

# Trophic role of gulf menhaden *Brevoortia patronus* examined with carbon and nitrogen stable isotope analysis

Zachary Olsen<sup>1,4,\*</sup>, Richard Fulford<sup>2</sup>, Kevin Dillon<sup>1</sup>, William Graham<sup>3</sup>

<sup>1</sup>Department of Coastal Sciences, University of Southern Mississippi, Ocean Springs, Mississippi 39564, USA

<sup>2</sup>United States Environmental Protection Agency, Gulf Ecology Division, Gulf Breeze, Florida 32561, USA

<sup>3</sup>Department of Marine Science, University of Southern Mississippi, Stennis Space Center, Mississippi 39529, USA

<sup>4</sup>Present address: Texas Parks and Wildlife Department, Coastal Fisheries Division, Corpus Christi, Texas 78412, USA

**ABSTRACT:** The gulf menhaden *Brevoortia patronus* is an important species of the coastal ecosystem and the target of the largest fishery by landings in the Gulf of Mexico. Menhaden species forage on a variety of plankton and detritus and, by grazing plankton stocks, may provide an important regulatory ecosystem service by reducing organic material loadings. This study used stable isotope analysis to examine the spatial, temporal, and ontogenetic dynamics of food selectivity and trophic role observed in gulf menhaden. The most important dietary item for juvenile (<100 mm total length) fish was phytoplankton (74.0% dietary composition), while that of sub-adults (100–200 mm) and adults (>200 mm) was zooplankton (61.6% for sub-adults and 52.4% for adults). Juvenile fish also utilized detritus when present in the water column, and their diet was more varied among individuals than sub-adult and adult age classes. Juveniles occupied a trophic level approximately one step lower ( $2.65 \pm 0.31$ ; mean  $\pm$  SE) than sub-adults ( $3.50 \pm 0.21$ ) and adults ( $3.39 \pm 0.19$ ). Spatial dietary variation was related to known ontogenetic habitat shifts (i.e. onshore to offshore stratification of size classes), while temporal variation was minimal, especially in the larger size classes. Since the fishery largely targets age 1+ fish (sub-adults and adults), these results suggest that if overfishing occurs to the extent that it impacts recruitment, it may decrease the resiliency of the inshore Gulf of Mexico ecosystem to eutrophication by decreasing the abundance of juvenile fish seasonally present in this environment.

**KEY WORDS:** *Brevoortia patronus* · Stable isotopes · Trophic position · Bayesian mixing model · Ecosystem role

Resale or republication not permitted without written consent of the publisher

## INTRODUCTION

The gulf menhaden *Brevoortia patronus* is a small clupeid distributed in the shelf and estuarine waters of the Gulf of Mexico. Because of their large numbers and defensive schooling behavior in surface water (Vaughan et al. 2000), menhaden play dual ecosystem roles as a filter feeder (Durbin & Durbin 1975, Friedland et al. 1984, Friedland 1985) and a main prey item for many economically and ecologically important species of fish, marine mammals, and birds

(McLean & Byrd 1991, Fertil & Wursig 1995, Scharf & Schlicht 2000). As filter feeders, they are believed to forage on a range of phytoplankton and zooplankton as well as vascular plant detritus (Durbin & Durbin 1983, Friedland et al. 1984, Deegan et al. 1990, Castillo-Rivera et al. 1996). Because of the large numbers of these fish found seasonally inshore and the resulting filtration potential (Durbin & Durbin 1975, Deegan 1993), it has been suggested that menhaden may influence local water quality via grazing controls on phytoplankton and zooplankton (Lynch et

al. 2010), but the importance of this effect is dependent, in part, on the dietary selection of the menhaden population.

Gulf menhaden support the largest fishery by landings in the Gulf of Mexico (NMFS 2012). This commercial industry, termed a reduction fishery, uses small aircraft to locate schools of menhaden, usually in coastal waters, and captures the located fish using large purse seining vessels. At dockside reduction factories located in Mississippi and Louisiana, the fish are off loaded and processed into fish oil and fish meal, which has various uses as industrial lubricants, industrial additives, food supplements, fertilizers, and animal feeds (Smith 1991). While the most current assessment of the fishery reports *Brevoortia patronus* are not overfished or undergoing overfishing (Vaughan et al. 2007), this assessment does not consider the ecological role of the species, and the potential exists for such a large fishery to yield an ecological impact, so that role should be well understood.

Despite the ecological importance of gulf menhaden as a dominant prey fish (Hoese & Moore 1998) and the economic importance of this organism in the Gulf of Mexico, there is surprisingly little species specific trophic data. Most available trophic level and dietary data are reported for the congener Atlantic menhaden *Brevoortia tyrannus*, which has no distributional overlap with *B. patronus*. Further, diet data for *B. tyrannus* is based largely on gut content analysis. While gut content information is useful, it relies heavily on the assumption that what is found and identified in the stomach is both non-biased and metabolically important (Darnell 1961, June & Carlson 1971, Jeffries 1975, Castillo-Rivera et al. 1996). Filter feeders may consume a variety of potential food items when feeding, and utilize indirect means of selection such as increasing swimming speed in response to preferred prey, differential retention efficiency, and selective digestion (Durbin & Durbin 1975, Friedland et al. 1984, Friedland et al. 2005). As a result, dietary information on *B. patronus* is somewhat incomplete, and studies have often not taken into account spatial, temporal, or ontogenetic shifts that may occur (Deegan et al. 1990, Castillo-Rivera et al. 1996).

Stable isotope analysis bypasses many of the assumptions of traditional gut content analysis (Fry 2006) and provides a way to quantify the metabolic assimilation of available planktonic particles in the species and system of interest. In the present study, we utilized carbon and nitrogen isotope ratios to quantify the relative contribution of various plank-

tonic food sources to gulf menhaden. Additionally, we examined the relative similarity of gulf menhaden diet and trophic level to 2 other specialist planktivores found in the northern Gulf of Mexico ecosystem, bay anchovy *Anchoa mitchilli* and eastern oyster *Crassostrea virginica*, as these organisms have well-documented feeding behaviors as zooplanktivores and phytoplanktivores, respectively (Johnson et al. 1990, Newell 2004). We also examined the ontogenetic, spatial, and temporal variation in trophic dynamics of *Brevoortia patronus* to better understand dietary plasticity of this species within the estuary and relate observed patterns back to the potential for an ecological impact of the fishery.

## MATERIALS AND METHODS

Gulf menhaden and plankton samples were collected monthly from June to August 2010 and March to September 2011 in 3 study regions along the Mississippi coast in the northern Gulf of Mexico: West Pascagoula River (WPR), Biloxi Back Bay (BB), and Bay Saint Louis (BSL). Within each region, samples were collected systematically from nearshore out to adjacent portions of the Mississippi Sound in 3 strata (dock, bay, sound; Fig. 1).

Fishery independent sampling of sub-adult (100–200 mm total length [TL]) and adult (>200 mm) menhaden was conducted monthly utilizing a stratified random sampling design by region with sampling locations randomly selected within each bay strata and adjacent sound strata. These size classes were collected with a 150 m long monofilament gill net. Because of low sample size, sub-adult and adult menhaden samples in bay and sound strata were supplemented by fishery-dependent samples collected by personnel from the National Marine Fisheries Service and Mississippi Department of Marine Resources.

Since juvenile menhaden (<100 mm) primarily utilize the farthest inshore reaches of the estuary (Deegan 1990), sites were selected along the immediate shoreline of each study region (dock strata) to target collections of this size class. Fishery independent juvenile collections were conducted monthly using a 2 m diameter monofilament cast net.

Planktonic prey sampling was conducted in conjunction with the fishery-independent sampling. Triplicate plankton samples were collected in the immediate vicinity of each gill net or cast net set by either 2 to 4 min oblique surface tows of 0.5 m, 200  $\mu$ m and 64  $\mu$ m nitex mesh plankton net or a 19 to

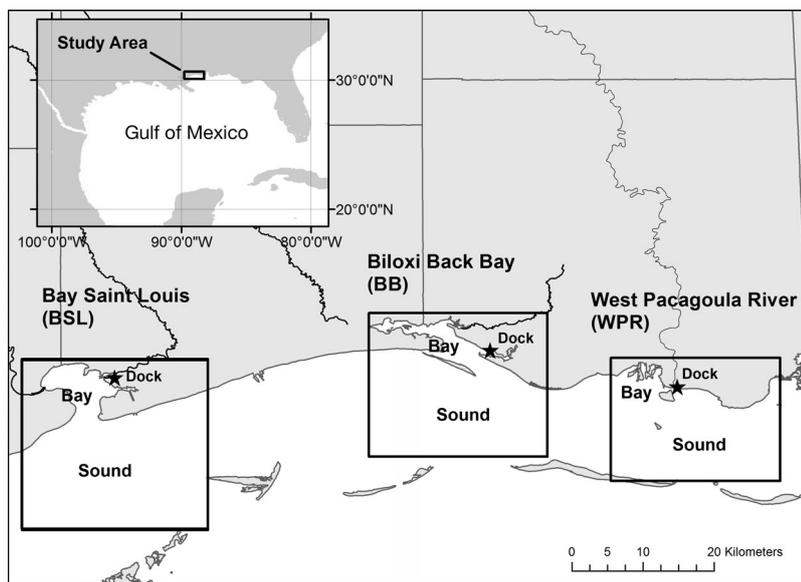


Fig. 1. Study area along the Mississippi coast in the northern Gulf of Mexico showing the 3 study regions along with the 3 strata (dock, bay, and sound) within each region

38 l whole water sample collected with a water pump. The samples were size-fractionated post-collection using a series of brass sieves (355, 212, 64, and 20  $\mu\text{m}$ ) to yield 4 size fractions of plankton: >355  $\mu\text{m}$  (hereafter referred to as 355  $\mu\text{m}$ ), 355–212  $\mu\text{m}$  (hereafter referred to as 212  $\mu\text{m}$ ), 212–63  $\mu\text{m}$  (hereafter referred to as 63  $\mu\text{m}$ ) and 63–20  $\mu\text{m}$  (hereafter referred to as 20  $\mu\text{m}$ ). These samples were preserved on ice for analysis. Samples of black needle rush (*Juncus roemerianus*; hereafter referred to as *Juncus*) were also collected adjacent to study sites. This is generally considered to be the dominant marsh grass and detrital source of Mississippi Gulf coast estuaries (Hackney & Haines 1980) and because of the similarity in isotopic composition to upland plants, was chosen to represent a ‘model’ vascular plant detrital source.

Reference consumers were also collected for trophic and dietary comparison. *Anchoa mitchilli* were collected in the Mississippi Sound adjacent to BB with a 4.5 m otter trawl in May of 2011 and *Crasostrea virginica* were collected at Marsh Point in BB with a 12 prong half dredge in January of 2012.

### Sample preparation

Juvenile menhaden and all anchovies were processed whole due to the difficulty of obtaining a sample large enough for isotopic analysis. To avoid contamination by organ tissue and stomach contents,

these samples were eviscerated prior to analysis. For sub-adult and adult fish, a dorsal muscle sample was excised and processed for isotope analysis (Schielke & Post 2010). Skin and bone were carefully removed from white muscle samples and both white muscle and whole samples rinsed with deionized water to remove shell fragments, blood, and other bodily fluids. Oysters were removed from their shells for analysis to avoid carbonate contamination.

All samples were freeze-dried and homogenized to a fine powder. Homogenized whole fish, shellfish, and potential food sources were rinsed in 10% HCl to remove inorganic carbonates (Chanton & Lewis 1999, Pinnegar & Polunin 1999). Lipids were extracted from muscle samples as is generally suggested (Post et al. 2007) using a

method similar to that described by Ruiz et al. (2007). Sub-adult and adult gulf menhaden are particularly high and quite variable in body lipids (Deegan 1986), and lipid extraction is a necessary step to minimize analytical variability. Acid washed portions of whole fish tissue and oyster tissue were utilized for carbon isotope analysis, while non-acid washed portions of whole fish were utilized for nitrogen isotope analysis because of the bias often introduced to the  $\delta^{15}\text{N}$  values by the acid washing procedures (Pinnegar & Polunin 1999). Lipid extracted portions of white muscle tissue (sub-adult and adult fish) were utilized for both carbon and nitrogen isotope analysis, and  $\delta^{15}\text{N}$  values were then ‘back corrected’ to pre-extraction values using the multiple linear regression correction ( $p < 0.001$ ;  $r^2 = 0.582$ ) outlined in Eq. (1):

$$\delta^{15}\text{N}_{\text{MC}} = 1.392 + (0.769 \times \delta^{15}\text{N}_{\text{ME}}) + (0.308 \times \text{C:N}_{\text{ME}}) \quad (1)$$

where  $\delta^{15}\text{N}_{\text{MC}}$  is the  $\delta^{15}\text{N}$  value for unaltered muscle tissue,  $\delta^{15}\text{N}_{\text{ME}}$  is the  $\delta^{15}\text{N}$  value for lipid extracted muscle tissue, and  $\text{C:N}_{\text{ME}}$  is the carbon to nitrogen ratio of lipid extracted muscle tissue. This model was based on an empirical comparison of extracted and non-extracted portions of 30 gulf menhaden muscle samples and then tested for accuracy based on 15 additional gulf menhaden muscle samples and a comparison of unaltered-corrected  $\delta^{15}\text{N}$  values to extracted  $\delta^{15}\text{N}$  values. Corrected and non-extracted  $\delta^{15}\text{N}$  values were found to be statistically indistinguishable ( $t = -0.899$ ,  $df = 27.126$ ,  $p = 0.3766$ ). This

correction was applied to all lipid extracted  $\delta^{15}\text{N}$  values.

### Isotope analysis and statistical procedures

All samples were analyzed using continuous flow stable isotope ratio mass spectrometry (CF-IRMS) with a Costech Elemental Combustion System coupled to a Thermo-Fisher Scientific Delta V Advantage Isotope Ratio Mass Spectrometer at the Gulf Coast Research Laboratory's stable isotope facility. Isotope values are reported relative to established standards for each element and expressed in standard  $\delta$  notation as outlined in Eq. (2):

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3 \quad (2)$$

where  $X$  is the isotope of interest ( $^{13}\text{C}$  and  $^{15}\text{N}$ ) and  $R$  is the corresponding ratio of heavy to light isotopes ( $^{13}\text{C}/^{12}\text{C}$  and  $^{15}\text{N}/^{14}\text{N}$ ) for the sample being analyzed or for the established standard material (PeeDee limestone carbon or atmospheric nitrogen).

A non-parametric Kruskal-Wallis test was used to assess differences in raw isotope values between size classes of menhaden and also plankton size fractions due to both deviations from normality and equal variance. A 2-way ANOVA was used to test for spatial (among study regions) and temporal differences in isotopic values of menhaden and plankton. A student's  $t$ -test was used to examine differences in sub-adult and adult menhaden isotope values between bay and sound strata, and a 1-way ANOVA and Wilcoxon signed-rank test used to test for differences in phytoplankton and zooplankton isotope values, respectively, between strata. Results were deemed significant at  $\alpha = 0.05$ .

The functional trophic level of gulf menhaden was estimated by Eq. (3):

$$\text{Trophic Level} = 1 + (\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{primary producer}})/\Delta^{15}\text{N} \quad (3)$$

where  $\delta^{15}\text{N}_{\text{consumer}}$  is the  $\delta^{15}\text{N}$  (‰) of the consumer,  $\delta^{15}\text{N}_{\text{primary producer}}$  is the baseline or average  $\delta^{15}\text{N}$  (‰) of the primary producers (phytoplankton/detritus, represented by the 20  $\mu\text{m}$  size fraction), and  $\Delta^{15}\text{N}$  (‰) or the nitrogen isotopic fractionation factor between trophic levels (Fredriksen 2003, Rooker et al. 2006). The trophic fractionation factor for nitrogen isotopes utilized in this study was 2.3‰ (McCutchan et al. 2003), as this was determined for aquatic organisms from a variety of sources. Additionally, this value falls between that calculated for organisms utilizing vascular plants and those utilizing other diets and also

between those utilizing a high protein based diet and those utilizing a low protein based diet (McCutchan et al. 2003). Past work has suggested that gulf menhaden are, to some extent, omnivorous (Castillo-Rivera et al. 1996) and, as a result, trophic fractionation factors most likely vary depending on the food source utilized by the fish. For this reason, utilizing an averaged trophic enrichment factor which falls between those of organisms with specialized diets, as the one chosen for this study, will most likely yield accurate results.

To estimate the cumulative importance of pre-defined planktonic food sources available to gulf menhaden and the relative similarity of gulf menhaden to the reference consumer groups (oysters and bay anchovy), we examined multivariate dietary mixing with a Bayesian isotopic mixing model applied in the program Stable Isotope Analysis in R (SIAR, <http://cran.r-project.org>, Parnell et al. 2010). The outcome of this analysis was an estimate of the relative proportional importance of phytoplankton (20  $\mu\text{m}$  fraction), zooplankton (355  $\mu\text{m}$  fraction), and detritus (*Juncus*) to menhaden diet based on the comparison of menhaden to prey isotope ratios. Trophic corrections of  $0.4 \pm 1.2\text{‰}$  for  $\Delta^{13}\text{C}$  and  $2.3 \pm 1.6\text{‰}$  for  $\Delta^{15}\text{N}$  from McCutchan et al. (2003) were used once again based on the argument presented above. The outcome of the comparison of gulf menhaden to reference consumer groups consists of percent similarity of menhaden dietary composition to the reference consumers. This use of consumer data in mixing models allows for direct dietary comparisons among species in a given ecosystem and, to our knowledge, is the first time they have been used in such a way. This comparison was conducted utilizing average isotopic values for *Anchoa mitchilli* and *Crassostrea virginica* as sources in the Bayesian mixing model (no trophic correction applied in this case). The Bayesian approach is most informative as it provides a measure of uncertainty about the estimates.

## RESULTS

### Menhaden stable isotopes

Ontogenetic differences were shown to be the largest source of variation within the gulf menhaden population. Differences in carbon and nitrogen isotope ratios were detected among the 3 size classes of menhaden examined. Juveniles were shown to be most similar in isotopic composition to phytoplankton, and sub-adult and adults most similar in isotopic com-

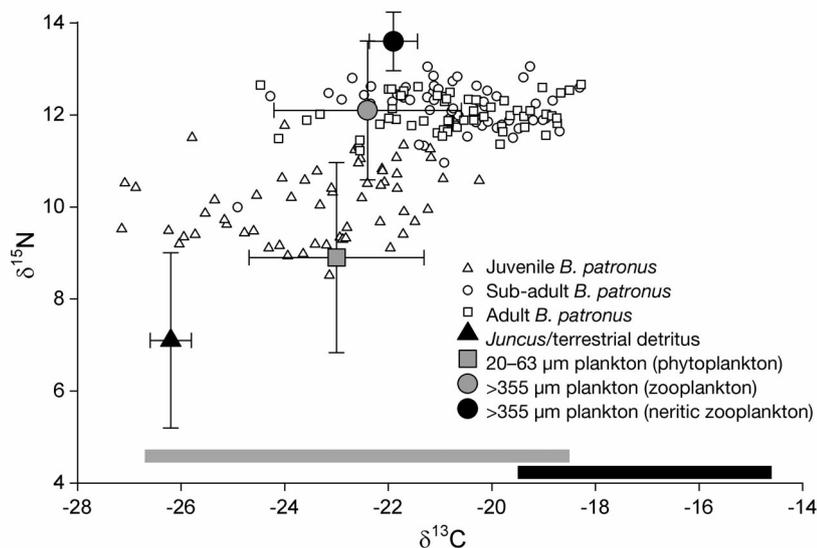


Fig. 2. *Brevoortia patronus*.  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of juvenile, sub-adult, and adult *B. patronus* along with the 3 potential food sources ( $\pm$ SD). Isotope values for neritic zooplankton ( $\pm$ SD) have been added along with a range of neritic (gray) and oceanic (black) particulate organic matter  $\delta^{13}\text{C}$  values (Dorado et al. 2012; shown on the x-axis) for comparison. Food source isotope values are corrected for trophic enrichment

position to zooplankton. The overall range of menhaden  $\delta^{13}\text{C}$  enrichment was coincident with ranges of neritic, but not oceanic carbon isotope values reported by Dorado et al. (2012), but oceanic carbon may potentially explain the highly enriched values of some

Table 1. *Brevoortia patronus*. Statistical analysis of stable isotope data for gulf menhaden. Samples were analyzed separately for juvenile and sub-adult/adult fish among region (Bay Saint Louis, Biloxi Back Bay, and West Pascagoula River), and month (March to August for juveniles and June to August for sub-adult/adults). Due to the fact that juvenile menhaden were only collected from a single strata (dock), only sub-adult/adult fish were analyzed

		df	Test statistic	p-value
<b>Menhaden</b>				
Size class	$\delta^{13}\text{C}$	2	$H = 71.95$	<0.0001
	$\delta^{15}\text{N}$	2	$H = 109.49$	<0.0001
<b>Juvenile</b>				
Region	$\delta^{13}\text{C}$	2	$F = 8.76$	0.0005
	$\delta^{15}\text{N}$	2	$F = 5.37$	0.0075
Month	$\delta^{13}\text{C}$	1	$F = 5.61$	0.022
	$\delta^{15}\text{N}$	1	$F = 0.39$	0.533
<b>Sub-adult/adult</b>				
Region	$\delta^{13}\text{C}$	2	$F = 3.97$	0.022
	$\delta^{15}\text{N}$	2	$F = 12.11$	<0.0001
Month	$\delta^{13}\text{C}$	1	$F = 0.59$	0.444
	$\delta^{15}\text{N}$	1	$F = 5.16$	0.025
Strata	$\delta^{13}\text{C}$	111	$t = -4.94$	<0.0001
	$\delta^{15}\text{N}$	111	$t = 0.86$	0.392

sub-adult and adult menhaden (Fig. 2). Juvenile fish were depleted in  $\delta^{13}\text{C}$  compared to sub-adults and adults, which were comparable in their carbon isotope ratios. Similarly, juveniles were depleted in  $\delta^{15}\text{N}$  ratios compared to sub-adults and adults, while adult fish were observed to be depleted relative to sub-adults. As a result of this analysis and known migratory patterns of this species, adult and sub-adults have been grouped for spatial and temporal comparisons of raw isotopic values.

Spatial and temporal differences were also observed, but were weaker and differed among the 2 groups. Isotopic ratios of  $\delta^{13}\text{C}$  for juvenile fish were found to differ among study regions and months showing greater depletion at site BSL and the longer time spent inshore after the initial arrival as larvae sometime during the winter months (Deegan 1990). However, 2 of these months had small sample sizes

(March,  $n = 4$  and July,  $n = 5$ ) which may bias results. Isotopic ratios of  $\delta^{15}\text{N}$  for juvenile fish were also found to differ among study regions with fish from BSL showing more depletion compared to BB but not WPR. Differences were not observed among months for juvenile fish. For sub-adult and adult fish,  $\delta^{13}\text{C}$  values were found to vary slightly among regions but not among months with fish from site WPR showing more depletion than those from BB but not BSL. Isotopic ratios of  $\delta^{15}\text{N}$  were found to differ among regions and months with BB showing greater enrichment than both BSL and WPR. Sub-adult and adult  $\delta^{13}\text{C}$  values were significantly depleted in the bay strata compared to sound strata, while  $\delta^{15}\text{N}$  were not found to be significantly different. In some cases, significance or non-significance of raw isotope values were not related to those determined by trophic level and mixing model outputs, as these alternative calculations take into account multiple parameters associated with the specific trophic or dietary relationship. Outputs from all statistical tests conducted on menhaden isotope values are given in Table 1.

### Plankton stable isotopes

Isotope values for both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  were found to be significantly different between plankton size fractions with variation observed between the 355  $\mu\text{m}$

Table 2. *Brevoortia patronus*. Statistical analysis of stable isotope data for plankton collected as potential food sources of gulf menhaden *B. patronus*. Samples were analyzed separately for phytoplankton and zooplankton among region (Bay Saint Louis, Biloxi Back Bay, and West Pascagoula River), and month (March to August for phytoplankton and June to August for zooplankton). Phytoplankton were collected in all 3 strata (dock, bay and sound), while zooplankton were only collected in 2 strata (bay and sound)

		df	Test statistic	p-value
<b>Plankton</b>				
Size class	$\delta^{13}\text{C}$	3	$H = 10.50$	0.015
	$\delta^{15}\text{N}$	3	$H = 148.49$	<0.0001
<b>20 <math>\mu\text{m}</math> (phytoplankton)</b>				
Region	$\delta^{13}\text{C}$	2	$F = 10.85$	<0.0001
	$\delta^{15}\text{N}$	2	$F = 3.71$	0.030
Month	$\delta^{13}\text{C}$	4	$F = 0.99$	0.421
	$\delta^{15}\text{N}$	4	$F = 1.81$	0.139
Strata	$\delta^{13}\text{C}$	2	$F = 4.36$	0.016
	$\delta^{15}\text{N}$	2	$F = 6.89$	0.002
<b>355 <math>\mu\text{m}</math> (zooplankton)</b>				
Region	$\delta^{13}\text{C}$	2	$F = 8.17$	0.0005
	$\delta^{15}\text{N}$	2	$F = 1.43$	0.244
Month	$\delta^{13}\text{C}$	1	$F = 0.84$	0.360
	$\delta^{15}\text{N}$	1	$F = 0.80$	0.374
Strata	$\delta^{13}\text{C}$		$W = 533$	0.0002
	$\delta^{15}\text{N}$		$W = 658$	0.007

and 20  $\mu\text{m}$  size fractions. Enrichment observed in  $\delta^{15}\text{N}$  values between these size fractions (Peterson & Fry 1987) suggest that the 20  $\mu\text{m}$  fraction consists mainly of phytoplankton, while the 355  $\mu\text{m}$  fraction consists mainly of zooplankton and 63  $\mu\text{m}$  and 212  $\mu\text{m}$  size fractions a mixture of these 2 trophic levels. This was further verified by microscopic examination of samples and fully presented in Olsen (2012). For this reason, only the 20  $\mu\text{m}$  and 355  $\mu\text{m}$  size fractions were utilized for comparison with menhaden data.

Spatial variation among study regions was observed in 20  $\mu\text{m}$  plankton (phytoplankton) isotope values though it was much weaker for  $\delta^{15}\text{N}$  than  $\delta^{13}\text{C}$ . Temporal variation across months (March to August) was not observed in phytoplankton values. Spatial variation among study regions was also observed in 355  $\mu\text{m}$  plankton (zooplankton)  $\delta^{13}\text{C}$  values though not in  $\delta^{15}\text{N}$  values. Temporal variation across months (June to August) was not observed in zooplankton values. Phytoplankton and zooplankton isotope values were found to be slightly different between strata. Note that we were

unable to collect sufficient zooplankton in the dock strata to allow for isotopic analysis. Outputs from all statistical tests conducted on plankton isotope values are given in Table 2.

### Menhaden trophic variation

Due to the potential for movement of adult and sub-adult menhaden among sites, an evenly weighted average  $\delta^{15}\text{N}$  baseline (20  $\mu\text{m}$  phytoplankton size fraction) value of the 3 study regions (6.5‰) was utilized in the trophic level calculations. However, we assumed juveniles migrate much less among sites and these isotopic  $\delta^{15}\text{N}$  baseline values were found to be significantly different. Because of this potential difference in movement patterns and site  $\delta^{15}\text{N}$  baselines, we chose to utilize site-specific values in the trophic level calculations for this size class. Plankton values from strata within each region were averaged together due to potential movement to deeper waters throughout the summer months (Deegan 1990). The baseline nitrogen value used for BSL was 5.6‰, while that of BB was 6.8‰ and that of WPR was 7.0‰.

Juvenile menhaden had the lowest trophic level and sub-adults had the highest (Table 3). Calculated trophic levels showed a similar relationship among size classes with a general trend of decreasing trophic level observed between sub-adult and adults and a general increase from juveniles to sub-adults. This difference between juveniles and sub-adults may have been more distinct had there been a larger number of fish of 100–150 mm TL in the data set (Fig. 3). Overall, sub-adult and adult menhaden from site BSL occupied a slightly lower trophic level compared to the other sites, while a slightly higher trophic level was calculated for the juvenile size class at this site (Table 3). Trophic level calculations among months showed little variation especially for

Table 3. *Brevoortia patronus*. Calculated trophic levels for the 3 size classes of *B. patronus* ( $\pm$ SE). Trophic level calculation is based on shifts in  $\delta^{15}\text{N}$  relative to an evenly weighted average of the 3 site baselines for sub-adults and adults (6.5‰) and site-specific baselines for juveniles (Bay Saint Louis 5.6‰, Biloxi Back Bay 6.8‰, and West Pascagoula River 7.0‰)

	Juveniles		Sub-adults		Adults		All fish	
	Mean trophic level $\pm$ SE	n						
BSL	2.88 $\pm$ 0.06	20	3.36 $\pm$ 0.04	25	3.32 $\pm$ 0.03	44	3.23 $\pm$ 0.03	89
BB	2.58 $\pm$ 0.06	25	3.56 $\pm$ 0.03	30	3.48 $\pm$ 0.04	19	3.21 $\pm$ 0.06	74
WPR	2.44 $\pm$ 0.05	13	3.58 $\pm$ 0.04	28	3.47 $\pm$ 0.05	15	3.28 $\pm$ 0.07	56

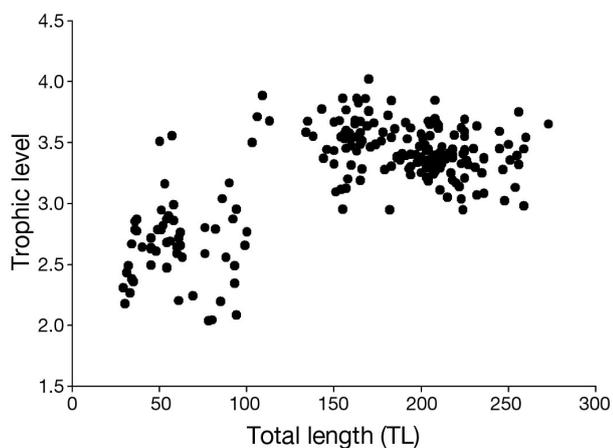


Fig. 3. *Brevoortia patronus*. Trophic level by total length. Trophic level calculation is based on shifts in  $\delta^{15}\text{N}$  relative to an evenly weighted average of the 3 site baselines for sub-adults and adults (6.5‰) and site-specific baselines for juveniles (Bay Saint Louis 5.6‰, Biloxi Back Bay 6.8‰, and West Pascagoula River 7.0‰)

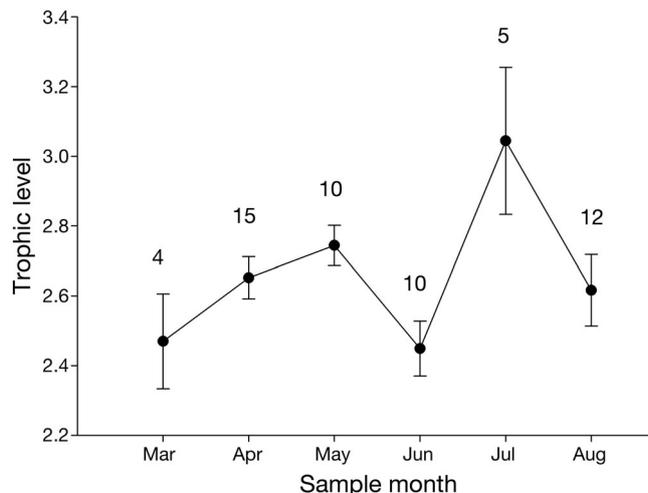


Fig. 4. *Brevoortia patronus*. Mean trophic level calculations ( $\pm$ SE) for juvenile *B. patronus* from March to August 2011. Trophic level calculation is based on shifts in  $\delta^{15}\text{N}$  relative to site-specific baseline values of 5.6‰ (Bay Saint Louis), 6.8‰ (Biloxi Back Bay), and 7.0‰ (West Pascagoula River). Sample size for each month is given

sub-adult and adult fish (Olsen 2012), while those of juvenile fish showed some variation with a slight decrease in trophic level in June followed by an increase in July (Fig. 4).

### Menhaden mixing models

In order to simplify interpretation of this analysis, averaged food source values across sites, months, and strata were utilized for all size classes of men-

haden. Quantitative mixing model outputs showed a higher use of phytoplankton and detritus for juvenile menhaden relative to sub-adult and adult fish (Table 4). Additionally, the surrounding 95% posterior intervals for relative dietary use of phytoplankton and zooplankton were smaller for juvenile gulf menhaden than for sub-adults and adults.

Relative dietary contributions to menhaden were similar among all sites with the exception of *Juncus* detritus within the diet of the juvenile size class (Table 4). Juvenile fish captured at site BSL were found to have 5 to 10 times higher detrital contributions to their diets compared to juveniles from the other study regions. The higher contribution of detritus in the diet of juvenile menhaden as a size class can be largely attributed to fish from this site. Relatively little change was seen in dietary contributions of menhaden among months aside from dietary shifts of juvenile fish similar to those seen in the trophic level data (Olsen 2012).

Table 4. *Brevoortia patronus*. Bayesian mixing model inputs ( $\pm$ SD) and outputs for the 3 size classes of *B. patronus* relative to 3 potential food sources (Zooplankton, Phytoplankton, and *Juncus* detritus) and to 2 reference consumers (*Crassostrea virginica* and *Anchoa mitchilli*). 95% posterior intervals are given in parentheses

	Zoo-plankton n = 101	Phyto-plankton n = 88	<i>Juncus</i> n = 3	<i>C. virginica</i> n = 16	<i>A. mitchilli</i> n = 10
<b>Model inputs</b>					
$\delta^{13}\text{C}$	-22.8 $\pm$ 1.8	-23.4 $\pm$ 1.5	-26.6 $\pm$ 0.4	-25.6 $\pm$ 0.5	-21.3 $\pm$ 0.6
$\delta^{15}\text{N}$	9.8 $\pm$ 1.5	6.6 $\pm$ 1.8	4.8 $\pm$ 1.9	8.8 $\pm$ 0.4	13.1 $\pm$ 0.5
%C	38.7 $\pm$ 12.8	10.2 $\pm$ 6.2	47.6 $\pm$ 0.97	42.8 $\pm$ 0.8	40.5 $\pm$ 1.7
%N	7.1 $\pm$ 3.5	1.7 $\pm$ 1.8	0.94 $\pm$ 0.03	5.0 $\pm$ 0.3	11.7 $\pm$ 0.5
<b>Model outputs</b>					
	Percent dietary composition			Percent dietary similarity	
<i>B. patronus</i> , Juvenile	16.7 (11.3–22.1)	74.0 (64.7–83.1)	9.3 (3.1–15.8)	82.5 (79.4–85.8)	17.5 (14.2–20.6)
<i>B. patronus</i> , Sub-adult	61.6 (44.4–80.4)	37.8 (18.7–55.3)	0.6 (0–1.8)	30.9 (24.8–36.9)	69.1 (63.1–75.2)
<i>B. patronus</i> , Adult	52.4 (37.2–68.5)	47.0 (30.8–62.4)	0.6 (0–1.8)	43.2 (39.8–46.3)	56.8 (53.7–60.2)

### Planktivorous filter feeder comparison

Isotope ratios and dietary composition of *Anchoa mitchilli* and *Crassostrea virginica* determined

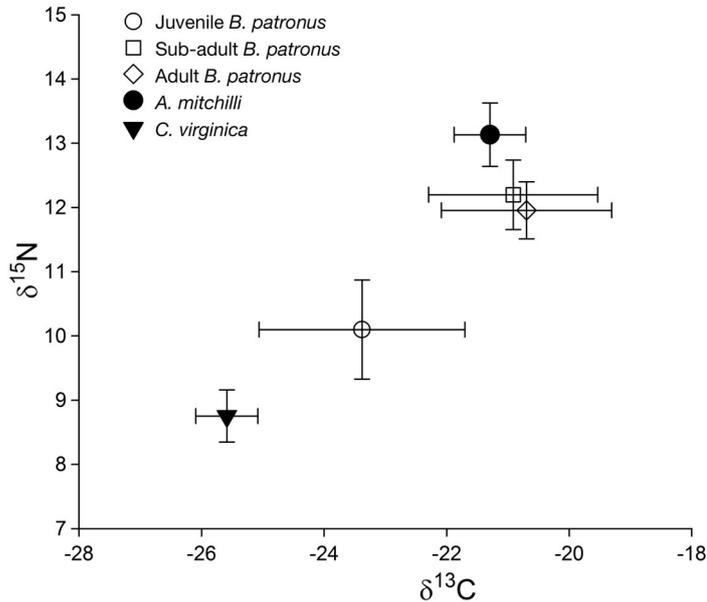


Fig. 5.  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values ( $\pm\text{SD}$ ) for *Anchoa mitchilli* and *Crassostrea virginica* along with the 3 size classes of *Brevoortia patronus*

by our study (Fig. 5) are comparable to those outlined in the literature (Johnson et al. 1990, Newell 2004). Juvenile menhaden were observed to be more balanced in dietary composition similar to *C. virginica*, while sub-adults and adults possessed a dietary composition close to but less enriched than that of *A. mitchilli* (Fig. 5). Both juveniles and adults showed comparable variation in relative dietary similarity for both *A. mitchilli* and *C. virginica*, while sub-adults possessed a wider 95% posterior interval for each (Table 4).

## DISCUSSION

### Ontogenetic and spatial dietary variation

Juvenile gulf menhaden have distinctly different diets than sub-adults and adults; juveniles feed on proportionately 2 to 3 times more phytoplankton than the larger size classes. This size class arrives in nearshore nursery grounds from offshore spawning grounds in late winter followed by sub-adults and adults in early spring. They spend the summer feeding and growing before migrating offshore the following fall (Deegan 1986). The dietary shift observed between juvenile and sub-adult gulf menhaden seems to occur during the first winter offshore, as suggested by the lack of small sub-adults (100–150 mm) observed nearshore during our study.

Our findings are consistent with past studies (Durbin & Durbin 1975, Friedland et al. 1984, Friedland et al. 2006, Lynch et al. 2010, Friedland et al. 2011). Friedland et al. (2006) found that the first major increase in branchiospinule spacing in Atlantic menhaden occurred at approximately 100 mm fork length (FL,  $\approx 116$  mm TL). Spacing increased until fish reached approximately 200 mm FL ( $\approx 231$  mm TL). This suggests that juveniles filter smaller phytoplankton quite efficiently during estuarine residency. This changed with increased branchiospinule spacing after moving offshore with the adult population (Friedland et al. 2006).

The increase in phytoplankton usage of adult menhaden compared to sub-adults suggests that the filtration apparatus becomes more efficient, larger aggregates of phytoplankton become available to adults as gill raker spacing grows, or possibly adult menhaden behaviorally seek out phytoplankton. Friedland et al. (2006) suggested that this was an eco-morphological characteristic that enabled adult Atlantic menhaden to avoid competition for smaller phytoplankton when migrating northward into competitive foraging grounds. While such migration is not reported for gulf menhaden (Ahrenholz 1991), adults may still take advantage of larger phytoplankton species or aggregates of smaller phytoplankton (e.g. Kiørboe et al. 1990, Alldredge et al. 1995) throughout their range. As for behavioral changes in adult menhaden, Durbin et al. (1981) and Durbin & Durbin (1975) determined that adult Atlantic menhaden *ex situ* do have the ability to behaviorally select various size fractions of plankton and so may not entirely rely on passive means of food selection in the wild.

Juvenile menhaden showed a shift in carbon source that reflects a spatial shift from offshore larvae to nearshore juveniles. This pattern of depleted carbon utilization, and a wider range of carbon sources compared to sub-adult and adult fish, reflects the 20  $\mu\text{m}$  plankton fractions collected nearshore. This is likely related to higher levels of terrestrial detritus in the nearshore food web (*Juncus* or upland plants), which varies among sites. The influence of *Juncus* terrestrial carbon was most clearly seen when we examined juvenile menhaden from site BSL, where juveniles were estimated to consume approximately 5 to 10 times more detritus than those captured at other sites. The 20  $\mu\text{m}$  plankton size fractions collected from BSL dock strata were slightly more depleted in  $\delta^{13}\text{C}$  compared to the other sites. This may imply a larger detrital input (Hackney & Haines 1980, Peterson & Fry 1987) or a lack of other food sources (phyto-

plankton/zooplankton) in the water column. Regardless, this agrees with past work done by Deegan et al. (1990) on juvenile gulf menhaden in Fourleague Bay, Louisiana. Their study determined that juvenile gulf menhaden were physiologically able to digest plant based detritus and that it made up roughly 30% of their diet. Although their study utilized *Spartina* as the vascular plant detrital source, we assume that *Juncus* and upland plant detritus can be digested and utilized in a similar manner. Additionally, Friedland et al. (1984) determined that detritus may have a clogging effect on the gill rakers of juvenile Atlantic menhaden allowing them to filter larger particles less efficiently and smaller particles more efficiently. While a decrease in dietary phytoplankton contribution of approximately 18% was observed for juvenile menhaden, a slight increase in dietary phytoplankton and decrease in trophic level were observed for sub-adult and adult fish collected at this site. These larger size classes were not shown to metabolically utilize detritus to a significant extent and this dietary increase in phytoplankton could be related to the aforementioned clogging effects.

A few individual fish in the sub-adult and adult size classes showed fairly enriched carbon isotope values relative to the food sources utilized in our study, suggesting a potential impact from offshore sources before the seasonal inshore migration of these size classes (see neritic and oceanic carbon sources from Dorado et al. 2012 shown in our Fig. 2 for comparison). These sources were not taken into account in the mixing model analysis. Additionally, offshore 'new' nitrogen sources such as *Trichodesmium* may impact interpretation of the trophic level by introducing a nitrogen source not utilized in this calculation (Capone et al. 1997, Holl et al. 2007). This source of nitrogen would be depleted in  $\delta^{15}\text{N}$  (possessing a  $\delta^{15}\text{N}$  value of approximately 0‰) compared to terrigenous sources generally associated with the coastal environment in which this study took place. Dorado et al. (2012) suggested that this cyanobacterium should be taken into account in pelagic food web studies utilizing stable isotope analysis; however, based on the enriched  $\delta^{15}\text{N}$  values observed in all size classes of menhaden in our study, it is doubtful that this particular nitrogen source had a measurable impact. Nitrogen sources utilized in both the mixing model analysis and trophic level analysis seemed to account for the full variation observed in menhaden  $\delta^{15}\text{N}$  values. Additionally, calculated trophic levels were in agreement with mixing model outputs suggesting that these conclusions were sound.

Trophic patterns based on carbon isotope incorporation were similar among sites for sub-adult and adult gulf menhaden. While this may have been due to close proximity of our sites to one another, D'Ambra (2012) found a similar pattern over a greater longitudinal range in the northern Gulf of Mexico. This likely also reflects more uniform isotopic signatures farther offshore and away from the influence of terrestrial sources where sub-adult and adult fish are generally found.

Trophic level variation was observed within size classes with the largest variation observed in the juvenile size class. Sub-adult fish showed much less variation in trophic level, and even less than observed in the adult size class. The trophic level calculations and their respective baseline values take into account ontogenetic differences in fish movement. While gulf menhaden do not show any extensive east-west migration (Kroger & Pristas 1975, Pristas et al. 1976), we assumed that sub-adult and adult menhaden possessed the ability to migrate on a smaller scale among our study sites and so utilized the differing  $\delta^{15}\text{N}$  baselines associated with each. Conversely, we assumed that juvenile menhaden migrated much less among study sites because of their smaller size and use of the nearshore habitat as a refuge from predation (Boesch & Turner 1984). It should be noted that these trophic level calculations are very sensitive to the  $\delta^{15}\text{N}$  baselines used. Nonetheless, both methods of calculating baseline values (weighted average among sites and site-specific) were considered and the methods used here deemed most appropriate based on these assumptions. Additionally, we understand that interpretation of spatial variation may be confounded by the fact that we do not have precise isotopic turnover rates associated with this species. For this reason, we suggest a conservative interpretation of such spatial variation in isotopic values.

We also note the relatively narrow posterior intervals associated with the phytoplankton and zooplankton food sources in the mixing model outputs of the juvenile fish as compared to those of the sub-adults and adults. While the juvenile size class was more trophically variable, the smaller variation in relative dietary breakdown suggests that this size class also showed less 'evenness' in dietary selection than larger fish (Bearhop et al. 2004). While sub-adults and adults are omnivorous as individuals feeding on similar mixtures of phytoplankton and zooplankton, juveniles are omnivorous as a group with some individuals showing dietary specialization, most likely related to spatial availability of food sources.

The trophic comparison between menhaden and 2 specialist planktivores suggests that juvenile *Brevoortia patronus* are trophically balanced between phytoplanktivore and zooplanktivore, but more similar to *Crassostrea virginica*, while the larger size classes are more similar to *Anchoa mitchilli*. The selectivity of these comparison species is well documented, which allowed us to further refine our analysis. *C. virginica* is known to be a dominant herbivore that selectively ingests small (10–100  $\mu\text{m}$ ) particulates in the water column (largely phytoplankton/detritus) (Newell & Jordan 1983, Newell 2004), while *A. mitchilli* selectively ingests larger sized zooplankton (Johnson et al. 1990, Luo & Brandt 1993). Our study is consistent with this literature, and the dietary similarity of juvenile menhaden to *C. virginica* suggests that a similar ecosystem level effect of this size class may be possible.

This unconventional use of the mixing model framework exploits the life history of consumers with specialized diets compared to that of menhaden and allows for use of these mixing models without relying on the assumption of a specific trophic fractionation factor, which is often cited as a weakness in stable isotope trophic studies (Gannes et al. 1997, Post 2002). However, this method does assume that fractionation factors and isotopic turnover rates for all 3 of these consumers are similar, which may not always be valid. Additionally, these comparison consumers were collected at different times and over a smaller temporal range which could impact dietary interpretation and comparisons. Nonetheless, the results of both uses of these models and the trophic level calculations were consistent, suggesting that the trophic fractionation factors and baseline values selected for the traditional Bayesian mixing models and trophic level calculations were consistent.

### Temporal variation

Sub-adult and adult  $\delta^{13}\text{C}$  values stayed consistently enriched throughout the months of June, July, and August suggesting that these fish did not utilize the same carbon sources as juvenile fish. Though juvenile menhaden collected in March showed enriched  $\delta^{13}\text{C}$  values similar to those of sub-adults and adults (presumably due to feeding farther offshore as larvae), these values became increasingly depleted throughout the spring and summer suggesting uptake of nearshore/terrestrial carbon. Additionally, no major differences in dietary composition were observed for sub-adult or adult menhaden, nor were

trophically relevant differences observed in the trophic level calculations during the months they were collected. This was surprising considering the documented seasonal change in the planktonic composition of the northern Gulf of Mexico due to spring and summer phytoplankton blooms. However, sub-adult and adult fish are not present in the nearshore environment for as long as the juvenile size class and so were collected over a smaller temporal range. This could be seen as a lack of isotopic turnover in menhaden tissue. Understanding an organisms turnover rate is important to accurately interpret isotopic data in food web studies and the fact that we do not have precise turnover values for menhaden in this study may impact interpretation of these results. However, due to their high metabolic rate (Durbin et al. 1981) and the lack of temporal trend observed in carbon isotope values, we feel that this interpretation of the data is sound.

Juvenile menhaden displayed some temporal variation in the relative contribution of diet sources possibly suggestive of an opportunistic feeding strategy. Juvenile fish were collected over a larger range of months and a slight decrease in trophic level was observed in June followed by a spike in trophic level in July samples, which is possibly related to changing abundances of phytoplankton and zooplankton in the environment and, as a result, in the diet of the fish. Elevated phytoplankton content in the diet of juvenile menhaden was observed in April and slightly elevated levels observed in May and June with an increase in zooplankton dietary contribution in July that suggests this size class may have been taking advantage of seasonal bloom and bust cycles of phytoplankton observed in the nearshore Gulf of Mexico (Lohrenz et al. 1997). It is interesting to note a much lower contribution of detritus in the diet of juvenile menhaden observed in April suggesting that the presence of phytoplankton may have resulted in a sharp decrease in dietary detrital contribution, while that of zooplankton contribution remained the same. In interpreting temporal trends, it should be kept in mind that stable isotope values reflect dietary changes over time and are delayed based on tissue and species specific turnover rates. While we have not attempted to estimate turnover rates for gulf menhaden in this study, changes in dietary patterns suggested by the stable isotope data are consistent with the idea that juveniles are highly opportunistic and variable in their feeding strategy as a size class relative to sub-adults and adults. Nonetheless, we suggest a conservative interpretation of temporal trends observed here.

### Ecological and fishery applications

The unique status of gulf menhaden as both an important ecosystem component and a fishery resource leads to the concern that these 2 needs may be in conflict. While fishing mortality of gulf menhaden seems to be rising, and population fecundity may be experiencing slight declines, recent assessments suggest that the stock is not overfished or undergoing overfishing (Vaughan et al. 2007), yet this assessment does not account for ecological impacts. Due to the fact that menhaden are such a numerous and densely schooling seasonal resident of inshore environments (Ahrenholz 1991), it is often suggested that they could play a localized role similar to the eastern oyster (Cerco & Noel 2007). Our study suggests that, similar to *Crassostrea virginica*, juvenile menhaden may have the ability to impact water quality by foraging on a relatively large proportion of phytoplankton, though the individual dietary variability in this size class may impact the ecosystem effects, spatially or temporally. Additionally, the effect that oysters tend to have on local water quality is not only due to their feeding selectivity and specific behavior as a filter feeder, but also to the fact that they are long lived, slow-growing, and sessile benthic organisms, which gives them the ability to act as a benthic nutrient sink (Newell et al. 2005). While gulf menhaden are not similar in these respects, they do possess the ability for large scale offshore migration. This presents the possibility (especially the juvenile size class) to remove nitrogen from the nearshore environment through grazing and deliver it offshore in the form of menhaden biomass (Deegan 1993). For an impact to occur, these processes would have to outweigh any inshore excretion of nitrogen or inshore mortality of menhaden, as some authors have suggested that excessive nitrogenous waste and consumption of zooplankton by Atlantic menhaden in the inshore environment may actually increase primary production locally (Lynch et al. 2010, Lynch et al. 2011).

Whether this ecosystem impact occurs in the Gulf of Mexico to any measureable extent is beyond the scope of our study; however, this work suggests that a reduction in the juvenile gulf menhaden population could decrease the resiliency of the inshore Gulf of Mexico ecosystem to summer eutrophication events, which can lead to localized hypoxia. Recent management restrictions set on the Atlantic menhaden reduction fishery (ASMFC 2011) highlight the importance of understanding these possible scenarios, as these limitations may increase fishing pressure in the

Gulf of Mexico. To fully understand the impact of the gulf menhaden population on the local environment, additional work is necessary, including accurately quantifying the biomass of juvenile menhaden and a thorough understanding of the nitrogen budget of this size class. Until now, it has been difficult to accurately estimate the impact of the entire gulf menhaden population on surrounding water quality due largely to the uncertainty of their feeding habits. Without a thorough understanding of these environmental impacts, a decline in numbers or a shift in the ecological role of this species may create problems unforeseen by fishers and managers alike.

*Acknowledgements.* We thank all those who aided in field and laboratory work including personnel from the Mississippi Department of Marine Resources (MDMR) and the National Marine Fisheries Service (NMFS) for their help in collecting fishery dependent samples and Omega Protein Inc. for allowing us to do so. The views expressed in this paper are those of the authors and do not necessarily reflect the views or policies of the US Environmental Protection Agency. The use of named analytical equipment in this manuscript does not imply endorsement from such corporations.

### LITERATURE CITED

- Ahrenholz DW (1991) Population biology and life history of the North American menhadens, *Brevoortia* spp. Mar Fish Rev 53:3–19
- Allredge AL, Gotschalk C, Passow U, Riebesell U (1995) Mass aggregation of diatom blooms: insight from a mesocosm study. Deep-Sea Res II 42:9–27
- Atlantic States Marine Fisheries Commission (ASMFC) (2011) Addendum V to Amendment 1 to the Atlantic menhaden fishery management plan. ASMFC, Washington, DC, p 1–12
- Bearhop S, Adams CE, Waldrons S, Fuller RA, Macleod H (2004) Determining trophic niche width: a novel approach using stable isotope analysis. J Anim Ecol 73: 1007–1012
- Boesch DF, Turner RE (1984) Dependence of fishery species on salt marshes: the role of food and refuge. Estuaries 7: 460–468
- Capone DG, Zehr JP, Paerl HW, Bergman B, Carpenter EJ (1997) *Trichodesmium*, a globally significant marine cyanobacterium. Science 276:1221–1229
- Castillo-Rivera M, Kobelkowsky A, Zamayoa V (1996) Food resource partitioning and trophic morphology of *Brevoortia gunteri* and *B. patronus*. J Fish Biol 49:1102–1111
- Cerco CF, Noel MR (2007) Can oyster restoration reverse cultural eutrophication in Chesapeake Bay? Estuaries Coasts 30:331–343
- Chanton JP, Lewis FG (1999) Plankton and dissolved inorganic carbon isotopic composition in a river dominated estuary: Apalachicola Bay, Florida. Estuaries 22:575–583
- D'Ambra I (2012) Application of stable isotopes in the analysis of trophic interactions between jellyfish and fish. PhD thesis, University of South Alabama, Mobile

- Darnell RM (1961) Trophic spectrum of an estuarine community, based on studies of Lake Ponchartrain, Louisiana. *Ecology* 42:553–568
- Deegan LA (1986) Changes in body composition and morphology of young-of-the-year gulf menhaden, *Brevoortia patronus* Goode, in Fourleague Bay, Louisiana. *J Fish Biol* 29:403–415
- Deegan LA (1990) Effects of estuarine environmental conditions on population dynamics of young-of-the-year gulf menhaden. *Mar Ecol Prog Ser* 68:195–205
- Deegan LA (1993) Nutrient and energy transport between estuaries and coastal marine ecosystems by fish migration. *Can J Fish Aquat Sci* 50:74–79
- Deegan LA, Peterson BJ, Portier R (1990) Stable isotopes and cellulase activity as evidence for detritus as a food source for juvenile Gulf menhaden. *Estuaries* 13:14–19
- Dorado S, Rooker JR, Wissel B, Quigg A (2012) Isotope baseline shifts in pelagic food webs of the Gulf of Mexico. *Mar Ecol Prog Ser* 464:37–49
- Durbin AG, Durbin EG (1975) Grazing rates of the Atlantic menhaden *Brevoortia tyrannus* as a function of particle size and concentration. *Mar Biol* 33:265–277
- Durbin AG, Durbin EG, Verity PG, Smayda TJ (1981) Voluntary swimming speeds and respiration rates of a filter-feeding planktivore, the Atlantic menhaden, *Brevoortia tyrannus* (Pisces: Clupeidae). *Fish Bull* 78:877–886
- Durbin EG, Durbin AG (1983) Energy and nitrogen budgets for the Atlantic menhaden, *Brevoortia tyrannus*, (Pisces: Clupeidae), a filter-feeding planktivore. *Fish Bull* 81:177–199
- Fertl D, Wursig B (1995) Coordinated feeding by Atlantic spotted dolphins (*Stenella frontalis*) in the Gulf of Mexico. *Aquat Mamm* 21:3–5
- Fredriksen S (2003) Food web studies in a Norwegian kelp forest based on stable isotope ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) analysis. *Mar Ecol Prog Ser* 260:71–81
- Friedland KD (1985) Functional morphology of the branchial basket structures associated with feeding in the Atlantic menhaden, *Brevoortia tyrannus* (Pisces: Clupeidae). *Copeia* 1985:1018–1027
- Friedland KD, Haas LW, Merriner JV (1984) Filtering rates of juvenile Atlantic menhaden *Brevoortia tyrannus* (Pisces: Clupeidae) with consideration of the effects of detritus and swimming speed. *Mar Biol* 84:109–117
- Friedland KD, Ahrenholz DW, Haas LW (2005) Viable gut passage of cyanobacteria through the filter-feeding fish Atlantic menhaden, *Brevoortia tyrannus*. *J Plankton Res* 27:715–718
- Friedland KD, Ahrenholz DW, Smith JW, Manning M, Ryan J (2006) Sieving functional morphology of the gill rakers feeding apparatus of Atlantic menhaden. *J Exp Zool* 305A:974–985
- Friedland KD, Lynch PD, Gobler CJ (2011) Time series mesoscale response of Atlantic menhaden *Brevoortia tyrannus* to variation in plankton abundance. *J Coast Res* 27:1148–1158
- Fry B (2006) *Stable isotope ecology*. Springer, New York, NY
- Gannes LZ, O'Brien DM, Martinez del Rio C (1997) Stable isotopes in animal ecology: assumptions, caveats, and a call for more laboratory experiments. *Ecology* 78:1271–1276
- Hackney CT, Haines EB (1980) Stable carbon isotope composition of fauna and organic matter collected in a Mississippi estuary. *Estuar Coast Mar Sci* 10:703–708
- Hoese HD, Moore RH (1998) *Fishes of the Gulf of Mexico, Texas, Louisiana, and adjacent waters*. Texas A&M University Press, College Station, TX
- Holl CM, Villareal TA, Payne CD, Clayton TD, Hart C, Montoya JP (2007) *Trichodesmium* in the western Gulf of Mexico:  $^{15}\text{N}_2$ -fixation and natural abundance stable isotope evidence. *Limnol Oceanogr* 52:2249–2259
- Jeffries HP (1975) Diets of juvenile Atlantic menhaden (*Brevoortia tyrannus*) in 3 estuarine habitats as determined from fatty acid composition of gut contents. *J Fish Res Board Can* 32:587–592
- Johnson WS, Allen DM, Ogburn MV, Stancyk SE (1990) Short-term predation responses of adult bay anchovies *Anchoa mitchilli* to estuarine zooplankton availability. *Mar Ecol Prog Ser* 64:55–68
- June FC, Carlson FT (1971) Food of young Atlantic menhaden, *Brevoortia tyrannus* in relation to metamorphosis. *Fish Bull* 68:493–512
- Kjørboe TK, Anderson KP, Dam HG (1990) Coagulation efficiency and aggregate formation in marine phytoplankton. *Mar Biol* 107:235–245
- Kroger RL, Pristas PJ (1975) Movement of tagged juvenile menhaden (*Brevoortia patronus*) in the Gulf of Mexico. *Tex J Sci* 26:473–477
- Lohrenz SE, Fahnenstiel GL, Redalje DG, Lang GA, Chen X, Dagg MJ (1997) Variations in primary production of northern Gulf of Mexico continental shelf waters linked to nutrient inputs from the Mississippi River. *Mar Ecol Prog Ser* 155:45–54
- Luo J, Brandt SB (1993) Bay anchovy *Anchoa mitchilli* production and consumption in mid-Chesapeake Bay based on a bioenergetics model and acoustic measures of fish abundance. *Mar Ecol Prog Ser* 98:223–236
- Lynch PD, Brush MJ, Condon ED, Latour RJ (2010) Net removal of nitrogen through ingestion of phytoplankton by Atlantic menhaden *Brevoortia tyrannus* in Chesapeake Bay. *Mar Ecol Prog Ser* 401:195–209
- Lynch PD, Brush MJ, Latour RJ (2011) Simulated short-term impacts of the Atlantic menhaden reduction fishery on Chesapeake Bay water quality. *N Am J Fish Manag* 31:70–78
- McCutchan JH, Lewis WMJ, Kendall C, McGrath CC (2003) Variations in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. *Oikos* 102:378–390
- McLean PK, Byrd MA (1991) The diet of Chesapeake Bay ospreys and their impact on the local fishery. *J Raptor Res* 25:109–112
- National Marine Fisheries Service (NMFS) (2012) *Fisheries of the United States, 2011*. Current fisheries statistics No. 2011, US Department of Commerce, Silver Spring, MD
- Newell RIE (2004) Ecosystem influences of natural and cultivated populations of suspension-feeding bivalve molluscs: a review. *J Shellfish Res* 23:51–61
- Newell RIE, Jordan SJ (1983) Preferential ingestion of organic material by the American oyster *Crassostrea virginica*. *Mar Ecol Prog Ser* 13:47–53
- Newell RIE, Fisher TR, Holyoke RR, Cornwell JC (2005) Influence of eastern oysters on nitrogen and phosphorus regeneration in Chesapeake Bay, USA. In: Dame R, Olenin S (eds) *The comparative roles of suspension feeders in ecosystems*, Book 47. Springer, Dordrecht
- Olsen ZT (2012) Determining the trophic role of Gulf menhaden using carbon and nitrogen stable isotopes. MSc thesis, University of Southern Mississippi, Gulf Coast Research Laboratory, Hattiesburg, MS
- Parnell AC, Inger R, Bearhop S, Jackson AL (2010) Source

- partitioning using stable isotopes: coping with too much variation. *PLoS ONE* 5:e9672
- Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. *Annu Rev Ecol Syst* 18:293–320
- Pinnegar JK, Polunin NVC (1999) Differential fractionation of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  among fish tissues: implications for the study of trophic interactions. *Funct Ecol* 13:225–231
- Post DM (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* 83:703–718
- Post DM, Layman CA, Arrington DA, Takimoto G, Quattrochi J, Montana CG (2007) Getting to the fat of the matter: models, methods, and assumptions for dealing with lipids in stable isotope analysis. *Oecologia* 152:179–189
- Pristas PJ, Levi EJ, Dryfoos RL (1976) Analysis of tag returns of tagged gulf menhaden. *Fish Bull* 74:112–117
- Rooker JR, Turner JP, Holt SA (2006) Trophic ecology of *Sargassum*-associated fishes in the Gulf of Mexico determined from stable isotopes and fatty acids. *Mar Ecol Prog Ser* 313:249–259
- Ruiz N, Dubois N, Wielgosz-Collin G, du Pont TR, Bergé JP, Pouchus YF, Barnathan G (2007) Lipid content and fatty acid composition of a marine-derived *Trichoderma longibrachiatum* strain culture by agar surface and submerged fermentations. *Process Biochem* 42:676–680
- Scharf FS, Schlicht KK (2000) Feeding habits of Red Drum (*Sciaenops ocellatus*) in Galveston Bay, Texas: seasonal diet variation and predator-prey size relationships. *Estuaries* 23:128–139
- Schielke EG, Post DM (2010) Size matters: comparing stable isotope ratios of tissue plugs and whole organisms. *Limnol Oceanogr* 8:348–351
- Smith JW (1991) The Atlantic and Gulf menhaden purse seine fisheries: origins, harvesting technologies, biostatistical monitoring, recent trends in fisheries statistics, and forecasting. *Mar Fish Rev* 53:28–41
- Vaughan DS, Smith JW, Prager MH (2000) Population characteristics of gulf menhaden, *Brevoortia patronus*. NOAA Tech Rep NMFS 149:1–19
- Vaughan DS, Shertzer KW, Smith JW (2007) Gulf menhaden (*Brevoortia patronus*) in the US Gulf of Mexico: fishery characteristics and biological reference points for management. *Fish Res* 83:263–275

*Editorial responsibility: Janet Ley,  
St. Petersburg, Florida, USA*

*Submitted: March 6, 2013; Accepted: August 15, 2013  
Proofs received from author(s): January 7, 2014*