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Ontogenetic patterns in resource use dynamics of bonefish (*Albula vulpes*) in the Bahamas

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Abstract We used stable isotope analysis to examine ontogenetic patterns in the resource use dynamics of bonefish (*Albula vulpes*) collected from two locations (Banks and Atlantic) within the coastal waters of Eleuthera, The Bahamas. A marked shift in $\delta^{13}C$ signatures between leptocephali and juveniles reflected a rapid change in resource use, likely from pelagic to alternate neritic sources of primary production. Ontogenetic shifts in habitat use were observed across bonefish from both sides of Eleuthera, but direction of the isotopic shifts varied. Bonefish from the Atlantic side demonstrated an enrichment in ^{13}C with size, whereas the opposite pattern was observed for individuals captured from the Banks. Differences are likely to be explained by the variability of primary production sources, which dominate each side of the island (i.e., more reliance on seagrass with ontogeny on the Atlantic side, versus a shift to macroalgal-dominated foodwebs with growth on the Banks side). Enrichment in ^{15}N with body size was observed for both locations and reflects the ability to utilize a broader range of prey items with increasing gape size. Trophic diversity (inferred through nitrogen range), however, was lower on the Banks side, suggesting that reduced prey diversity may limit the increase in dietary shifts that gape size increases typically allow. A significant positive relationship between $\delta^{13}C$ and whole-body energy density (MJ kg-1) in adults on the Banks side was observed. Adult bonefish that forage in seagrasses likely benefit from higher energy densities from selected prey items, and may explain this result. Data from this study reinforces the importance of a diversity of habitats in supporting bonefish throughout ontogeny.

Keywords Bonefish · *Albula vulpes* · Stable isotope analysis · Ontogenetic shifts

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Introduction

Examining patterns of resource use across life history stages is important for understanding the structure and

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function of ecological systems, as such processes vitally underpin and regulate ecosystem services (Jones et al. 1994; Mod et al. 2016). Many coastal marine vertebrates, including fish, undergo shifts in habitat and prey preference throughout ontogeny, and rely upon multiple resource pools to facilitate growth and maturation (Scharf et al. 2000; Graham et al. 2007; Kimirei et al. 2013). Coastal seascapes are one of many ecological realms subject to a multitude of anthropogenic stressors. While the negative impacts of coastal development (Lotze et al. 2006; Waycott et al. 2009), commercial fisheries exploitation (Pauly et al. 1998; Jackson et al. 2001), and widespread pollution have been established for some time, accurate prediction of the resulting ecological consequences has eluded scientists and policy makers. As the inability to predict is partially driven by the paucity of basic life history and other biological (e.g., trophic) data pertaining to many coastal species, a need exists to further improve understanding of the resource use patterns in coastal ecosystems. Understanding when and why different resource pools support specific life history stages for foraging therefore aids in holistic management and conservation of populations, communities, and ecosystems (Platell et al. 2010; Nunn et al. 2012; Usmar 2012).

Bonefish (*Albula* spp.) are a group of fishes which undergo shifts in habitat use (Pfeiler et al. 1988; Mojica et al. 1995; Danylchuk et al. 2011; Murchie et al. 2013) and diet throughout their life cycle (Colton and Alevizon 1983; Crabtree et al. 1998; Snodgrass et al. 2008). Bonefish also carry the distinction of being a prized sportfish throughout their circumtropical distribution (Colton and Alevizon 1983; Pfeiler et al. 2000), with this fishery making significant contributions to local and national economies (Humston 2001; Fedler 2010). Despite their economic and ecological significance (Murchie 2010), there are still major gaps in our understanding of bonefish ecology, which requires innovative approaches to gathering data on the habitat and ecological needs of the species (Adams and Cooke 2015).

Assessing resource use patterns economically important species, such as bonefish, allows for the identification of key habitats and biomes warranting protection and management. To date, only analyses of stomach contents have been used to elucidate the resource use dynamics of juvenile and adult bonefish (e.g., Warmke and Erdman 1963; Bruger 1974; Colton and Alevizon 1983; Crabtree et al. 1998;

Layman and Silliman 2002; Snodgrass et al. 2008). Although this approach is well established for examining foraging dynamics of fishes, it provides a temporally limited snap shot of resource acquisition, and partly digested prey items are often hard to identify (Kling et al. 1992; Polito et al. 2011). Further, differential digestion and variable feeding can lead to the importance of some prey categories being overemphasized (Hyslop 1980). Stable isotope analysis (SIA), however, is a complimentary and/or alternative approach, which can be used to assess food web structure and resource use dynamics of fishes (Layman et al. 2007, 2012). SIA provides a direct assessment of energy flow regimes, and a temporally-integrated signature of the assimilated energy sources used for tissue anabolism (Kling et al. 1992). Isotope signatures provide time-integrated signatures of dietary preferences, which are dependable at least on seasonal scales (Hesslein et al. 1993). Ratios of heavy to light isotopes of nitrogen (denoted as δ^{15}N) are used to estimate the relative trophic position of an organism, as a relatively consistent step-wise enrichment of ^{15}N by ~3–4‰ is exhibited through trophic transfer (DeNiro and Epstein 1981; Minagawa and Wada 1984; Peterson and Fry 1987). Ratios of heavy to light carbon (denoted as δ^{13}C) are distinct between marine primary producers but exhibit relatively low fractionation (i.e. 0–1‰ enrichment in ^{13}C) throughout trophic transfer (DeNiro and Epstein 1978; Minagawa and Wada 1984; Peterson and Fry 1987; Layman et al. 2007). Therefore, the simultaneous measurement of nitrogen and carbon stable isotopes provides a powerful insight, respectively, into trophic diversity and energy sources which underpin food web biomass (Peterson and Fry 1987).

Given the paucity of broader ecological and foraging information available for bonefish (*Albula vulpes*), the goal of this study was to use SIA to examine resource use patterns of individuals across all life history stages. Specifically, we examined: 1) ontogenetic shifts in habitats for leptocephali (larval stage), juvenile (post-metamorphosis, 20–299 mm fork length), and adult bonefish (≥300 mm fork length), 2) if stable isotope signatures are related to whole body energy density of adult fish and what that may imply, and 3) the relative trophic niche size and degree of overlap exhibited between juvenile and adult bonefish.

Methods

All research was conducted under permits MAF/FIS/17 and MAF/FIS/34 from the Bahamian Department of Marine Resources. Animal sampling followed the requirements of the UK Home Office Scientific Procedures (Animals) Act and Association for the Study of Animal Behavior (Rollin and Kessel 1998) and was in accordance with the policies of the Canadian Council on Animal Care and completed under an approval granted by the Carleton University Animal Care Committee (protocols B07–03, B07–05, B07–06), as well as the University of Massachusetts Amherst IACUC (protocol 2010–005).

Sample collection and preparation

Leptocephali (larval), juvenile (20–299 mm), and adult (≥300 mm) bonefish were collected from a number of tidal creek systems and tidal embayments located on the coast of Eleuthera, The Bahamas (Fig. 1). Leptocephali and juvenile fish were collected in 2012, whereas the majority (91%) of adult fish were collected in 2007 (with 1 fish collected in 2006, and 3 in 2012). The west side of Eleuthera is herein referred to as the "Banks" and the east side of Eleuthera is referred to as the "Atlantic". Leptocephali were collected using quatrefoil-style light traps (see McLeod and Costello 2017), moored overnight in probable settlement areas on or around the last quarter moon. Juvenile bonefish were collected using 15.2 m × 1.2 m seine nets with 3.175 mm mesh. Adult bonefish were collected using seine nets of various mesh size and length (see Murchie et al. 2009 for protocols and net details). Genetic analysis of a sub-set of bonefish (authors' unpublished data) samples confirmed that all captured individuals were *Albula vulpes*. All bonefish samples were measured (fork length, FL in mm) and weighed (g).

Leptocephali and juvenile bonefish <30 mm were wrapped in aluminum foil, labeled and frozen at −20 °C. For juvenile bonefish >30 mm and adult bonefish, dorsal muscle tissue was excised from each individual fish and stored as above. The adult bonefish included in this study were processed for proximate body
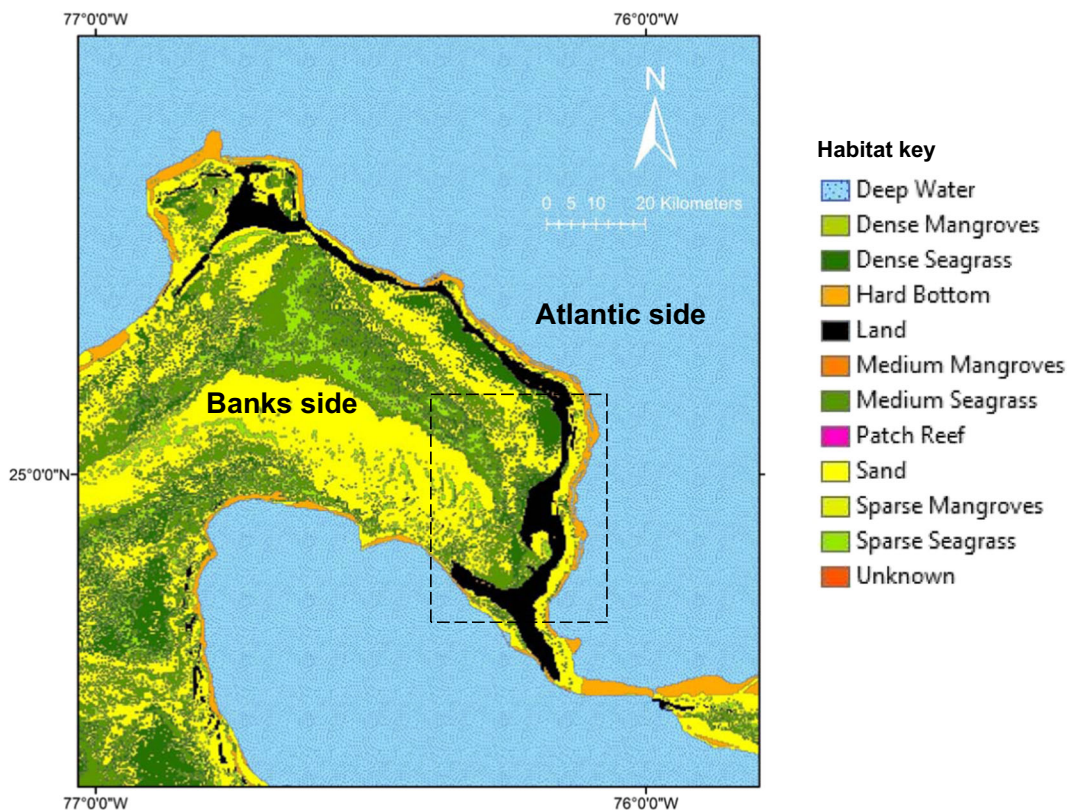
Fig. 1 Bonefish were collected in coastal waters within the dashed box on both the Atlantic and Banks side of Eleuthera, The Bahamas. The key habitat types are included courtesy of the Khaled bin Sultan Living Oceans Foundation

composition, including energy densities, as described in Murchie et al. (2010). Tissue samples for SIA were dried in a standard laboratory convection oven at 50–60 °C before being homogenized into a fine powder for simultaneous analysis of carbon (δ^{13}C) and nitrogen (δ^{15}N) stable isotopes at the Environmental Isotope Laboratory, University of Waterloo, Waterloo, Ontario, Canada. A Thermo-Finnigan Delta Plus continuous flow isotope mass spectrometer (Thermo-Finnigan, Bremen, Germany) coupled to a 4010 Elemental Analyzer (Costech International S. p. A., Milan Italy) was used, with analytical precision of ±0.1‰ and ± 0.2‰ for δ^{13}C and δ^{15}N, respectively. Analytical accuracy was validated against internal laboratory standards cross-calibrated against the International Atomic Energy Agency standards CH$_6$ for carbon and N1 and N2 for nitrogen. Error for δ^{13}C and δ^{15}N, during any given sample run did not exceed 0.2‰ and 0.3‰, respectively. Isotope values are denoted in delta notation (δ) and are measured in permil (‰), relative to international standards of Vienna Peedee Belemnite (VPDB) for δ^{13}C (Craig 1957), and atmospheric nitrogen for δ^{15}N (Mariotti 1983). While lipids are depleted in ^{13}C relative to pure protein and may artificially deplete δ^{13}C values of teleosts (Sweeting et al. 2006; Post et al. 2007), the C:N ratios (Table 1) of studied juvenile and adult bonefish were uniformly low (C:$N < 3.5$) and below the accepted limit where carbon isotope signatures can be left uncorrected for lipids (e.g., Post et al. 2007; Jardine et al. 2013).

Statistical analyses

Statistical analyses were performed in a combination of RStudio (version 1.0.143) and JMP version 13 (SAS Institute, Cary, NC). Generalized linear models (GLMs), with a backwards elimination of non-significant effects, were used to determine the effects of capture location on the isotopic composition of juvenile and adult bonefish tissue samples. The effect of capture location was used to inform whether subsequent analyses should be performed on the pooled community, or regional (i.e. Atlantic and Banks) populations. Generalized linear models revealed capture location as a highly significant predictor of δ^{13}C and δ^{15}N values ($t = 8.45$, $p < 0.001$; $t = 6.52$, p < 0.001) across the pooled juvenile and adult bonefish community (Table 1). As a result, all analyses on bonefish SIA data were separated by location (i.e., Atlantic and Banks side). It should be noted that statistical analyses including the leptocephali (larval) stage were limited to summary statistics as sample size was small ($n = 3$) and was limited to the Atlantic side only. Additionally, leptocephali undergo negative growth phase (i.e., shrink) as a result of the recruitment of endogenous carbon compounds during ossification processes associated with metamorphosis from the larval to juvenile stage (Pfeiler et al. 1998), and would confound the analyses of ontogenetic resource shifts related to size. Following tests of normality and homogeneity of variance [i.e., Shapiro-Wilk goodness of fit and Levene's test, respectively (Sokal and Rohlf 1995)] analyses of carbon and nitrogen SIA values including juvenile and adult life stages were assessed for significant differences using the Wilcoxon Mann-Whiney U-test. To examine the relationship between fish size (FL) and isotopic values of carbon and nitrogen, including the juvenile and adult life stages, least squares regression analyses were used.

For adult bonefish from the two broad sampling locations (i.e., Banks side and Atlantic side), we examined the relationship between energy density and isotopic composition, using least squares regression. As both variables may be influenced by size, we normalized isotope ratios and energy density values to reflect the mean size of bonefish within each community. Parameter values were only normalized if size-specific relationships were observed. Values were derived from the following equation:

$$X_{\text{standard}} = X_{\text{observed}} - a(\text{Size}_{\text{observed}} - \text{Size}_{\text{standard}})$$

Table 1 Results of full and reduced generalized linear models (GLMs) assessing drivers of juvenile and adult bonefish isotope signatures

Model	Intercept	Size	Location	df	AIC
δ^{13}C ~ size + location	−36.60 (< 0.001*)	1.25 (0.216)	8.55 (< 0.001*)	107	450.27
δ^{13}C ~ location	−49.54 (< 0.001*)	8.45 (<0 .001*)	–	108	449.85
δ^{15}N ~ size + location	55.17 (< 0.001*)	5.70 (< 0.001*)	6.52 (< 0.001*)	107	236.59

Models indicate t-values (p value [*significance at $\alpha = 0.05$]) for each variable. For δ^{15}N stepwise elimination of non-significant effects yielded the same model solution

where X = the parameter (i.e. $\delta^{13}C/\delta^{15}N$/Energy density), a = the slope of the relationship between X and size.

Core and total trophic niche dynamics (see Shipley et al. 2018) between different juvenile and adult stages of bonefish, across the Atlantic and Banks sides, were investigated. Core isotopic niche estimates for each life history stage (i.e., based upon 40% of the total data) were determined using maximum likelihood and Bayesian estimates of the standard elliptical area (SEA_C, and SEA_B respectively; Jackson et al. 2011). As core isotopic niche estimates are insensitive to variation in sample size, they provide an adequate relative estimation of niche size (i.e., the niche size of species A is scaled similarly to that of species B, regardless of the percentage of data included within each ellipse). To estimate the trophic overlap in isotopic niche space between bonefish of different life history stages, we used the total trophic niche (i.e. an ellipse incorporating approximately 95% of the data), as core trophic niche estimates may exclude natural variability within a species' realized niche (Jackson et al. 2011; Shipley et al. 2018). Estimates of total trophic niche overlap were calculated using the methods outlined in nicheROVER, which draws probable isotopic overlap estimates from the posterior distribution using a Bayesian framework, and is insensitive to sample size (Swanson et al. 2015).

Results

Stable isotope signatures were obtained from a total of 113 bonefish of various life stages (Table 2). Leptocephali were found to be the most depleted in both carbon and nitrogen signatures, relative to juvenile and adult stages on the Atlantic side (Table 2). There was a significant difference in the $\delta^{13}C$ values between juveniles and adult life stages in samples from both the Atlantic ($W = 788.5$; $z = 4.26$; $p < 0.0001$) and the Banks side ($W = 516$; $z = -2.32$; $p = 0.021$); however, on the Atlantic side the juveniles were more depleted in $\delta^{13}C$ compared to the adults and the inverse was the case on the Banks side (Table 2). For $\delta^{15}N$, there was a significant difference between juvenile and adult signatures on the Atlantic side ($W = 741.5$; $z = 3.42$; $p < 0.001$) with juveniles being more depleted in $\delta^{15}N$ (Table 2). There was no difference in $\delta^{15}N$ values for juvenile and adult bonefish from the Banks side $(W = 766.5$; $z = 1.84$; $p = 0.065)$ (Table 2).

Least squares regression revealed significant relationships between size and $\delta^{13}C$ and $\delta^{15}N$ for both the Atlantic ($F = 18.03$, $df = 1$, 52, $r^2 = 0.26$, $p < 0.001$; $F = 25.39$, $df = 1$, 52, $r^2 = 0.33$, $p < 0.001$) and the Banks side bonefish ($F = 5.25$, $df = 1$, 54, $r^2 = 0.09$, $p = 0.026$; $F = 8.46$, $df = 54$, $r^2 = 0.14$, $p = 0.005$) (Fig. 2). We observed a significant relationship between whole body energy density and $\delta^{13}C$ for the Banks adult bonefish ($F = 5.04$, $df = 1$, 24, $r^2 = 0.19$, $p = 0.036$) (Fig. 3). All other comparisons did not prove significant ($p > 0.060$) (Fig. 3).

Core trophic niche areas (SEA_C & SEA_B) yielded similar estimates of niche size, and were greatest for the >300 mm age class across both communities (Table 3). Significant total trophic niche overlap was exhibited between juvenile and adult bonefish, and this pattern was homogenous across Atlantic and Banks sampled bonefish (Table 3 and Fig. 4). Specifically, juvenile bonefish from the Atlantic side had a 68.73% total trophic overlap with adults, and on the Banks side, the juvenile trophic overlap with adult bonefish was 80.35% (Table 3 and Fig. 4). The adult niche overlapped the juvenile niche by 71.67% on the Banks side and by 42.52% on the Atlantic side (Table 3 and Fig. 4).

Table 2 Summary of $\delta^{13}C$, $\delta^{15}N$, and C:N ratios [mean values ± standard deviation (SD)] and minimum and maximum values of $\delta^{13}C$, $\delta^{15}N$ for life stages of bonefish collected from the two sides of Eleuthera, The Bahamas

Location	Life stage	n	$\delta^{13}C$ ± SD (‰)	$\delta^{13}C$ min/max	$\delta^{15}N$ ± SD (‰)	$\delta^{15}N$ min/max	C:N
Atlantic side	Leptocephali	3	−20.97 ± 0.17	−21.10/−20.77	4.81 ± 0.07	4.75/4.88	4.23 ± 0.07
	Juvenile	34	−13.18 ± 1.68	−16.91/−10.49	7.39 ± 0.51	6.19/8.10	3.15 ± 0.08
	Adult	20	−11.01 ± 1.32	−12.88/−8.72	8.37 ± 1.02	6.71/10.44	3.05 ± 0.04
Banks side	Leptocephali	0	N/A	N/A	N/A	N/A	N/A
	Juvenile	33	−8.94 ± 1.86	−13.07/−6.72	8.38 ± 0.61	7.02/9.16	3.16 ± 0.08
	Adult	23	−10.10 ± 1.49	−13.88/−7.20	8.80 ± 0.74	7.19/10.08	3.08 ± 0.05

Juvenile bonefish range from 20 to 299 mm fork length and adults are ≥300 mm fork length
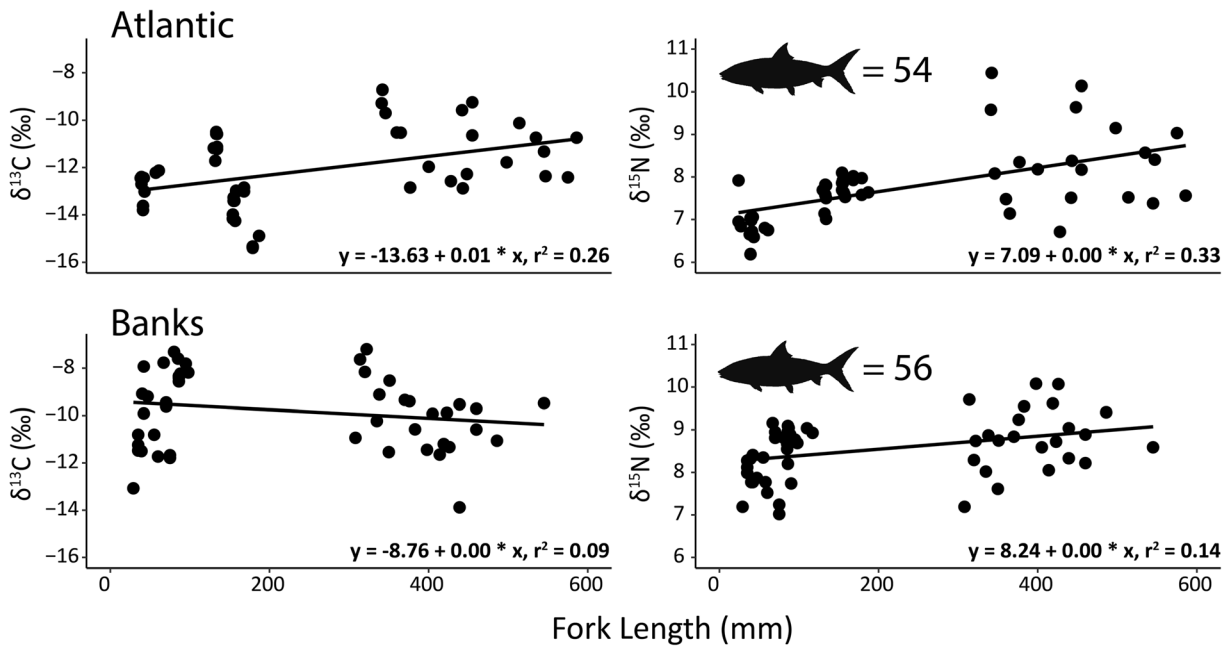
Fig. 2 Examination of the relationship between size and $\delta^{13}C$ and $\delta^{15}N$ for both the Atlantic side and Banks side locations

Discussion

This study is the first to utilize a stable isotope approach to examine resource use dynamics across ontogeny in bonefish. Shifts in $\delta^{13}C$ demonstrate a rapid change from the pelagic life stage of the larvae (Pfeiler et al. 1998) to the benthic neritic settlement of juvenile (post-metamorphosis bonefish), as

evidenced by a change from isotopically depleted ^{13}C leptocephali to a more enriched signature in juvenile bonefish. This is corroborated by pelagic phytoplankton values of approximately −20‰, which are exhibited across the sub-tropical Atlantic Ocean (Magozzi et al. 2017), compared to the isotopically heavier nature of neritic coastal resource pools (Shipley et al. 2018).
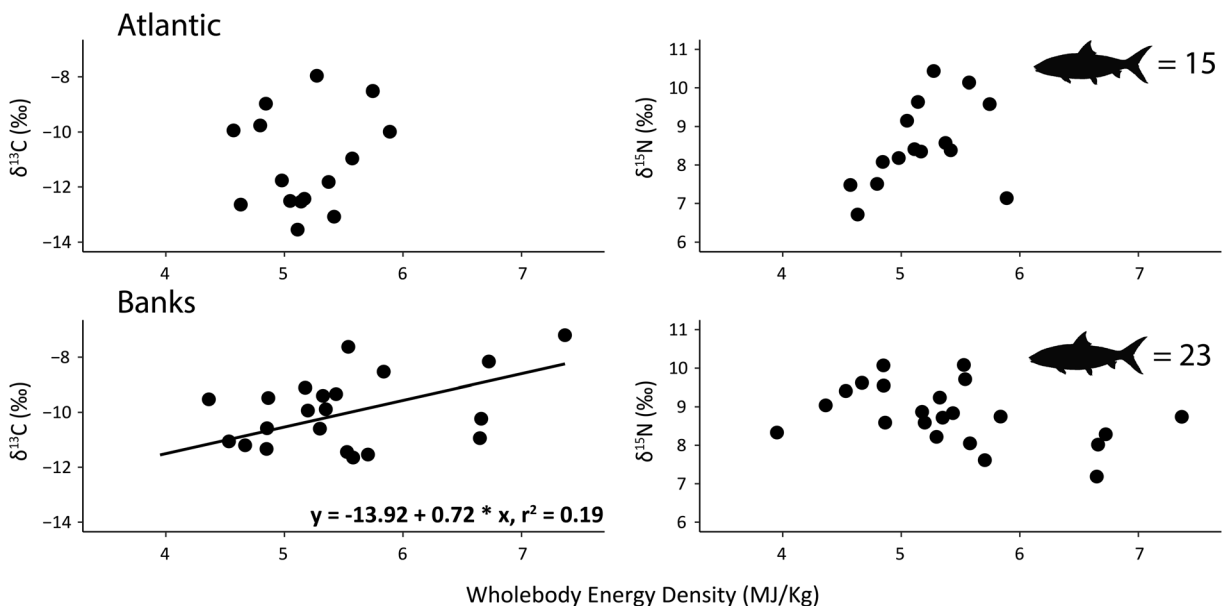
Fig. 3 Examination of the relationship between whole body energy density and $\delta^{13}C$ and $\delta^{15}N$ for both the Atlantic side and Banks side locations

Table 3 Summary of isotopic niche metrics for bonefish assemblages captured from the Atlantic and Banks sides of Eleuthera, The Bahamas; total isotopic area (TA), small sample size corrected standard ellipse area (SEAc), Bayesian SEA (SEA$_B$), and total trophic overlap estimates

Location	Life stage	n	TA	SEA$_C$	SEA$_B$	Total Trophic Overlap (%)
Atlantic side	<300 mm	34	8.4	2.8	2.7	68.73
	≥300 mm	20	10.5	4.4	4.3	42.52
Banks side	<300 mm	33	8.1	2.9	2.9	80.35
	≥300 mm	23	11.6	3.6	3.5	71.67

Ontogenetic shifts in habitat use ($\delta^{13}C$) were observed across bonefish populations sampled from the two sides of Eleuthera, however, distinct differences in the direction of the isotopic shifts throughout ontogeny were observed (Fig. 2). For example, individuals captured from the Atlantic side exhibited an enrichment of $\delta^{13}C$ throughout ontogeny, whereas the opposite pattern was observed for individuals captured from the Banks. Such patterns may, in part, be explained by variability in the dominating primary production pathways on the two sides. For example, even though all samples were collected in shallow nearshore sandy habitats typically surrounded by red mangroves (*Rhizophora mangle*), the Atlantic side has high densities of turtle grass (*Thalassia testudinum*), whereas seagrass is more sparsely distributed on the Banks side (Fig. 1). In addition to the sparsely distributed seagrass on the Banks side, the shoreline is more characteristically composed of extensive shallow, sandy flats with more tidal creeks in the littoral zone (see Murchie et al. 2015). Thus, on the Atlantic side, the enrichment of $\delta^{13}C$ from juvenile to adults is consistent with the enrichment that would occur if juveniles shifted from feeding in sparsely vegetated seagrass habitat to adults feeding more often in isotopically enriched and more densely vegetated seagrass habitats. For example, Stoner and Waite (1991) noted enrichment in both sediment and algal isotope values (*Batophora oerstedii*) when examining differences between low and moderate shoot density turtle seagrass (*Thalassia testudinum*) bed use by queen conch (*Strombus gigas*). In contrast the inverse Banks side relationship (i.e., a decline in $\delta^{13}C$ with size) is suggestive of adults feeding in less isotopically enriched food webs such as algal dominated food webs (see Stoner and Waite 1991; O'Farrell et al. 2014 for values of primary producers). Indeed, Kieckbusch et al. (2004) found that in fringe mangrove island ecosystems, that the majority of primary consumers diet was based on algae, while secondary consumers diets were both algal and seagrass based. Alternatively, a downward shift in

Fig. 4 Core trophic niche estimates (solid lines including ca. 40% of data, Jackson et al. 2011; Shipley et al. 2018) calculated for juvenile (<300 mm) and adult (>300 mm) bonefish from the Atlantic side and Banks side locations of Eleuthera, The Bahamas. Hashed lines represent the total trophic niche (ca. 95% of data) of sub-sampled populations used for Bayesian niche overlap calculations (Swanson et al. 2015). Leptocephali values are plotted for comparative purposes
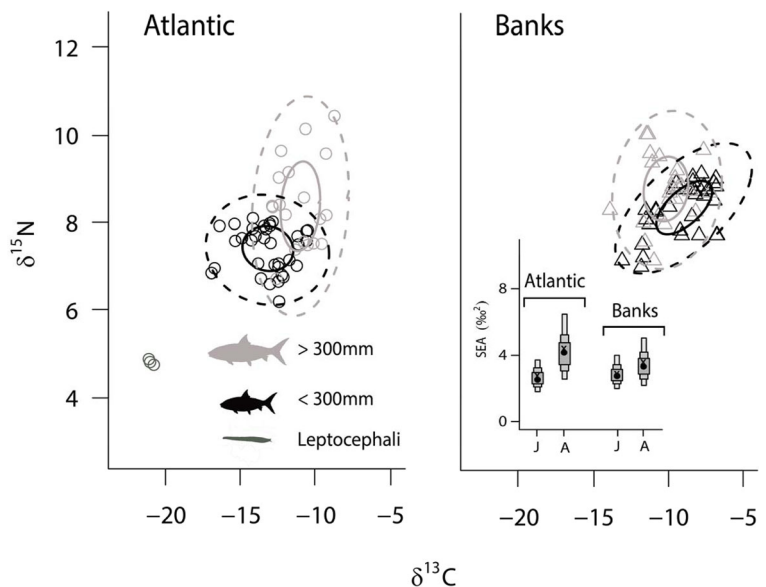
adult signatures may be driven by heavier use of molluscs, such as *Codakia orbicularis* known to be a dominant prey item (Colton and Alevizon 1983) and to be $\delta^{13}C$ depleted as a result of chemosynthetic production (Higgs et al. 2016). Telemetry data on adult bonefish on the Banks side does suggest adult bonefish remain in nearshore sand-flat and mangrove creeks for much of the tidal cycle (Murchie et al. 2013). And while samples were collected over a period of 6 years and isotopic baselines can shift, we deem it unlikely that any significant shifts in the basal primary production sources underpinning species' biomass will have occurred in that time-frame because of the minimal anthropogenic influences in the study area.

For both locations, a significant relationship between $\delta^{15}N$ and bonefish body size was observed. This is not surprising as gape size limits foraging of juveniles, and likely the bite force and ability to crush invertebrate shells varies between life stages (see Wainwright and Richard 1995). While juvenile and adult bonefish exhibit some overlap in prey items (e.g., *Caridea* shrimp, bivalves, and gastropods), gut content analysis suggests juveniles tend to rely more heavily on two prey taxa around Eleuthera – amphipods and *Caridea* shrimp (Griffin et al., A comparison of juvenile bonefish diets in Eleuthera, the Bahamas, and Florida, U.S., in review). Inclusion of small-bodied fish such as gobies, toadfish, and speckled worm eels has been documented for adult *A. vulpes* (Warmke and Erdman 1963, Colton and Alevizon 1983, Crabtree et al. 1998; this study), which would also explain a gradual enrichment of ^{15}N throughout ontogeny. However, as gut content analysis can only provide a temporal snapshot of fish diet (MacNeil et al. 2005; Weidner et al. 2017), further work should explore long-term estimates of the relative contribution of major prey groups to the diet of individuals across all life history stages. Such estimates could be achieved through analyzing the stable isotope composition of tissues exhibiting variable isotopic turnover rates (i.e., liver vs. white muscle, Sweeting et al. 2005), in combination with mixing models (Parnell et al. 2013; Philips et al. 2014).

Layman et al. (2007) proposed the use of carbon range (CR) and nitrogen range (NR) as metrics to examine important aspects of trophic structure. In both cases, the maximum values reported (i.e., most enriched) are subtracted from the minimum values (i.e., most depleted) obtained (Layman et al. 2007). In this study, the CR was greater for adults from the Banks, compared to adults from the Atlantic (Table 2). This implies that adults

residing on the Banks side may feed on prey items for which biomass is supported by a broader range of primary production sources. A recent compilation by Shipley et al. (2018) illustrated the isotopic diversity exhibited across dominant primary producers such as seagrass ($\sim -6‰$) and macroalgae ($\sim -12‰$), from The Bahamas, and thus provides a plausible range of values to contextualize those observed in this study. Future work incorporating the use of Bayesian mixing models may allow for a more thorough determination of dominant production pathways supporting bonefish biomass, but were beyond the scope of this study due to a lack of data for isotopic end-member species (see McCauley et al. 2012). Colton and Alevizon (1983) determined seagrass areas had both higher densities and diversity of prey, and as such, bonefish sampled in grassy areas tended to be more selective in their foraging compared to those captured over sandy habitats. Bonefish foraging in sandy areas tended to feed less discriminately and processed large amounts of substrate to pick up buried prey items (Colton and Alevizon 1983). Combined, these observations may also, at least in part, explain the discrepancy in CR exhibited by individuals across both communities. Overall isotopic niche width increased with increasing life-history stage, for bonefish communities on both side of Eleuthera (Table 2). Visual inspection of isotope ellipses suggest that the trends were primarily driven by enrichment in ^{15}N in adults compared to juveniles, suggesting ingestion of a greater prey diversity by larger individuals (Table 3). For adults, estimates of isotopic niche width were greater for the Atlantic community, compared to the banks, and may imply a reduced diversity of potential prey resources within the Banks. Indeed, Griffin et al. (A comparison of juvenile bonefish diets in Eleuthera, the Bahamas, and Florida, U.S., in review) found a difference in prey species diversity, evenness and richness between juvenile bonefish collected on the Banks versus the Atlantic, with lower indices on the Banks. Although we provide the first indication of inter-site variability of prey diversity, combining indices of species diversity with direct stomach content analyses are required to segment our hypotheses.

The relationships between isotopic composition and metrics of proximate body composition, such as energy densities, has yet to be explored in wild fishes. Our results demonstrated a significant relationship between $\delta^{13}C$ and whole-body energy density (MJ kg-1) in adults on the Banks. The observed relationship is likely explained by the fact that there

are less high-quality foraging resources (i.e., seagrass habitats) relative to sandy habits; thus, adult bonefish that forage more often in seagrass may benefit from higher energy densities if they are being selective for prey (see Colton and Alevizon 1983).

The unique mosaic of coastal habitats found in The Bahamas provides a variety of resource pools, which species such as bonefish can exploit. This study suggests that bonefish rely critically on the different resource pools through ontogeny, and this variation in life-stage specific demands has consequences for conservation and management of these fish. While bonefish exhibit a degree of trophic plasticity that is habitat dependent, they are unlikely to be immune to habitat loss. Moreover, given that there is concern regarding the status of various bonefish species across their respective ranges (see Adams et al. 2014), our study emphasizes the importance of protecting different habitat types, as habitat is the foundation for healthy and productive fisheries. Knowledge from this study is timely as The Bahamas moves to protect 20% of their marine habitat by 2020 (Moultrie 2012). Using economically important species such as the bonefish to justify protection of diverse habitats types would benefit bonefish and an array of other nearshore species that similarly require habitat mosaics (see Adams and Murchie 2015).

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