

Dietary overlap between jellyfish and forage fish in the northern Gulf of Mexico

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ABSTRACT: Despite the speculations that jellyfish (hydromedusae, siphonophores, scyphomedusae and ctenophores) may compete with forage fish for prey, there are few direct comparisons of their diets. To determine the dietary overlap between *Aurelia* sp. (Cnidaria, Scyphozoa) and *Brevoortia patronus* (Goode, 1878) (Pisces, Clupeidae) in the northern Gulf of Mexico, we collected monthly samples in Louisiana, Mississippi and Alabama coastal waters (USA) during summer and early fall 2009–2010. We determined carbon and nitrogen stable isotope ratios in predators and their potential prey, including small plankton (<200 µm) and mesozooplankton (200–2000 µm), and identified prey in the stomachs of adult *Aurelia* sp. and *B. patronus*. Trophic niche overlap was defined using the stable isotope Bayesian ellipses in R (SIBER) procedure and ranged from 0–28% for *Aurelia* sp. and 0–64% for *B. patronus* across the 3 sites. While stable isotope values in *B. patronus* clearly reflected the range of mesozooplankton, those for *Aurelia* sp. indicated a high individual variability, which likely accounted for the niche separation in Louisiana. Copepods were numerically the most abundant prey in the stomachs of predators at all sites, resulting in a percent similarity index of 93% in Louisiana, 87% in Mississippi and 86% in Alabama. Our results highlight that, despite local and species-specific variability, dietary overlap between *Aurelia* sp. and *B. patronus* is high across the northern Gulf of Mexico. Our data contribute to the definition of trophic interactions between jellyfish and forage fish in the Gulf of Mexico region and other ecosystems where they co-occur.

KEY WORDS: Stomach contents · Stable isotopes · Niche overlap · SIBER · MixSIAR · *Aurelia* sp. · *Brevoortia patronus*

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INTRODUCTION

Jellyfish (hydromedusae, siphonophores, scyphomedusae and ctenophores) and forage fish potentially share middle trophic levels in marine food webs (Purcell & Arai 2001). Except for a few species, most jellyfish are zooplanktivorous and include a large variety of prey taxa within their diets (Purcell 1997, 2009). Because detecting and identifying gelatinous tissues in stomach contents is difficult, predators of

jellyfish, which include sea turtles, sea birds, sharks and several fish species, have likely been underestimated (Arai 2005). Forage fish are schooling fish and serve as a critical link between plankton and higher trophic level predators within marine food webs worldwide (Springer & Speckman 1997). Based on the similarity of their diets, trophic niches of jellyfish and forage fish are likely to overlap (Purcell & Arai 2001), but the dietary composition and degree of overlap between jellyfish and forage fish diets have

rarely have defined (Purcell & Grover 1990, Purcell & Sturdevant 2001, Brodeur et al. 2008, Shoji et al. 2009, Nagata et al. 2015).

When examined, stomach contents of co-occurring jellyfish and forage fish showed significant dietary overlap. For example, analysis of stomach contents showed a high degree of overlap between the diets of the hydromedusae *Obelia* sp., *Proboscoidactyla flavicirrata* and *Aglantha digitale* and the diet of larval Pacific herring *Clupea pallasii* in Kullest Bay, British Columbia (Purcell & Grover 1990). Stomach contents of adult scyphomedusae and ctenophores had a percent similarity index (PSI) >60% with different species of age-0 forage fishes in the northern California Current (Brodeur et al. 2008) and juvenile forage fishes in Prince William Sound, Alaska (Purcell & Sturdevant 2001). The similarity of results from different ecosystems suggests that dietary overlap between jellyfish and forage fish may be a common trait within marine food webs, but conclusions are limited by the small number of ecosystems where dietary overlap of co-occurring jellyfish and forage fish has been defined.

Determining the dietary overlap between jellyfish and forage fish may present some challenges due to methodological constraints. The time framework of dietary composition provided by stomach content analysis has been extended by combining or replacing this approach with stable isotope analysis (SIA; Brodeur et al. 2008, Shoji et al. 2009, Nagata et al. 2015). Although sample processing protocols have been refined (Fleming et al. 2011, D'Ambra et al. 2014, Kogovšek et al. 2014), the interpretation of stable isotope values in jellyfish is challenged by the unusual diet-tissue discrimination factors (DTDFs) from scyphomedusae to their prey. The DTDFs of a large variety of invertebrates and fish fall within the range $1.4 \pm 1\%$ (mean \pm SD) for carbon (C) and $3 \pm 1\%$ for nitrogen (N) (McCutchan et al. 2003). Conversely, laboratory-determined DTDFs for *Aurelia* sp. were $4.3 \pm 0.2\%$ (mean \pm SD) for C and $0.1 \pm 0.2\%$ for N (D'Ambra et al. 2014). Laboratory-based DTDFs for *Aurelia* sp. appear to be supported by field data (Frost et al. 2012), but their application has resulted in apparently unrealistic trophic-level assignments (Fleming et al. 2015, Nagata et al. 2015). Hence, the resulting definitions of dietary composition and trophic niche remain uncertain (Nagata et al. 2015, Javidpour et al. 2016).

The Gulf menhaden *Brevoortia patronus* (Goode, 1878) (Pisces: Clupeidae) is an ecologically and economically important forage fish in the northern Gulf of Mexico. Gulf menhaden transfer energy from

plankton to piscivorous fishes, sharks, sea turtles and sea birds (Ahrenholz 1991) and sustain the second-largest commercial fishery by mass in the USA (Vaughan et al. 2007). In the Gulf of Mexico and other highly productive ecosystems, scyphomedusae replace forage fish on inter-decadal cycles, with decreased fish landings corresponding to high biomass of scyphomedusae (Robinson et al. 2014). While *Aurelia* sp. appears to prey on mesozooplankton in the northern Gulf of Mexico (Graham & Kroutil 2001), the diet of *B. patronus* has been defined in detail only for the larval stage, which appears to feed mainly on detritus and phytoplankton (Govoni et al. 1983, Deegan et al. 1990, Olsen et al. 2014). Given the relevance of *B. patronus* to the ecology and economy of the northern Gulf of Mexico, clearly determining the dietary composition of the adult stage is crucial to correctly define their trophic interactions with other taxa and their position within the food web. Within this framework, in the present study we made a direct comparison of the diets of adult *Aurelia* sp. and *B. patronus* and defined the degree of dietary overlap between them when they co-occurred in the northern Gulf of Mexico. Our data will aid to refine the definition of trophic interactions between jellyfish and fish in this region and other ecosystems alike.

MATERIALS AND METHODS

Sample collection

Sampling was conducted monthly at 1 station each in Louisiana and Mississippi and 3 stations in Alabama coastal waters (Fig. 1) from June to October 2009–2010 (summer–early fall). This sampling frequency was sufficient to yield discrete dietary intervals based on the known half-life for $\delta^{13}\text{C}$ (11 d) and $\delta^{15}\text{N}$ (10 d) estimated for *Aurelia* sp. (D'Ambra et al. 2014). *Aurelia* sp. specimens (availability was constrained by their unpredictable appearance at the sampling events) were collected from surface waters using a dip net and their bell diameter was measured on the boat as the distance between opposite rhopalia (± 0.5 cm). For SIA, freshly caught *Aurelia* sp. scyphomedusae were transported to the laboratory in buckets with filtered seawater from the sampling site to allow gut evacuation. For analysis of stomach contents, *Aurelia* sp. scyphomedusae were preserved in a buffered 4% formaldehyde solution. *Brevoortia patronus* were caught by purse seining from vessels equipped for large-scale commercial

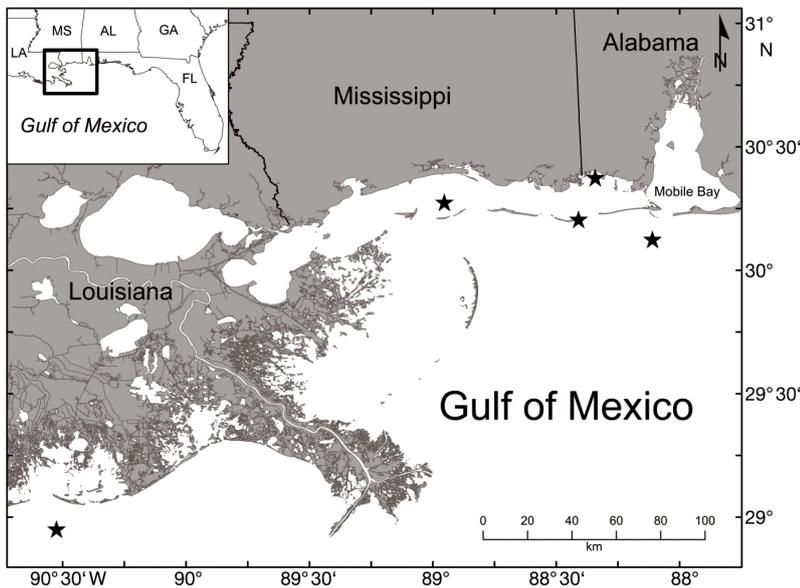


Fig. 1. Sampling stations in Louisiana, Mississippi and Alabama (USA) coastal waters where the scyphomedusa *Aurelia* sp. and the forage fish *Brevoortia patronus*, along with their potential prey—small plankton (<200 μm) and mesozooplankton (200–2000 μm)—were collected monthly from June to October 2009–2010

fishing within the same month and near the stations where *Aurelia* sp. were collected. Nets were 17–22 mm bar mesh, up to 365 m long and 18–22 m deep (Smith 1991). Fish were kept on ice until they were landed on shore, where they were measured (fork length, ± 0.5 cm) and frozen until further processing within 6 mo.

Small plankton (<200 μm ; detritus, microphytoplankton, microzooplankton) and mesozooplankton (200–2000 μm) known to be potential prey of *Aurelia* sp. and *B. patronus* (Matlock & Garcia 1983, Graham & Kroutil 2001) were collected at the same locations and times as *Aurelia* sp. A 2 l Niskin bottle was deployed at 1 m depth below the surface to collect water samples. To size-fractionate plankton, replicate water samples were filtered on the boat through a 200 μm mesh and the filtrate was stored on ice in acid-washed plastic bottles. Mesozooplankton samples were collected using duplicate vertical (according to the depth of stations) net hauls (200 μm mesh), size-fractionated by filtering them through a 2000 μm mesh and stored on ice in acid-washed plastic jars containing filtered seawater from the sampling site.

Stable isotope analyses

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in freshly caught *Aurelia* sp. were determined in the bell, from which the stom-

ach and gonads were removed. After dissection, the bell was rinsed with ultrapure water to remove any detritus or plankton from the sample (D'Ambra et al. 2014). The bell was used because a previous study demonstrated that the bell is isotopically representative of the whole body of *Aurelia* sp. (D'Ambra et al. 2014). Frozen *B. patronus* were slightly thawed, dissected, and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were determined in the dorsal muscle free from skin and bones (Pinnegar & Polunin 1999). Small plankton (<200 μm) were concentrated by filtering water samples under a vacuum through pre-combusted (4 h at 500°C) Whatman GF/F grade glass fiber filters (2.5 cm diameter, 0.2 μm nominal pore size). Mesozooplankton samples (200–2000 μm) were concentrated through a 200 μm mesh. All samples were dried to constant mass at 60°C to avoid changes in the isotopic composition. Tissues of *Aurelia* sp., *B.*

patronus and mesozooplankton were individually homogenized using a mortar and a pestle.

On average, 4.0 ± 0.3 mg (mean \pm SD) of dried *Aurelia* sp. and 1.0 ± 0.2 mg of dried *B. patronus* and plankton were used to determine $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in samples. A higher quantity of *Aurelia* sp. tissue was required to account for the low organic content of scyphomedusae compared to other fish and zooplankton (D'Ambra et al. 2014). Samples were sent to the stable isotope facility at the University of California (UC), Davis (USA) in 2009 and the stable isotope facility for environmental research (SIRFER) at the University of Utah (USA) in 2010. The long-term standard deviations were 0.2‰ for $\delta^{13}\text{C}$ and 0.3‰ for $\delta^{15}\text{N}$ at UC Davis and 0.1‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ at SIRFER. To ensure that determinations between the 2 laboratories were comparable, 15 samples were analyzed in both laboratories. The mean difference in $\delta^{13}\text{C}$ was 0.1‰ ($t_{27} = 0.42$, $p = 0.68$); the mean difference in $\delta^{15}\text{N}$ was 0.2‰ ($t_{27} = 0.71$, $p = 0.48$), indicating that differences were within the range of variability of data.

The effect of lipid content, which results in lower $\delta^{13}\text{C}$ values than in lipid-free tissues, was corrected in samples with C:N > 3.5 (Post et al. 2007) using the specific equation determined for *Aurelia* sp. (D'Ambra et al. 2014). Specific corrections for *B. patronus* and mesozooplankton were defined following the same protocol used for *Aurelia* sp. Small

plankton samples were not included in this analysis due to small sample size. Lipids were removed from 30 homogenized samples (5 mg) of each group (*Aurelia* sp. bell, *B. patronus* muscle and mesozooplankton) using 2:1 chloroform:methanol and removing the solvent by centrifuging samples in ultrapure water. Samples were dried at 60°C to constant mass and re-homogenized using a mortar and pestle. The equations applied for each species were:

Aurelia sp. (D'Ambra et al. 2014):

$$\delta^{13}\text{C}_{\text{corrected}} = \delta^{13}\text{C} - 9.43 + 2.69 \times \text{C:N} \quad (1)$$

B. patronus:

$$\delta^{13}\text{C}_{\text{corrected}} = \delta^{13}\text{C} - 3.34 + 1.16 \times \text{C:N} \quad (2)$$

plankton:

$$\delta^{13}\text{C}_{\text{corrected}} = \delta^{13}\text{C} - 2.45 + 0.62 \times \text{C:N} \quad (3)$$

Stomach content analysis

Formalin-preserved *Aurelia* sp. were dissected and their stomachs were isolated to obtain their contents. The fixative from original preservation was filtered through a 10 µm mesh to further collect prey regurgitated by scyphomedusae during preservation. To isolate stomach contents of *B. patronus*, the stomachs of thawed fishes were preserved in a buffered 4% formaldehyde solution and contents were identified to the lowest taxon possible under a dissecting microscope.

Data analysis

The trophic niches of *Aurelia* sp. and *B. patronus* based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were defined using the SIBER procedure within the package stable isotope analysis in R (SIAR; v. 4.2), which incorporates the uncertainty due to small sample size (Jackson et al. 2011). The percentage of ellipses overlap was calculated as the ratio between the area of overlap between paired ellipses (estimated by the SIBER procedure) and each ellipse area for *Aurelia* sp. and *B. patronus* separately at each site. To fulfill the assumption that DTDFs of predators were similar (Jackson et al. 2011), $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in *Aurelia* sp. and *B. patronus* were corrected using the laboratory-determined DTDFs for *Aurelia* sp. ($\Delta^{13}\text{C} = 4.3 \pm 0.2\text{‰}$ and $\Delta^{15}\text{N} = 0.1 \pm 0.2\text{‰}$; D'Ambra et al. 2014) and expected DTDFs ($\Delta^{13}\text{C} = 1.4 \pm 1\text{‰}$ and

$\Delta^{15}\text{N} = 3 \pm 1\text{‰}$; McCutchan et al. 2003) for *B. patronus*, because specific DTDFs were not available for this species.

To ensure that multiple trophic levels of predators were not pooled, we calculated the Pearson's correlation coefficient between the bell diameter and $\delta^{15}\text{N}$ of *Aurelia* sp. and the fork length and $\delta^{15}\text{N}$ of *B. patronus*. Neither correlation was statistically significant ($r^2 = 0.16$, $p = 0.23$ for *Aurelia* sp.; $r^2 = 0.005$, $p = 0.95$ for *B. patronus*). We estimated the assimilated dietary composition of *Aurelia* sp. and *B. patronus* at each site using the MixSIAR GUI (version 2.1.2), a graphical user interface within the MixSIAR mixing model framework (<https://github.com/brianstock/MixSIAR>). MixSIAR models were run for each sampling when scyphomedusae and fish co-occurred by applying the DTDFs used for trophic niches (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m587p031_supp.pdf). Small plankton and mesozooplankton were considered as potential prey of *Aurelia* sp. and *B. patronus* and were included in the models along with their C and N content (Table S1).

The relative importance of each prey taxon to the dietary composition of *Aurelia* sp. and *B. patronus* based on analysis of stomach contents was calculated as the numerical proportion of each prey taxon (the number of individuals of a prey taxon divided by the total number of prey in each stomach; Hyslop 1980) for *Aurelia* sp. and *B. patronus* separately for 2009 and 2010. Stomach contents were compared between the 2 years separately for *Aurelia* sp. and *B. patronus* using a permutational analysis of variance (PERMANOVA) in R (version 3.1.2; Comprehensive Archive Network: <http://cran.r-project.org/>), based on 1000 permutations and a Bray-Curtis matrix. Stomach contents were statistically different only for *B. patronus* in Alabama coastal waters between 2009 and 2010 (Table S2). Because this difference did not change the overall biological significance of the analysis (i.e. *B. patronus* prey on mesozooplankton), the proportions of each prey taxon were pooled for 2009 and 2010, and mean proportions (\pm SD) were calculated for each predator at every site.

The dietary overlap between *Aurelia* sp. and *B. patronus* was determined at each sampling site as the PSI (Schoener 1974, Mathur 1977):

$$\text{PSI}_{jk} = [1 - 0.5 (\sum |P_{ij} - P_{ik}|)] \times 100 \quad (4)$$

between the proportions of the prey taxon i found in the stomachs of *Aurelia* sp. (P_{ij}) and *B. patronus* (P_{ik}) at the same site (Purcell & Sturdevant 2001, Brodeur et al. 2008).

RESULTS

Stable isotope analyses

Most stable isotope values of *Aurelia* sp. corrected using laboratory-determined DTDFs (D'Ambra et al. 2014) fell between the stable isotope ranges of small plankton and mesozooplankton in Louisiana and Alabama coastal waters, with only a few values within the range of mesozooplankton (Fig. 2). Conversely, in Mississippi, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of *Aurelia* sp. were within the range of mesozooplankton values at all sampling events (Fig. 2). Stable isotope values of *B. patronus* corrected using DTDFs by McCutchan et al. (2003) consistently fell within the range of mesozooplankton $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in 2009 and 2010 at all 3 sites considered in this study (Fig. 2).

The MixSIAR GUI estimated that the mean (\pm SD) contribution of small plankton dominated the dietary composition of *Aurelia* sp. in Louisiana during August 2009 ($91 \pm 21\%$) but was small in October 2009 and 2010 ($30 \pm 34\%$ and $4 \pm 16\%$, respectively) (Table 1). Because stable isotope values of *Aurelia* sp. in Mississippi coastal waters fell within the range of stable isotope values in mesozooplankton throughout the study, the assimilated dietary composition estimated by the mixing model was based mainly on mesozooplankton in 2009 and 2010 (Table 1). In Louisiana coastal waters, the assimilated diet of *Aurelia* sp. was based on mesozooplankton in August 2009, whilst the proportions of small plankton and mesozooplankton were similar in September 2009 and 2010 and in October 2010 (Table 1).

The MixSIAR GUI estimated that $99 \pm 1\%$ (mean \pm SD) of the assimilated diet of *B. patronus* in Louisiana coastal waters consisted of mesozooplankton in August 2009 and August and October 2010 when they co-occurred with *Aurelia* sp. (Table 1). According to the results of the mixing model, small plankton provided a contribution of $\sim 60\%$ to the dietary composition of *B. patronus* in Mississippi. In Alabama coastal waters, *B. patronus* assimilated mainly mesozooplankton in August and September 2009, while their diet was balanced between small plankton and mesozooplankton in 2010 (Table 1).

Overall, stable isotope Bayesian ellipses of *Aurelia* sp. corrected for sample size were slightly larger than non-corrected ellipses. Both corrected and non-corrected ellipses of *Aurelia* sp. were larger than Bayesian ellipses of *B. patronus*. The SIBER procedure estimated that trophic niche overlap based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ranged from 0–28% for *Aurelia* sp. and 0–64% for *B. patronus* across the 3 sites (Table 2).

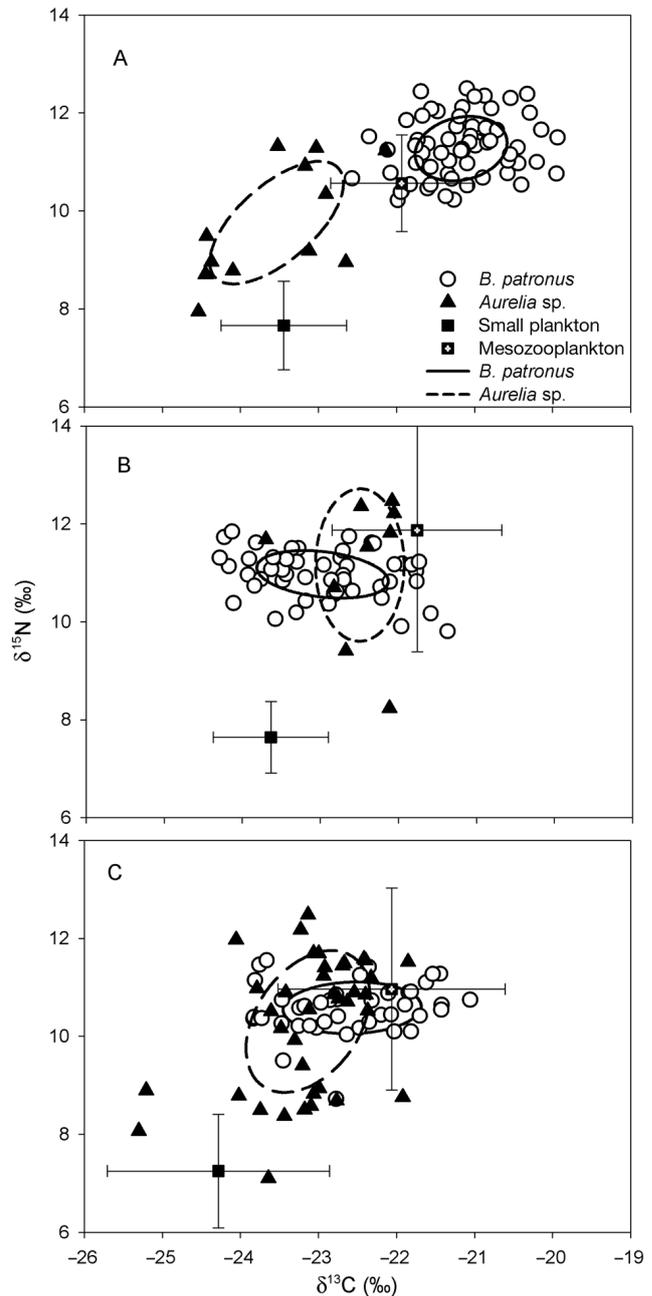


Fig. 2. Corrected $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and resulting trophic niches (indicated by solid and dashed ovals) estimated using the stable isotope Bayesian ellipses in R (SIBER) procedure of the scyphomedusa *Aurelia* sp. and the forage fish *Brevortia patronus*, along with their potential prey—small plankton ($< 200\ \mu\text{m}$) and mesozooplankton ($200\text{--}2000\ \mu\text{m}$)—collected monthly from June to October 2009–2010 in (A) Louisiana, (B) Mississippi and (C) Alabama coastal waters

Stomach content analysis

PSIs between stomach contents of *Aurelia* sp. and *B. patronus* were 93% in Louisiana, 87% in Mississippi and 86% in Alabama coastal waters (Table 3). Only

Table 1. Mean (\pm SD) and 95 % confidence interval (in parentheses) contribution of small plankton (<200 μ m) and mesozooplankton (200–2000 μ m) to the assimilated diets of the scyphomedusa *Aurelia* sp. and the forage fish *Brevoortia patronus* collected in Louisiana, Mississippi and Alabama coastal waters from June to October 2009–2010. Dietary compositions were estimated using the MixSIAR GUI based on stable isotope values of predators and their potential prey and only for the months when *Aurelia* sp. and *B. patronus* co-occurred

	<i>Aurelia</i> sp.		<i>B. patronus</i>	
	Small plankton	Mesozooplankton	Small plankton	Mesozooplankton
Louisiana				
Aug 2009	91 \pm 21 (37–100)	9 \pm 21 (0–63)	1 \pm 1 (0–3)	99 \pm 1 (97–100)
Oct 2009	30 \pm 34 (0–80)	70 \pm 34 (30–100)	1 \pm 1 (0–2)	99 \pm 1 (97–100)
Oct 2010	4 \pm 16 (4–21)	96 \pm 16 (79–00)	1 \pm 1 (0–2)	99 \pm 1 (98–100)
Overall	48 \pm 28 (5–4)	52 \pm 28 (6–95)	10 \pm 20 (0–59)	90 \pm 20 (41–100)
Mississippi				
Oct 2009	35 \pm 28 (0–77)	65 \pm 28 (23–100)	60 \pm 5 (51–68)	40 \pm 5 (32–49)
Oct 2010	20 \pm 21 (0–57)	81 \pm 21 (44–100)	60 \pm 5 (51–69)	40 \pm 5 (31–49)
Overall	44 \pm 25 (6–88)	56 \pm 25 (12–94)	60 \pm 5 (52–68)	40 \pm 5 (33–48)
Alabama				
Aug 2009	16 \pm 18 (0–51)	84 \pm 18 (49–100)	10 \pm 14 (0–38)	90 \pm 14 (62–100)
Sep 2009	62 \pm 17 (26–84)	38 \pm 17 (16–74)	6 \pm 10 (0–27)	94 \pm 10 (73–100)
Sep 2010	52 \pm 7 (40–62)	48 \pm 7 (37–60)	52 \pm 11 (32–68)	48 \pm 11 (32–68)
Oct 2010	39 \pm 19 (0–64)	61 \pm 19 (38–60)	54 \pm 11 (36–71)	46 \pm 11 (29–64)
Overall	45 \pm 8 (31–58)	55 \pm 8 (42–69)	45 \pm 5 (36–53)	55 \pm 5 (47–64)

mesozooplankton prey were found in the stomachs of both *Aurelia* sp. and *B. patronus*. Copepods were numerically the most abundant prey in the stomachs of both predators at the 3 sites considered in the present study. In addition to copepods, unidentified eggs, ostracods and crab zoea were found in the stomachs of both predators at the same site and, therefore, were accounted for in the calculation of PSI. Gastropod veligers, bivalve larvae, cladocerans, amphipods and decapods were identified only in small numbers and in one of the predator species' stomachs at the same

site, and hence were not included in the calculation of dietary overlap (Table 3).

DISCUSSION

Analysis of stable isotope values and stomach contents indicated that the overall degree of dietary overlap between the adult stages of the scyphomedusa *Aurelia* sp. and the forage fish *Brevoortia patronus* was high (0–64 % trophic niche overlap estimated from stable isotope values and 86–93 % based on analysis of stomach contents) across the northern Gulf of Mexico during summer-early fall 2009–2010. Even in Louisiana coastal waters, where stable isotope ratios indicated no trophic niche overlap between assimilated diets, the 93 % PSI between stomach contents in *Aurelia* sp. and *B. patronus* suggested potential for a high degree of dietary overlap. Scyphomedusae and forage fish co-occur in several coastal areas, including highly productive ecosystems (Brodeur et al. 2008, Robinson et al. 2014). The inverse correlation between the abundance of scyphomedusae and forage fish found in a previous study (Robinson et al. 2014), along with the dietary overlap observed during this study, suggest potential for competition for prey between these taxa. Based on the assumption that scyphomedusae and forage fish compete for prey, recent food web models have included jellyfish as potential competitors of forage fish in the Northern California Current (Ruzicka et al.

Table 2. Stable ellipses area corrected (SEAc) and non-corrected (SEA) for small sample size (in δ^2 units) and area overlap (in δ^2 units and percentage) between the SEA of the scyphomedusa *Aurelia* sp. and the forage fish *Brevoortia patronus* in Louisiana, Mississippi and Alabama coastal waters based on stable isotope values of scyphomedusae and fish (n = number of samples) collected from June to October 2009–2010 and estimated using the stable isotope Bayesian ellipses in R (SIBER) procedure

	n	SEA (δ^2)	SEAc (δ^2)	Area overlap (δ^2)	Percentage overlap (%)
Louisiana					
<i>Aurelia</i> sp.	12	2.3	2.6	0	0
<i>B. patronus</i>	64	1.2	1.2	0	0
Mississippi					
<i>Aurelia</i> sp.	9	2.4	2.8	0.7	25
<i>B. patronus</i>	50	1.2	1.2	0.7	56
Alabama					
<i>Aurelia</i> sp.	38	3.2	3.3	0.9	28
<i>B. patronus</i>	43	1.4	1.5	0.9	64

Table 3. Number of samples (n), size (in cm; bell diameter for scyphomedusae; fork length for fish), percentage (mean \pm SD) and number of mesozooplankton prey (in parentheses) in the stomach and percent similarity index (PSI) of the scyphomedusa *Aurelia* sp. and the forage fish *Brevoortia patronus* in Louisiana, Mississippi and Alabama coastal waters based on analysis of stomach contents collected from June to October 2009–2010

	n	Size (cm)	Mesozooplankton prey (%)								PSI (%)
			Copepoda	Eggs	Cladocera	Ostracoda	Crab zoea	Amphipoda	Decapoda	Gastropoda	
Louisiana											
<i>Aurelia</i> sp.	16	28.3 \pm 3.4	69 \pm 27 (141)	11 \pm 16 (40)	–	20 \pm 28 (37)	–	–	–	–	93
<i>B. patronus</i>	34	19.3 \pm 0.8	66 \pm 22 (1649)	4 \pm 9 (48)	6 \pm 11 (135)	15 \pm 21 (315)	6 \pm 8 (117)	2 \pm 5 (24)	–	–	–
Mississippi											
<i>Aurelia</i> sp.	10	25.5 \pm 3.4	62 \pm 45 (34)	3 \pm 7 (3)	–	25 \pm 36 (14)	3 \pm 11 (1)	6 \pm 13 (3)	–	–	87
<i>B. patronus</i>	27	19.0 \pm 0.8	64 \pm 35 (1548)	–	–	16 \pm 28 (383)	18 \pm 26 (597)	–	–	–	2 \pm 5 (54)
Alabama											
<i>Aurelia</i> sp.	26	26.9 \pm 4.2	78 \pm 31 (394)	8 \pm 12 (21)	–	1 \pm 3 (3)	1 \pm 5 (3)	8 \pm 25 (20)	–	1 \pm 5 (2)	3 \pm 9
<i>B. patronus</i>	44	18.5 \pm 0.8	75 \pm 29 (6608)	3 \pm 11 (269)	–	7 \pm 17 (593)	9 \pm 22 (751)	1 \pm 8 (89)	5 \pm 14 (410)	–	–

2012), the Gulf of Mexico (Robinson et al. 2015) and marine coastal ecosystems under diverse future scenarios (Schnedler-Meyer et al. 2016). However, a direct comparison of the diets of jellyfish and forage fish is only available for a limited number of ecosystems (Purcell & Grover 1990, Purcell & Sturdevant 2001, Brodeur et al. 2008, Shoji et al. 2009, Nagata et al. 2015). The present study demonstrates potential for dietary overlap between 2 abundant species of jellyfish and forage fish in an important coastal ecosystem by direct comparison of their diets across the northern Gulf of Mexico region.

Trophic niches of *Aurelia* sp. and *Brevoortia patronus* and their overlap

Except for Louisiana coastal waters, trophic niches defined using C and N stable isotope ratios in tissues of the scyphomedusa *Aurelia* sp. overlapped 25–28% with trophic niches of the forage fish *B. patronus*, while the percentage of overlap was 56–64% for trophic niches of *B. patronus* in the northern Gulf of Mexico (Table 2). These ranges are consistent with the observed percentages of overlap between trophic niches of the forage fish *Chloroscombrus chrysurus* with the scyphomedusae *Lychnorhiza lucerna* (56%) and *Chrysaora lactea* (65%) in the Cananéia Lagoon Estuary System, Brazil (Nagata et al. 2015). Trophic niche overlap of *Aurelia* sp. in the present study was smaller than the percentage estimated for *L. lucerna* (50%) and *C. lactea* (45%) (Nagata et al. 2015). Al-

though trophic niches were not defined, stable isotope values of *Aurelia aurita* overlapped with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of the Japanese anchovy *Engraulis japonicas* in the Seto Inlet Sea, Japan (Shoji et al. 2009). Also, the range of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values determined in the scyphomedusa *Chrysaora fuscescens* and forage fishes (herring *Clupea pallasii*, saury *Cololabis saira*, sardine *Sardinops sagax*) were similar and indicated that these species feed at similar trophic levels in the Northern California Current (Brodeur et al. 2008). This agreement of results from diverse ecosystems suggests that dietary overlap between scyphomedusae and forage fish may be a common trait within marine food webs.

Feeding strategies of *Aurelia* sp. and *B. patronus* are different. Scyphomedusae use a combination of ambush and filter-feeding strategies, promoting the encounter of prey with their tentacles using feeding currents, as does *Aurelia* sp. (Kiørboe 2011). Feeding currents are generated by the rhythmical pulsation of their bell, and current intensity increases with increasing bell diameter for a specific bell shape (Costello & Colin 1994, 1995, Kiørboe 2011). The escape velocity of prey contribute, in part, to determining the success of prey capture and ingestion by scyphomedusae. Most forage fish species, including *B. patronus*, filter water through their gill rakers and retain prey as they swim. The spacing within and between gill rakers in adult *B. patronus* is sufficiently large to retain larger zooplankton (e.g. mesozooplankton; Deegan et al. 1990, Castillo-Rivera et al. 1996, Olsen et al. 2014). This basic difference of feeding strategies between scyphomedusae and forage

fish has been indicated to play a key role in determining the interplay between these taxa in marine ecosystems (Schnedler-Meyer et al. 2016), but further study is required to define the consequences of different feeding strategies in *Aurelia* sp. and *B. patronus* on trophic interactions between them in the northern Gulf of Mexico.

Our data indicate that *Aurelia* sp. and *B. patronus* generally fed at mid-trophic levels, with some site and species-specific variation. Stable isotope values in *B. patronus* consistently fell within the range of mesozooplankton, which clearly indicated that mesozooplankton provided the major contribution to their diet (Fig. 2). Conversely, stable isotope values of *Aurelia* sp. showed a high degree of individual variability at all 3 sites and largely fell between the stable isotope ranges of small plankton and mesozooplankton (Fig. 2), which may have different interpretations. To satisfy their metabolic requirements, scyphomedusae prey on a variety of plankton sizes (Purcell 1997, 2009). Based on this observation, stable isotope values of *Aurelia* sp. falling between the stable isotope values of small plankton and mesozooplankton may suggest that *Aurelia* sp. preyed upon a combination of the 2 prey. This interpretation of stable isotope values of *Aurelia* sp. is supported by the dietary compositions defined using the MixSIAR GUI, which included variable proportions of small plankton and mesozooplankton in their diet. An alternative interpretation of stable isotope values in *Aurelia* sp. may be that scyphomedusae were transported to the sampling site by currents within the half-life of the stable isotopes. Therefore, the stable isotope values in *Aurelia* sp. may reflect the isotope composition of prey at a distant feeding site. In addition to horizontal movements, scyphomedusae may migrate from the surface to deeper layers to prey on carbon-rich prey to satisfy their energetic costs (D'Ambra et al. 2013), or they may wait for carbon-rich, emergent zooplankton to reach the surface (Pitt et al. 2008). The specific movements of *Aurelia* sp. and zooplankton in the northern Gulf of Mexico are not known, but the consistency of findings among locations in this study suggests that the potential for dietary overlap throughout the region was not substantially diminished by local variation in diet and movements. Nevertheless individual variability and movements within different areas remain an important consideration when defining the dietary composition in *Aurelia* sp. and other scyphomedusae.

Stable isotope values of *Aurelia* sp. and *B. patronus* likely reflect different time scales. While a laboratory experiment indicated that the bell tissues in *Aurelia*

sp. of comparable size to specimens in the present study have a half-life 10.8 ± 2.4 d (mean \pm SD) for C and 9.7 ± 3.1 d for N at 28°C (D'Ambra et al. 2014); half-life rates for *B. patronus* are not available. The muscle tissues of the Pacific herring *Clupea pallasii*, a clupeid filter-feeder, showed a half life 46.2 d for N at 10.6°C (Miller 2006). *B. patronus* likely experienced warmer water temperatures in the northern Gulf of Mexico during summer and early fall (Carasou et al. 2011) and are smaller than the *C. pallasii* in the laboratory determinations (~46 cm; Miller 2006), which may reduce the half-life of stable isotopes in *B. patronus* compared to *C. pallasii*. Therefore, half-life rates in *Aurelia* sp. may be at least 2 times faster than in *B. patronus*. As a consequence, trophic niches and dietary reconstructions, which are based on stable isotope values, reflect a shorter time scale in *Aurelia* sp. compared to *B. patronus*.

Dietary compositions based on stable isotope values and stomach contents provide different information about the diet of predators and may be affected by methodological constraints. The dietary compositions estimated using the MixSIAR GUI may be affected by the limited spacing between end-members. Mixing models ensure the best performance when potential prey have distinct stable isotope ranges (Phillips et al. 2014). In the present study, the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ranges of small plankton and mesozooplankton almost overlapped in Mississippi and Alabama coastal waters. The overlap of prey ranges may have caused the mixing model to overestimate the contribution of small plankton in the diet of predators. On the other hand, by preserving stomach contents in formalin, which damages small and soft-bodied prey, the numerical abundance of small plankton in the stomachs of *Aurelia* sp. and *B. patronus* may have been underestimated, particularly in fish stomachs, where the digestive process may have continued during transport on land. Potential protracted digestion may explain, at least in part, why small plankton was not found in the stomach contents whilst the output of the MixSIAR GUI included a contribution of small plankton to the dietary composition of *B. patronus*.

Dietary overlap between *Aurelia* sp. and *B. patronus* based on analysis of stomach contents

Stomach contents indicated that the diets of adult *Aurelia* sp. and *B. patronus* were based on mesozooplankton, which yielded PSIs ranging from 86–93% across the 3 sampling sites (Table 3). Our results are

slightly higher than the range determined between *Aurelia labiata* and walleye pollock *Theragra chalcogramma*, Pacific sand lance *Ammodytes hexapterus*, and Pacific herring *Clupea pallasii* (67–75%) or between *Cyanea capillata* and pink salmon *Oncorhynchus gorbuscha* (78%) in Prince William Sound, Alaska (Purcell & Sturdevant 2001). In line with the findings by Purcell & Sturdevant (2001), PSIs ranged from 60–74% between the scyphomedusae *Aurelia labiata* and *Chrysaora fuscescens* and herring, saury, anchovy and sardine in the Northern California Current (Brodeur et al. 2008). The PSIs in the present study were likely due to the large proportion of copepods, which dominated the stomach contents of *Aurelia* sp. and *B. patronus* at all 3 sites. In agreement with our results, copepods were numerically the most abundant prey in previous analyses of stomach contents in adult *Aurelia* sp. across the northern Gulf of Mexico (Graham & Kroutil 2001), while a detailed analysis of stomach contents in adult *B. patronus* is lacking across the region.

CONCLUSIONS

Our results indicate a high degree of dietary overlap between the scyphomedusa *Aurelia* sp. and the forage fish *B. patronus* in the northern Gulf of Mexico. Food web models have identified scyphomedusae and forage fish as key pathways of energy transfer within coastal food webs. Forage fish transfer energy to higher trophic levels, while scyphomedusae appear to direct energy toward the microbial loop or the benthic food web (Condon et al. 2011, Robinson et al. 2015). Recent studies have highlighted that the contribution of scyphomedusae to the dietary composition of their predators may have been underestimated (Utne-Palm et al. 2010, Cardona et al. 2012, D'Ambra et al. 2015). Our results indicate that *Aurelia* sp. and *B. patronus* likely share middle trophic levels within the pelagic food web. Hence, the interplay between these and similar species may regulate energy flow within the food web of the northern Gulf of Mexico. Further studies are required to determine whether the high degree of trophic overlap is primarily driven by resource competition (which occurs when prey are limiting) or an abundance of similar prey (such as copepods) among locations. Data are also needed to better define how factors such as life cycles, larval recruitment, feeding strategies, predation rates and fishery pressure regulate the interactions between jellyfish and forage fish. Given the importance of *B. patronus* and similar

species to the ecology and economy of coast regions, the data gathered in this study will be useful to refine understanding of food web structure and energy transfer that has broad implications for fisheries management in the northern Gulf of Mexico and beyond.

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