 2).

Gray snapper exhibited the most diverse diet (Table 3). In the dry season, mojarras *Eucinostomus* spp., pink shrimp *Farfantepenaeus duorarum* and caridean shrimp constituted about 60% of gray snapper diet. However, in the wet season, their diet was made up of a greater variety of crustaceans and teleosts, with gulf toadfish *Opsanus beta*, hardhead silverside *Atherinomorus stipes*, caridean shrimp, blue crab *Callinectes sapidus*, mojarras, rainwater killifish *Lucania parva* and pink shrimp accounting for 60% of food items consumed. Of the primary prey items consumed, significantly more silversides were consumed in the wet season than in the dry season; however, there was no statistically significant seasonal difference in gray snapper consumption of rainwater killifish, pink shrimp, caridean shrimp, blue crab or mojarras.

For bluestriped grunt, a large amount of unidentifiable, highly digested material was found in their stomachs, likely due to the relatively rapid digestion of invertebrate skeletons (Table 3). Of the identifiable items, caridean shrimp and vegetation accounted for 60% of their diet in the dry season, and about 50% of their diet in the wet season. This seasonal difference was not statistically significant.

Aquatic vegetation, particularly seagrass *Thalassia testudinum* and macroalgae, dominated the diet of seabream in both seasons (%V = 76.92 dry, 86.36 wet; Table 3). However, significantly more vegetation was consumed in the wet season.

The diet of great barracuda was composed almost exclusively of teleosts in both seasons (Table 3D). In the dry season, hardhead silversides and rainwater killifish constituted 72% of barracuda diet. However, in the wet season, their diet was made up of a greater



Table 3. *Lutjanus griseus*, *Haemulon sciurus*, *Archosargus rhomboidalis* and *Sphyraena barracuda*. Seasonal diet in late-stage juveniles collected at night for stomach content analysis. Data are percent volume of food items in diet

Fish species	Dry season	Wet season
<b>Food items</b>		
<b>Gray snapper</b>		
Teleosts		
<i>Atherinomorus stipes</i>	0	11.83
<i>Eucinostomus</i> spp.	2.84	4.94
<i>Lucania parva</i>	0	4.24
<i>Floridichthys carpio</i>	0	0.26
<i>Opsanus beta</i>	0	23.15
Unknown or other	34.09	21.37
Crustaceans		
<i>Farfantepenaeus duorarum</i>	34.09	1.31
Caridean shrimp	24.15	9.28
<i>Callinectes sapidus</i>	0	5.14
Amphipod	0	0.05
Unknown or other	0	13.04
Echinoderm	0	0.13
Vegetation	1.70	2.37
Other	0	0.03
Unknown	3.13	2.85
<b>Bluestriped grunt</b>		
Crustaceans		
Caridean shrimp	15.38	47.67
Amphipod	15.38	0
Unknown or other	23.08	7.77
Mollusc	0	0.52
Vegetation	30.77	1.04
Other	0	0.52
Unknown	15.38	42.49
<b>Seabream</b>		
Teleosts		
<i>Atherinomorus stipes</i>	0	0.61
Crustaceans		
Caridean shrimp	22.62	1.60
Amphipod	0	0.10
Unknown or other	0.45	0.15
Mollusc	0	0.02
Vegetation	76.92	86.36
Other	0	1.84
Unknown	0	9.31
<b>Great barracuda</b>		
Teleosts		
<i>Atherinomorus stipes</i>	64.62	41.25
<i>Eucinostomus</i> spp.	0	5.82
<i>Lucania parva</i>	6.46	0.86
<i>Strongylura notata</i>	0	13.69
<i>Anchoa</i> sp.	0	17.12
Unknown or other	27.63	16.09
Crustaceans		
Caridean shrimp	0	0.68
Unknown or other	0.16	0
Vegetation	0.16	1.61
Unknown	0.97	2.88

variety of teleosts, with *Anchoa* sp., redbfin needlefish *Strongylura notata*, mojarras and hardhead silversides accounting for 78% of food items consumed. Of the primary prey items consumed, significantly more silversides were consumed in the wet season versus dry; however, there was no significant seasonal difference in consumption of mojarras and rainwater killifish.

#### Food abundance in the environment and consumption by fishes

Table 4 presents seasonal summaries of environmental abundances of major food items. Significant seasonal differences in mean abundances of silversides, mojarras and pink shrimp were found (Table 4). In terms of aggregate food abundance for gray snapper and great barracuda (i.e. all consumed primary food types combined for a particular species), we did not find any significant seasonal differences (Table 4).

Seasonal consumption of major prey items (Table 3) was compared with seasonal prey abundance in the environment (Table 4). For gray snapper, both consumption and abundance of silversides were significantly higher in the wet season. For all other primary prey items consumed by gray snapper, we failed to identify corresponding significant seasonal shifts in resource use and food supply. Consumption of rainwater killifish, pink shrimp and caridean shrimp tended to correlate with their abundance in the environment (Table 4), although the relationship was not significant. In contrast, consumption of both mojarras and blue crabs was highest when their abundance was lowest. For bluestriped grunt, consumption of caridean shrimp was highest in the dry season, when abundances were lowest. Bluestriped grunt consumption of vegetation was highest in the dry season, while mean vegetation cover at our site was equivalent with a tendency for increase in the dry season. For seabream, ingestion of vegetation (their primary food) was significantly higher in the wet season, although mean vegetation cover was similar in both seasons. Consumption of silversides and rainwater killifish by great barracuda was higher in the dry season, while their environmental abundances tended to be higher in the wet season. Abundances of mojarras declined from the dry to the wet season, while their importance in great barracuda diet tended to be higher in the wet season.

#### Population trophic niche breadth

Population trophic niche breadth was higher in the wet season versus the dry for gray snapper and great barracuda (Fig. 3A). In contrast, niche breadth of blue-

Table 4. Environmental abundance of primary food resources (individually and aggregate); data are ind. per seine haul of 142 m<sup>2</sup> (mean ± SE; range in parentheses), except for vegetation (percent cover). GS: gray snapper, GB: great barracuda. Aggregate: sum of food resources consumed—GS fed mainly on *A. stipes*, *L. parva*, *F. duorarum*, *Eucinostomus* spp. and caridean shrimp, and GB on *A. stipes*, *L. parva* and *Eucinostomus* spp.; bluestriped grunt fed almost exclusively on caridean shrimp, and seabream almost exclusively on vegetation (seagrass, mostly *Thalassia testudinum*, and algae). p: probability of a seasonal difference in environmental food supply, based on *t*-tests in which experiment-wise error rate was held at  $p = 0.10$  using the Bonferroni method; \*significant, ns: not significant

	Dry season	Wet Season	p
<i>Atherinomorus stipes</i>	44.3 ± 6.3 (1–346)	89.4 ± 7.6 (2–237)	*
<i>Eucinostomus</i> spp.	58.9 ± 4.5 (0–167)	40.7 ± 5.0 (0–244)	*
<i>Lucania parva</i>	15.3 ± 1.6 (0–71)	16.4 ± 3.4 (0–160)	ns
<i>Farfantepenaeus duorarum</i>	32.5 ± 4.2 (0–153)	17.1 ± 2.2 (0–88)	*
Caridean shrimp	172.0 ± 16.5 (0–877)	140.0 ± 23.5 (0–922)	ns
<i>Callinectes sapidus</i>	0.3 ± 0.1 (0–3)	0.1 ± 0.0 (0–1)	ns
Vegetation	91.7 ± 1.1 (40–100)	89.7 ± 1.1 (25–100)	ns
Aggregate GS	323.3 ± 23.3 (59–1197)	304.6 ± 29.6 (13–1038)	ns
Aggregate GB	118.6 ± 8.7 (10–479)	146.5 ± 11.6 (3–391)	ns

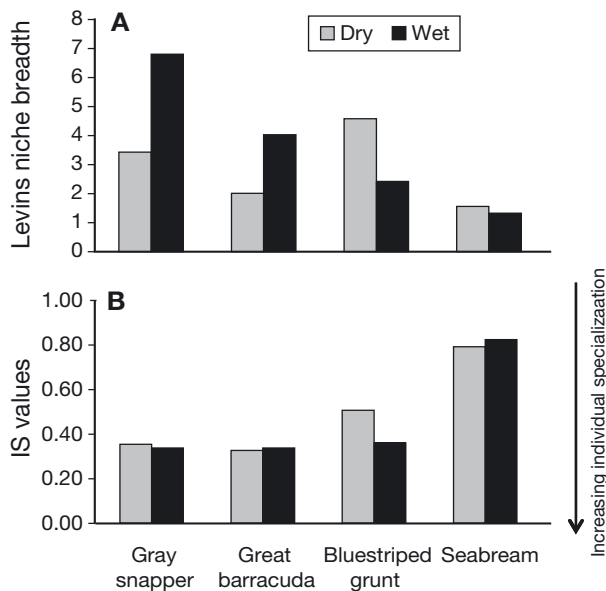


Fig. 3. *Lutjanus griseus*, *Haemulon sciurus*, *Archosargus rhomboidalis* and *Sphyraena barracuda*. (A) Levins' index of population niche breadth and (B) individual specialization (IS) index calculated for gray snapper, bluestriped grunt, seabream and great barracuda in Biscayne Bay, Florida. Niche breadth values were calculated on the percent by volume contribution of different food items in fish diets. The IS index provides a population-wide measure of individual specialization, which ranges from 0 (maximum individual specialization) to 1 (no individual specialization)

striped grunt was higher in the dry season. For seabream, trophic niche breadth was similar between seasons.

Comparing population niche breadth (Fig. 3A) with seasonal food abundance in the environment (Table 4),

trophic niche breadth of gray snapper increased from the dry to the wet season, but their primary food supply tended to show the opposite pattern. For great barracuda, trophic niche breadth and food supply both tended to be higher in the wet season compared to the dry season. Trophic niche breadth of both bluestriped grunt and seabream was higher in the dry season; their primary food supply showed a similar trend.

### Individual diet specialization

We found evidence of individual specialization, with the IS index ranging from 0.33 to 0.83. Fig. 3B presents seasonal summaries of IS values for each of the focal species. The greatest seasonal difference in IS values was for bluestriped grunt

(dry: 0.51; wet: 0.36), whereas season IS values for the other fishes were highly similar across seasons (Fig. 3b).

Comparing population niche breadth and IS values (Fig. 3) for gray snapper, niche breadth values increased from the dry to wet season; however, IS values remained constant (dry: 0.36; wet: 0.34). Similarly, for great barracuda, population trophic niche breadth was higher in the wet season, while IS values were similar across seasons (dry: 0.33; wet: 0.34). For bluestriped grunt, both population niche breadth and IS values were higher in the dry season. In contrast, population niche breadth and IS values for seabream were similar across seasons (Fig. 3). Based on our diet data, we constructed simple trophic diagrams for both the wet and dry seasons (Fig. 4).

## DISCUSSION

In the present study, we conducted a diet analysis of juvenile gray snapper, bluestriped grunt, seabream and great barracuda inhabiting the shallows of subtropical Biscayne Bay, Florida. Gray snapper was a generalist forager, feeding on a variety of small fishes and crustaceans, while bluestriped grunt fed primarily on caridean shrimp and, in the dry season, also vegetation. Seabream fed mostly on vegetation and great barracuda was almost entirely piscivorous. These feeding habits are consistent with previous studies from nearby areas (gray snapper: Starck & Schroeder 1970, Harrigan et al. 1989; bluestriped grunt: Randall 1967, Layman & Silliman 2002; seabream: Vaughan 1976, Sierra et al. 2001, Vega-Cendejas & Arreguín-Sánchez 2001; great barracuda: de Sylva 1963, Schmidt 1989). Because sea-

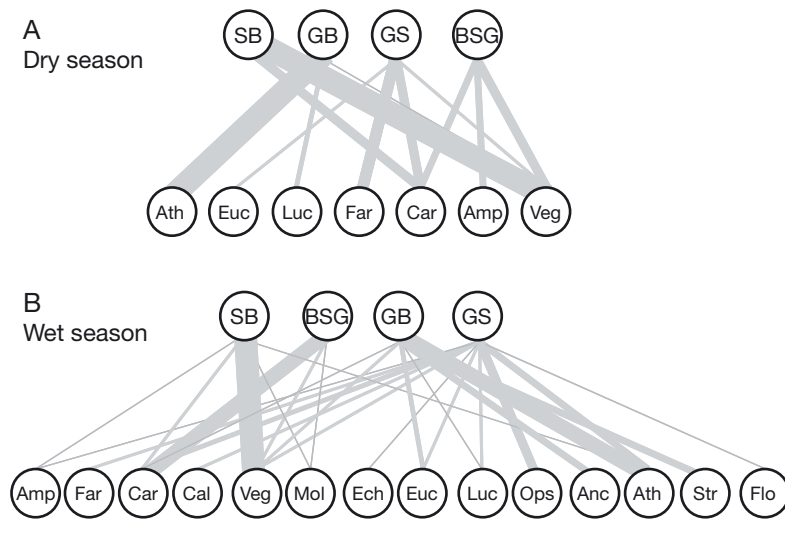


Fig. 4. Trophic model of fishes and their prey from Biscayne Bay, Florida (USA), in the (A) dry and (B) wet seasons. Fishes (top) are arranged from left to right in order of increasing population dietary niche breadth with based on data presented in Fig. 3A. The width of linking lines, correspond to the contribution by volume of different food items to fish diets, based on the data in Table 3. GS: gray snapper; BSG: bluestriped grunt; SB: seabream; GB: great barracuda. Abbreviations for food types (bottom) are the first 3 letters of taxa listed in Table 3

sonal changes in resource availability and environmental conditions can influence fish feeding patterns, we analyzed diet data for seasonal differences in feeding intensity, diet composition, population niche breadth and individual specialization to address 4 questions (see 'Introduction').

#### Fish feeding intensity is lower in the cool dry season

Feeding intensity was significantly lower during the dry season, when water temperatures were on average 8°C cooler than the wet season. Our data are consistent with others' suggesting fish feeding rates decrease as water temperature drops (Tyler 1971). Jardas et al. (2004) reported that feeding intensity of horse mackerel *Trachurus trachurus* collected from the Adriatic Sea was lower in the winter, due to both reduced food abundance and lowered fish metabolism. Because aggregate food abundances did not vary substantially across seasons for any of the 4 fish species (Table 4), we hypothesize that reduced feeding intensity during the dry season was primarily due to their depressed metabolic rates. Our data is supported by the  $Q_{10}$  expression, which is used to describe the effects of temperature on physiological rates, such as metabolism. The  $Q_{10}$  is defined as the increase in the rate of physiological processes resulting from a 10°C temperature increase (Jobling 1994). For fishes, it has been generally shown that with a 10°C temperature increase,  $Q_{10}$  is 2 and

metabolic rate doubles. In the present study we measured an 8°C average increase in temperature during the wet season compared to the dry season, and fish metabolic rate would be expected to nearly double. Indeed, at our site, species-specific fish feeding intensity increased 6- to 27-fold from the dry to the wet season. Yearly variation in temperature and/or salinity can affect fish feeding and metabolic rates. However, previous and ongoing studies at our site monitoring temperature and salinity (Serafy et al. 2003, 2007) have failed to find any evidence of significant interannual variation in temperature and salinity.

Diet studies from back-reef systems rarely report the percentage of fish sampled with empty stomachs. Of those that have presented this information, relatively high percentages of fishes with empty stomachs have been found. Previous studies have reported that between 52% (Starck & Schroeder 1970) and 69% (Randall 1967) of gray snapper sampled had empty stomachs, as did between 44% (Randall 1967) and 47% (Schmidt 1989) of great barracuda and 43% of bluestriped grunt (Randall 1967). In the present study (Table 2), we found a relatively lower proportion of fishes with empty stomachs, especially during the wet season. This may be due to 2 factors. (1) We used a sampling method that permitted rapid removal of fish from gear and immediate preservation, which minimized post-capture digestion (Bowen 1996). (2) Our sampling took place at night—a time when the fishes are likely foraging (Rooper & Dennis 1991, Nagelkerken et al. 2000, Hammerschlag & Serafy 2010). Most studies examining stomach contents of nearshore fishes have made collections during daylight hours, when many mangrove- and reef-associated species such as snappers and grunts predominantly shelter in mangroves and are not, for the most part, feeding. Our results are consistent with those reported by Odum (1970) who also conducted some diel sampling using seine nets, fish traps and poison in nearby Florida Bay. Odum (1970) found that nocturnal sampling resulted in nearly 19% more gray snapper with stomach contents present (empty: ~20% day versus 5% night).

Arrington et al. (2002) reviewed a large data set of African, neotropical and North American fishes to compare frequency of empty stomachs among different fish taxa and relate these differences to trophic guild. They found that fish trophic position was positively correlated with percentage of empty stomachs, with piscivores consistently showing the highest frequency of empty stom-



achs. In the present study, we found no evidence of this relationship, either within or across seasons (Table 2). A potential discrepancy between results may reflect that fishes examined by Arrington et al. (2002) were mainly collected from freshwater and brackish systems (e.g. rivers and estuaries), compared to purely subtropical marine systems (present study). Our results suggest that further work is needed in a variety of aquatic systems and climatic regions to further evaluate the relationship described by Arrington et al. (2002).

### Seasonal shift in resource use

Our data suggest that, for the most part, shifts in seasonal food abundance are not driving shifts in fish resource use at our study site. To further explore this relationship, we recommend future studies employing similar techniques at other sites in the area. One factor that could influence seasonal resource use at our site is competition. The mangrove shorelines of Biscayne Bay are inhabited by a diverse group of juvenile fishes which may be competing for food resources (Serafy et al. 2003, 2007). Winemiller (1989) studied the feeding habits of 9 piscivores from a diverse tropical fish assemblage in a Venezuelan creek. He suggested that during certain times of year, competition among fishes was high and this was ultimately driving their resource use. Another unmeasured variable that may have influenced seasonal fish feeding decisions at our site was predation risk. If predation risk varies spatially or seasonally, foragers should forego foraging opportunities for relative safety (see Lima & Dill 1990, Lima 1998 for reviews). For example, Dahlgren & Eggleston (2000) found that in Bahamian tidal creeks, juvenile Nassau grouper *Epinephelus striatus* trade-off food for safety by feeding in algal clumps offering relatively less nutrition, but greater protection from predators. Recent studies are challenging the notion that shallow, back-reef habitats, including mangroves and seagrass beds, harbor low piscivore densities (Newman et al. 2007, Dorenbosch et al. 2009, Payne & Gillanders 2009, Unsworth et al. 2009). A recent study at our site suggests that nocturnal predation risk to juvenile fishes varies spatially and is relatively high at night (Hammerschlag et al. 2010). Future experiments manipulating both food and predation risk at our site may provide valuable insights into fish foraging decisions.

### Population niche breadth vs. food abundance

Basic optimal foraging theory predicts that population trophic niche breadth should expand as food abundance decreases (Emlen 1966, Schoener 1971,

Stephens & Krebs 1986, Rodel et al. 2004). This is because when food is scarce, theory predicts that foragers cannot afford to bypass available prey items. Several studies have obtained results consistent with this hypothesis (e.g. McKaye & Marsh 1983, Rodel et al. 2004). Examining seasonal feeding habits of piscivorous fish in a swamp creek in Venezuela, Winemiller (1989) found that fish niche breadth increased seasonally when fish population densities were highest and availability of invertebrate prey was reduced. However, our data generally failed to support this scenario. In fact, for great barracuda, bluestriped grunt and seabream, there was a tendency for the opposite pattern: higher population niche breadth in the season when their primary food abundance was also higher. Only trophic niche breadth of gray snapper was higher in the season when food supply tended to be lower, but the seasonal differences in their food supply were not statistically significant. Sih & Christensen (2001) conducted a review of 134 studies examining optimal diet theory. Based on their analysis, they generally found relatively little support for optimal foraging theory to predict forager diet shifts in response to prey availability. However, they concluded that overall, optimal diet theory generally tended to work well for foragers that feed on immobile prey versus those that attack mobile prey. Although our results were not consistent with optimal foraging theory, we also found no support for the general conclusion proposed by Sih & Christensen (2001), since seasonal population niche breadth shifts in response to food availability were not consistent for our 4 species regardless of foraging tactic and prey type (mobile versus immobile). The lack of consistency between our results and basic foraging theory predictions may be due to the fact that seasonal food abundances may not be limiting at our site. Individuals are predicted to only add new prey types to their diet as preferred prey become scarce. Our data may reflect that densities of food are relatively high during both seasons, despite apparent seasonal differences. Recent advances in niche theory (Bolnick et al. 2002, 2003) predict that seasonal changes in population niche breadth may be achieved through changes in individual diet specialization (discussed below).

### Expansion of niche breadth vs. individual specialization

For fishes, individual specialization in movement (Hammerschlag-Peyer & Layman 2010) and diet (Bolnick et al. 2003) have been found. Here we conducted the first examination of seasonal differences in fish individual diet specialization. Our results revealed that in 3 of 4 species examined (gray snapper, great bar-

racuda and bluestriped grunt), individuals consistently fed on a narrow subset of the prey taxa consumed by the population, indicating the existence of relatively high degrees of individual diet specialization (IS < 0.5 across both seasons; Fig. 3B). In contrast, seabream showed a relatively low degree of individual specialization in either season, which is likely reflective of this species being herbivorous, with its diet dominated by vegetation in both seasons. The exact mechanisms and reasons for individual specialization remain unknown; however, it is likely related to the presence of functional trade-offs, either morphological, behavioral or physiological, e.g. learning in searching and handling prey, or in avoiding predation risk (Bolnick et al. 2003, Svanback & Bolnick 2005, Araújo et al. 2007).

Our data also gave us the opportunity to examine the interplay between population niche breadth and individual specialization and test if seasonal expansion in niche breadth corresponded with higher degrees of individual specialization. Such a pattern has been found in several taxa, including hunting wasps *Trypoxylon albonigrum* (Araújo & Gonzaga 2007), finches *Pinarolaxias inornata* (Werner & Sherry 1987), perch *Perca fluviatilis* (Svanback & Persson 2004) and fruit flies *Drosophila melanogaster* (Bolnick 2001). Our results generally failed to support this relationship. Gray snapper showed relatively high and consistent degrees of individual specialization in both seasons, although population niche breadth increased from the dry to the wet season. This implies that population niche breadth in the wet season was not expanded via increased inter-individual diet, but rather via increased within-individual variation in resource use (i.e. individuals consumed broader resources, while IS remained constant). The same pattern appears to be true for great barracuda. For bluestriped grunt, broader population niche breadth in the dry season was accompanied by lower individual specialization (higher IS values). This also implies that in the dry season, population niche breadth expanded by individuals consuming a broader array of resources versus increased specialization.

Despite this investigation into individual specialization, we caution for 2 reasons. (1) We only used stomach contents to determine individual specialization, which are only a snapshot of individual feeding habits. This type of data can be subject to sampling error and can lead to overestimated levels of diet variation. As suggested by Araújo et al. (2007), the use of a complementary measure, such as stable isotopes, would be useful to calculate individual specialization, since stable isotopes provide data on the individual's long-term diet. (2) In some species–season combinations, sample sizes were relatively small, which may have influenced our results. Thus we recommend additional sampling

at our site to further examine individual dietary specialization.

We were unable to identify some prey items to the species level due to their highly digested state. Future diet studies may consider genetic techniques that are available for identifying stomach contents. In the present study, we also only considered the percent volume contribution of different prey items to fish diet. However, prey caloric content likely plays a factor in influencing fish foraging decisions, which could have influenced our results. Future studies at this site may consider also using prey caloric content as a metric for calculating contribution of different prey items towards a fish's nutrition. Although the cumulative resource curves indicated that the number of stomachs analyzed in the present study was adequate for accurately describing the diet of each species in both seasons, sample sizes for a few of our species–season combinations were relatively small (e.g. great barracuda in the dry season), which may have influenced our findings and interpretations. Further sampling at our site across multiple seasons would verify our results.

The results of the present study have implications for fisheries management and conservation. Recent work has aimed at evaluating effects of habitat change on trophodynamics. For example, working in Bahamian Tidal creeks, Layman et al. (2007) found that the trophic niche width of gray snapper declined due to the loss of food diversity following anthropogenic habitat fragmentation. Biscayne Bay has lost over 80% of its fringe mangrove habitats; our study area within the Bay has not yet been similarly impacted by any noticeable anthropogenic habitat modifications (Milano et al. 2007). However, the present study provides baseline data on fish feeding intensity, diet composition and niche breadth to compare against any possible future ecosystem changes at our site. Data from the present study may also be useful for developing trophic models as tools for understanding multi-species fisheries (e.g. Christensen & Pauly 1992, Walters et al. 1997). The food webs we constructed for both the wet and dry season (Fig. 4) here may be useful for future studies exploring predator–prey interactions at this site, investigating impacts of environmental change or for testing various environmental or anthropogenic scenarios using ecosystem models. These types of models and other modeling approaches are expected to be more heavily utilized as management agencies move towards more ecosystem-oriented approaches to resource management.

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