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Hydrodynamic and isotopic niche differentiation between juveniles of two sympatric cryptic bonefishes, *Albula vulpes* and *Albula goreensis*

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Abstract We employed numerical wave models, GIS, and stable isotope analyses of otolith material to identify interspecific differences in habitat and resource use among juveniles of two sympatric and morphologically indistinct bonefishes, *A. goreensis* and *A. vulpes* in littoral zones of The Bahamas. Both species occurred in similar water temperatures; however, *A. goreensis* juveniles occupied habitats characterized by greater wave-driven flow velocities and closer proximity to coral reefs than *A. vulpes*. Likewise, *A. goreensis* was present across a broader range of flow environments and sampling stations than *A. vulpes*, which was typically confined to sheltered, low-flow habitats. The results of stable isotope analyses were consistent with the species' relationships with environmental parameters, providing support for differential habitat and/or resource utilization. Otolith $\delta^{18}O$ did not differ significantly between species, suggesting they experience comparable thermal regimes. However, $\delta^{13}C$ varied substantially, with the otoliths of *A. goreensis* depleted in ^{13}C relative to *A. vulpes* by approximately 1‰, potentially signifying a greater reliance on pelagic carbon sources by the former, in agreement with observed distinctions in habitat use. In linear models, otolith $\delta^{13}C$ was negatively correlated with ambient flow velocity and positively related to distance from coral reef habitats, and these relationships did not vary across species. After accounting for the effects of these variables, species-specific differences in otolith $\delta^{13}C$ remained, indicating that other unknown factors contributed to the observed disparities. Collectively, our findings suggest that niche partitioning between *A. goreensis* and *A. vulpes* is likely mediated by their differential abilities to compete across various flow environments, likely as a result of divergent behavioral and/or physiological adaptation.

Keywords Cryptic species · *Albula* spp. · Stable isotopes · Otolith · Wave exposure · Flow · Juvenile habitat · Niche partitioning · Behavior

Introduction

Bonefishes, *Albula* spp., are distributed throughout the world's tropical oceans, supporting valuable recreational fisheries across much of their ranges (Adams et al. 2014). Once thought to comprise just two species, the genus

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has undergone substantial phylogenetic revision in recent decades, and is now believed to include twelve distinct species, many of which share largely overlapping extents (Wallace 2014). This taxonomic uncertainty, however, remains due in large part to the unusually high degree of conservatism in morphological traits across members of the genus, among which observable distinguishing features are typically subtle or nonexistent (Pfeiler 1996; Colborn et al. 2001; Wallace 2014). Such cryptic species complexes can pose obvious difficulties for management efforts, potentially leading to false conclusions regarding conservation status or species-specific fundamental ecological requirements (Arlettaz 1999; Sattler et al. 2007). Accordingly, the relatively recent discoveries of several regional sympatric cryptic species complexes within the genus *Albula* (Pfeiler 1996; Colborn et al. 2001; Bowen et al. 2007; Wallace and Tringali 2010) has complicated efforts to conserve bonefishes, which are experiencing declines throughout much of their range (Adams et al. 2014).

One of the more problematic *Albula* cryptic species complexes occurs in the tropical Northwest Atlantic Ocean, where some of the most developed and lucrative recreational fisheries exist (Fedler 2010, 2013) and where stocks have undergone one of the most notable declines (Frezza and Clem 2015; Santos et al. 2017). In this region, molecular genetic analyses have documented the co-existence of at least three sympatric species with no distinguishing morphological characters (Colborn et al. 2001; Crabtree et al. 2003; Wallace and Tringali 2010; Wallace and Tringali 2016), with recreational fisheries supported almost entirely by a single species, *Albula vulpes* (Adams et al. 2007; Wallace and Tringali 2016). Despite clear genetic divergence among the species, there is little empirical evidence of ecological niche differentiation between them (Colborn et al. 2001; Wallace and Tringali 2010; Wallace 2014). Of the three species, *Albula* sp. cf. *vulpes (*Wallace and Tringali 2010) has the lowest incidence in fishery catches, may be the most ecologically distinct, and appears limited primarily to more turbid, estuarine waters (Wallace 2014). However, the differences in environmental preferences and habitat utilization between *Albula goreensis* (Wallace and Tringali 2016) and *A. vulpes* are more obscure.

Mature *A. goreensis* are infrequently encountered on the shallow tidal flats where bonefish (primarily *A. vulpes*) are typically targeted by anglers, and limited anecdotal evidence suggests that mature *A. goreensis* and *A. vulpes* may occupy distinct positions along a depth-related gradient (Bruger 1974; Colborn et al. 2001; Crabtree et al. 2003). This pattern is similar to that described for *A. virgata and A. glossodonta* in the Hawaiian Islands (Donovan et al. 2015), although there are no known distinguishing morphological characteristics for the Atlantic species. Nonetheless, the separation is not well-defined and may vary geographically (Colborn et al. 2001), leading to some degree of overlap in habitat utilization between adults of the two species, which have been found to co-occur in back-reef habitats (E. Wallace, pers. comm.). This apparent niche overlap is more pronounced in early life stages, where the co-occurrence of *A. goreensis* and *A. vulpes* is frequently observed in coastal habitats (Colborn et al. 2001; Crabtree et al. 2003; Adams et al. 2007; Snodgrass et al. 2008; Haak, unpubl. data).

For a species that occupies distinct habitats throughout ontogeny, determining the basic habitat requirements for each life stage is an essential step in the process of developing a comprehensive fishery management plan (Minello 1999; Levin and Stunz 2005). In the case of *Albula* spp., efforts to identify these requirements have been hindered by the aforementioned taxonomic dilemmas, and uncertainty exists regarding the habitats occupied by early life stages of bonefishes prior to their recruitment into the recreational flats fishery. Early efforts to identify juvenile habitats of bonefishes (initially assumed to be *A. vulpes*) in Florida suggested that they occupied sparsely vegetated, moderately-exposed windward beaches, yet subsequent genetic analyses determined that the vast majority of these individuals were in fact *A. goreensis* (Crabtree et al. 2003; Adams et al. 2007; Snodgrass et al. 2008). More recent efforts in The Bahamas have revealed that juvenile *A. vulpes* also occupy sparsely vegetated littoral zone habitats but are limited to largely enclosed, sheltered embayments exposed to minimal wave energy (Haak et al. 2018). Based on these observations, it appears that while juveniles of both species share preferences for similar depths and benthic microhabitats, they may exploit shorelines subject to distinct levels of wave exposure and varying degrees of connectivity with pelagic or coral reef habitats. Interspecific variation in the ability of fishes to negotiate wave driven flow is an important determinant of habitat use and assemblage structure in coastal marine habitats, even for closely related species (Bellwood and Wainwright 2001; Fulton et al. 2001). Accordingly, the preference for habitats subject to differential wave-driven flow regimes may constitute a fundamental niche difference between *A. vulpes* and *A. goreensis*, providing a much-needed ecologically-based descriptor from which species may be inferred.

Differences in resource use or ambient environmental parameters are often reflected in the isotopic composition of animal tissues, permitting retrospective inference about patterns of movement or habitat utilization (Hobson 1999; Rubenstein and Hobson 2004; McMahon et al. 2013). Ratios of stable carbon and oxygen isotopes in fish otoliths can provide information on broad scale geographic location, ambient temperature, resource utilization, and even physiology (Campana 1999). Consequently, isotopic ratios in otoliths are frequently employed as a tool for differentiating between fish stocks (Edmonds and Fletcher 1997; Gao et al. 2004; Correia et al. 2011) or elucidating patterns of migration or habitat utilization at a range of spatial scales (Hidalgo et al. 2008; McMahon et al. 2011a; Currey et al. 2014). Assuming that *A. vulpes* and *A. goreensis* juveniles do in fact exploit discrete habitats, it is probable that this will be reflected in the isotopic signatures recorded in otolith material, providing additional support for niche differentiation, and possibly permitting additional inference about the nature of interspecific differences in resource use.

In this study we compared environmental conditions, namely: (1) wave-driven water velocity; (2) proximity to coral reef habitats; (3) benthic vegetation coverage, and (4) ambient water temperature associated with the occurrence of *A. goreensis* and *A. vulpes* juveniles, with the goal of elucidating consistent distinctions in habitat use between the species. Additionally, we contrasted species-specific ratios of carbon and oxygen isotopes in otolith material from a subset of these individuals to further examine differences in habitat and resource utilization integrated over broader temporal scales. We expected the species to occupy distinct wave-driven flow regimes; expressly, that *A. goreensis* would be associated with more open, exposed habitats characterized by greater wave-driven water velocities (and concurrently reef proximities) than its counterpart, *A. vulpes*. Likewise, we expected that interspecific differences in otolith isotopic composition would be correlated with gradients in wave-driven flow and/or connectivity with reef habitats, reflecting disparities in flow-related habitat use between the species.

Methods

Fish sampling

Juvenile bonefishes were collected from six stations located along a roughly 40 km stretch of the windward (Atlantic-facing) shoreline of Eleuthera Island, situated on the eastern margin of the Bahamas Archipelago (Fig. 1), between January 2012 and April 2013. This coastline was directly exposed to prevailing easterly trade winds, with a largely uninterrupted fetch and little physical sheltering except for the adjacent fringing reef. With the exception of two largely enclosed sounds, littoral zones were characterized by relatively high-energy sandy beaches subject to long-period oceanic swells and locally generated wind-waves. Specimens were captured using a 15.2 m × 1.2 m, 3.2 mm mesh bagless beach seine, with each sample encompassing approximately 210 m^2 of seabed. During each haul, the composition of the seabed was monitored, and the proportion of moderately-to-densely vegetated bottom, defined following Harborne et al. (2008), was estimated and recorded. Seine hauls ranged in depth from 0 to 1.1 m. To permit subsequent estimation of wave-driven water velocities at the location of each sampling event, geographic coordinates for the approximate centroid of each seine haul were recorded using a handheld GPS receiver, and sea surface temperature was recorded in the vicinity of each seine haul using a digital handheld thermometer. Captured juvenile bonefish were immediately sacrificed and preserved on ice for transport, and then frozen at −20 °C. At a later date, specimens were thawed and measured to the nearest 1 mm fork length (FL). Fin clips were obtained from each fish, air-dried, and stored in acid-free filter paper for subsequent molecular genetic analysis at the University of Minnesota Genomics Center, following the methods outlined in Seyoum et al. (2008) and Wallace and Tringali (2010). For selected individuals, otoliths (sagittae) were extracted, rinsed in freshwater, air-dried, and stored in plastic vials until they could be prepared for stable isotope analysis (SIA).

Given that leptocephalus larvae of both species exploit similar pelagic environments prior to settling in coastal waters, their overlap during migration and settlement into neritic habitats is probable. As such, to limit the effects of habitat-mismatch; (i.e., to ensure that fishes were sampled from actively-selected settlement habitats rather than those they were incidentally

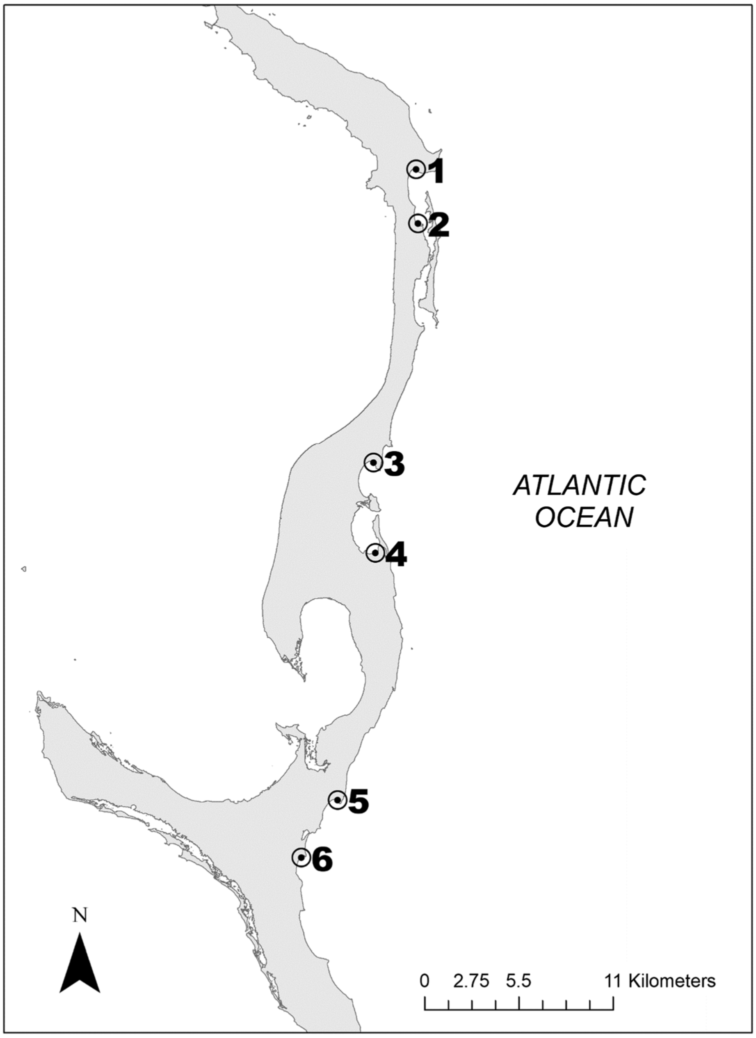

Fig. 1 Map of the study area on the east coast of Eleuthera, The Bahamas, depicting locations of sampling stations numbered 1–6

"passing through"), we limited our analysis to fully-metamorphosed individuals >30 mm in fork length (FL). Likewise, to minimize the potential of including fish from subsequent ontogenetic stages that may utilize distinct habitats, individuals larger than 150 mm FL were also excluded from consideration.

Environmental variables

Wave-associated hydrodynamic stress at the location of juvenile bonefish collections was quantified in terms of estimated maximum bottom orbital velocity (the peak near-bed wave-induced water velocity parallel to the seabed in the direction of dominant flow). Wave bottom orbital velocity provides a physically relevant measure of flow and has been employed extensively to represent the wave-related stresses experienced by demersal fishes (Fulton and Bellwood 2005; Gabel et al. 2011; Anton et al. 2014). Velocities were estimated using "response surface" or "surrogate" models (Box and Draper 1987) discretely relating local (wind) or remote (swell) forcing with hydrodynamic conditions experienced at each location of interest, based on a set of high-fidelity simulated wave fields produced using the numerical wave model SWAN (Booij et al. 1999). In SWAN, simulated surface gravity waves corresponding to forcing conditions are propagated through the model domain, where they are dynamically affected by bathymetry and coastal morphology based on physical principles and empirically-derived relationships, allowing the estimation of hydrodynamic parameters as waves travel to the shore. This approach permitted the high spatial resolution, large model domain, and physical accuracy necessary to resolve shallow-water wave processes in complex coastal habitats while keeping computational demands feasible. Wind and swell-driven bottom orbital velocities at seine haul locations were estimated independently, by interrogating the appropriate response surface model with the mean forcing (wind or swell) conditions corresponding to the time period of interest. For local (wind) forcing, these inputs comprised wind speed and direction recorded at NOAA station SPGF1 at Settlement Point on Grand Bahama Island, located 300 km NW of the study area. Remote (swell) forcing, inputs included swell direction, significant wave height, and dominant period recorded at NOAA NDBC 41047 located 500 km NE of Eleuthera. The greater of wind and swell-driven orbital velocities was then taken to reflect the most adverse conditions. Further information on the development and validation of these models can be found in Haak et al. (2018).

To examine the effects of both spatial and temporal variability in flow, we related the abundance of bonefishes to bottom orbital velocities at capture locations measured on two discrete temporal scales. To reflect incident wave stress on fine timescales, corresponding roughly to the moment of each sampling event, we estimated the mean wind or swell conditions corresponding to the 24-h period preceding each seine haul (U_{24}). This was deemed an appropriate temporal window, given not only the hourly to daily timescales at which wave conditions develop and subside in coastal habitats, but also the observations of others which suggest that temporal variability in the abundance of fishes is more closely correlated with sea state measured over the preceding hours to days than with instantaneous conditions (Lasiak 1984; Friedlander and Parrish 1998). To approximate spatial gradients in wave-driven flow integrated over broader temporal scales, likely to be more representative of the average conditions encountered at a location on a diel basis, long-term mean near-bed velocity (U_{mean}) at each capture location was determined by interrogating the surrogate models with hourly histories of forcing parameters recorded at their respective NOAA stations for a 4-year timespan encompassing the study period, (January 1, 2010 to January 1, 2014), and then calculating the mean of the resulting distribution. Spatial variation in U_{mean} across the study area is depicted in Fig. 2.

The minimum swimming distance from each seine haul location to the nearest coral reef habitat (heretofore referred to as Reef distance) was estimated to the nearest 100 m using a cost-distance function, with reef locations based on the 30 m spatial resolution United Nations Environment Programme-World Conservation Monitoring Centre global distribution of warm-water coral reefs database (UNEP-WCMC 2010). The estimated percent coverage of benthic vegetation characterizing the area sampled by each seine haul was obtained as described above under *Fish Sampling*.

Stable isotopes

Stable carbon isotope ratios (δ^{13}C) incorporated in animal structures are commonly used to determine the sources of organic carbon in food webs, based on the contrasting isotopic fractionations exhibited by different primary producers (Peterson and Fry 1987; Fry and Sherr 1989; Post 2002). Because the dominant primary producers at the base of marine food webs tend to vary among discrete habitats or microhabitats, δ^{13}C can function as a naturally-occurring intrinsic marker, linking fishes to distinct habitats through dietary intake and trophic transfer (Hobson 1999; Kieckbusch et al. 2004; Nagelkerken and van der Velde 2004; Lugendo et al. 2006). Although dissolved inorganic carbon (DIC) from ambient seawater generally comprises the dominant proportion of carbon in otolith aragonite, the remaining fraction is composed of metabolically-derived carbon (Solomon et al. 2006). Accordingly, bulk otolith δ^{13}C ($\delta^{13}C_{oto}$) can be reflective of dietary intake (Radtke et al. 1996) and thus may provide information about habitat use akin to that of muscle δ^{13}C (Jamieson et al. 2004; McMahon et al. 2011b).

However, the large DIC fraction of carbon in otolith aragonite results in a "dilution" effect, partially obscuring the dietary signal and making it difficult to draw conclusions about habitat or resource use from bulk otolith δ^{13}C values (McMahon et al. 2011b). In the case of the species considered here, isotopic data from an expanded collection of juvenile bonefishes taken from the study area demonstrates that $\delta^{13}C_{oto}$ correlates closely with muscle δ^{13}C within individuals (see Online Resource 1). Furthermore, in relatively stable oceanic environments such as the study area, the isotopic composition of DIC in seawater tends to vary little at the small scales encompassed by the present study (Hu and Burdige 2007). Therefore, it is reasonable to assume that variation in $\delta^{13}C_{oto}$ among the fishes examined here is largely attributable to dietary intake (Elsdon et al. 2010; Nelson et al. 2011), permitting insights into differential habitat or resource use via the sources of carbon

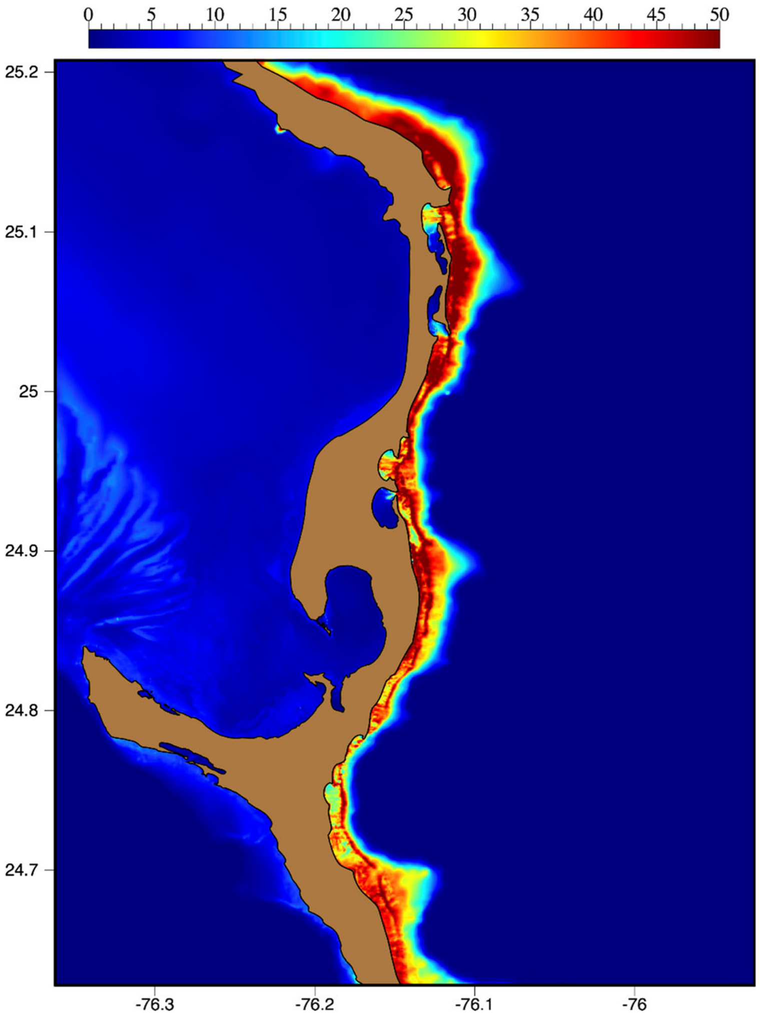

Fig. 2 Map illustrating the distribution of long-term mean wave-induced bottom orbital velocity (U_{mean}[cm s^{-1}]) across the study area as estimated by the numerical wave model SWAN. To highlight variability at sampling stations, the maximum value depicted by the color gradient ramp has been truncated to 50 cm s^{-1}

at the base of food webs they occupy. Likewise, the relative proportions of DIC (exogenous) and metabolically-derived (endogenous) carbon incorporated into otolith material is a function of metabolic rate, with a greater fraction of metabolic carbon included during periods of increased metabolism (Jamieson et al. 2004; Dufour et al. 2007; Tohse and Mugiya 2008). Because carbon in ambient DIC is isotopically heavy compared to metabolically-derived carbon, bulk otolith $\delta^{13}C$ is inversely related to metabolic rate (Kalish 1991; Schwarcz et al. 1998; Høie et al. 2003). Accordingly, variation in $\delta^{13}C_{oto}$ may also be indicative of inter-or-intra-specific discrepancies in metabolism, potentially providing insights into physiological differences among *A. goreensis* and *A. vulpes.*

Oxygen stable isotope ratios ($\delta^{18}O$) in otolith material also provide valuable information about the environment experienced by fishes, reflecting the isotopic composition of ambient seawater and environmental temperature at the time of deposition (Thorrold et al. 1997; Høie et al. 2004). While temperature histories can be approximated from $\delta^{18}O$, this cannot be accomplished without knowledge of the relationship between temperature and isotopic fractionation, which must be experimentally determined, can be non-linear, and may vary substantially even among related species (Stormsuke et al. 2007; Godiksen et al. 2010). Nonetheless, assuming interspecific differences in temperature-dependent fractionation do not exist between *A. vulpes* and *A. goreensis*, otolith $\delta^{18}O$ may indicate relative differences in the thermal regime of habitats occupied by the two species.

The subset of individuals selected for SIA were constrained to similar size classes, both within and across species, to limit the potential for any size-related or ontogenetic effects. Otoliths from selected individuals were scrubbed, sonicated, rinsed in deionized ultra-pure water, dried under a laminar flow hood, and stored in 1.5 ml plastic vials until analysis. Bulk SIA of otolith $\delta^{13}C$ and $\delta^{18}O$ was conducted at the University of Waterloo, following the methods described by Guiguer et al. (2003) and Storm-suke et al. (2007). Carbon and Oxygen isotope ratios are expressed in delta notation (δ) with concentrations measured in permil (‰), relative to Vienna Pee Dee Belemnite.

Statistical analyses

When observed data conformed to parametric assumptions, interspecific comparisons of fish size (FL), environmental variables at the time and place of capture, and otolith isotopic composition were conducted using Welch's unequal variances t-test for independent samples. If parametric distributional assumptions were not satisfied, as was the case for many environmental parameters, the non-parametric Mann-Whitney *U* test was instead employed for comparisons. To examine the relationship between otolith $\delta^{13}C$ and environmental factors, we employed a linear mixed model (LMM), approximating $\delta^{13}C_{oto}$ as a function of the continuous fixed variables U_{mean} and Reef distance, as well as of the fixed factor variables Station and Species. To evaluate the potential for interspecific differences in the relationship between $\delta^{13}C_{oto}$ and U_{mean}, an interaction term was included between U_{mean} and Species. Furthermore, to account for any potential interdependency in response among fishes co-occurring in the same seine haul (i.e., cluster sampling bias; Nelson 2014), seine haul was modeled as a random intercept. Model selection was performed using backward elimination of fixed effects via likelihood ratio tests. Statistical analyses were performed using RStudio (Version 1.0.143) and the lme4, car, and MASS packages. Unless otherwise noted, values displayed in the text are presented as mean ± SD, and fish sizes are given as fork length (FL).

Results

Fish collection and environmental variables

A total of 106 juvenile bonefishes were collected across 37 distinct seine hauls. Molecular genetic analyses classified six individuals as potential hybrids, and these were excluded from subsequent analyses. Of the remaining 100 specimens, 77 individuals from 26 seine hauls at three different stations (1, 2, and 4, as depicted in Fig. 1) were identified as *A. vulpes*, and 23 specimens, representing 13 distinct hauls at five different stations (1, 2, 3, 5, and 6) were classified as *A. goreensis*. The species co-occurred in three seine haul samples; twice at station 1, and once at station 2, comprising 23 and 13% of *A. vulpes* and *A. goreensis* specimens, respectively. While the lengths of *A. vulpes* (60 ± 34 mm) were more variable than those of *A. goreensis* (53 ± 9 mm), size did not differ substantively between species (Mann-Whitney *U* test, $U = 1088.5$, $Z = 1.66$, $p = 0.097$). Water temperatures associated with the occurrence of *A. vulpes* (27.5 ± 2.4 °C) were marginally lower than those corresponding to *A. goreensis* collections (28.9 ± 2.5 °C) (Table 1), however this difference was not statistically significant (Welch's *t*-test, $t = 1.589$, $df = 22.81$, $p = 0.1257$). Likewise, there was no significant difference in the coverage of benthic vegetation associated with the presence of each species (Mann-Whitney *U* test, $U = 147.5$, $Z = -0.99$, $p = 0.319$), with both occurring primarily in unvegetated or sparsely-vegetated habitats (Table 1).

Wave-driven flow regime at capture locations varied markedly and consistently between species (Table 2). Twenty-four-hour mean bottom orbital velocities, U_{24}, preceding the occurrence of *A. goreensis* (22.1 ± 11.5 cm s^{-1}) were on average more than three times those of corresponding *A. vulpes* collections (6.8 ± 6.5 cm s^{-1}), constituting a significant interspecific disparity (Mann-Whitney *U* test, $U = 293.5$, $Z = 3.69$, $p = 0.0002$). A similar degree of asymmetry was apparent in the long-term mean bottom velocities experienced at capture locations, U_{mean} (Mann-Whitney *U* test, $U = 301$, $Z = 3.92$, $p = <0.0001$), with *A. goreensis* taken from sites characterized by markedly greater mean velocities (21.6 ± 8.4 cm s^{-1}) than those associated with the presence of *A. vulpes* (7.5 ± 6.3 cm s^{-1}) (Fig. 3a). While typically occupying comparatively higher-flow habitats than *A. vulpes*, *A. goreensis* was also present in a notably broader range of water velocities, which spanned from near 0 up to a maximum of 46.7 cm s^{-1}, nearly twice that of *A. vulpes* (0–24.2 cm s^{-1}). Distance from coral reef habitats (Fig. 3b) also differed significantly between species (Mann-Whitney *U* test, $U = 57$, $Z = -3.37$, $p = 0.0007$), with *A. goreensis* (400 ± 600 m) regularly occurring in closer proximity than *A. vulpes* (1900 ± 900 m).

Table 1 Summary information on juvenile bonefishes (*A. vulpes* and *A. goreensis*) captured in seine hauls and corresponding environmental variables recorded at the time of collection, including ambient water temperature (Temp) and the coverage of moderate-to-densely vegetated seabed (Veg cover) within the sweep area. Lengths are reported as fork length

Species	*n indivs*	*n hauls*	Length ± SD (mm)	Length min/max (mm)	Temp ± SD (°C)	Temp min/max (°C)	Veg cover ± SD (%)	Veg cover min/max (%)
A. goreensis	23	13	53 ± 9	39/77	28.9 ± 2.5	24/32.1	0 ± 1.4	0/5
A. vulpes	77	26	60 ± 34	30/149	27.5 ± 2.4	21/32	9 ± 25	0/100

Stable isotopes

To control for any size-related or ontogenetic effects on isotope ratios, a reduced set of individuals ranging in length from 39 to 88 mm was selected for comparison of otolith isotopic composition (Table 3). This subset comprised twenty-three *A. vulpes* juveniles collected in 12 distinct seine hauls, and eighteen *A. goreensis* juveniles representing 12 discrete hauls. Within this group, the mean size of *A. vulpes* (55 ± 13 mm) corresponded closely to that of *A. goreensis* (54 ± 9 mm), with no significant difference in size between the two species (Welch's *t* test, $t = -0.403$, df = 39.398, $p = 0.688$). Examination of the data revealed no observable correlation between otolith $\delta^{13}C$ or $\delta^{18}O$ and fish length over the range of sizes considered, therefore no correction was applied to account for size effects on isotopic composition.

Mean $\delta^{13}C_{oto}$ values recorded for *A. vulpes* (−1.15 ± 0.53 ‰) were enriched in ^{13}C by approximately 1‰ compared to those of *A. goreensis* (−2.04 ± 0.51‰) (Fig. 4). This difference was highly significant (Welch's *t* test, $t = -5.428$, df = 37.232, $p < 0.0001$), signaling that the species exploited isotopically distinct environments and/or resources, or experienced contrasting metabolic demands. Although intraspecific variability in $\delta^{13}C_{oto}$ was similar between the species, *A. goreensis* displayed a slightly broader range of values overall, evidencing the utilization of a greater variety of habitats or resources. Otolith $\delta\ ^{18}O$ spanned a similar range of values for *A. vulpes* and *A. goreensis* and did not vary substantively between species (Welch's *t* test, $t = 0.783$, df = 34.274, $p = 0.438$), suggesting they inhabited comparable thermal environments.

In linear models relating $\delta^{13}C_{oto}$ to environmental variables (Tables 4 and 5), the fixed effect of sampling station did not contribute to explaining observed patterns in otolith $\delta^{13}C$. The high collinearity between U_{mean} and Reef distance ($r = 0.77$) and consequent variance inflation precluded the simultaneous inclusion of both continuous fixed predictors; however, in discrete reduced models, $\delta^{13}C_{oto}$ was negatively correlated with U_{mean} ($F = 3.027$, df = 38, $p = 0.089$) (Fig. 5a), and significantly positively correlated with distance from coral reef habitats ($F = 8.017$, df = 38, $p = 0.0073$) (Fig. 5b). The absence of an interaction between either U_{mean} or Reef distance with Species indicated that these relationships did not differ substantively between *A. goreensis* and *A. vulpes*. Nonetheless, after accounting for these effects, there was still a significant effect of Species in the presence of both U_{mean} ($F = 6.9992$, df = 38, $p = 0.01179$) and Reef distance ($F = 8.2412$, df = 38, $p = 0.0066$), indicating that interspecific differences in $\delta^{13}C_{oto}$ could not be explained entirely by variation in ambient flow velocities or coral reef proximity, and therefore that interspecific discrepancies in other, unmeasured factors likely contributed to observed differences in otolith $\delta^{13}C$.

Table 2 Summary information on environmental parameters corresponding to locations where juvenile bonefishes (*A. vulpes* and *A. goreensis*) were captured in seine hauls, as estimated by numerical wave models and GIS. Flow-related metrics (U_{mean} and U_{24}) reflect estimated wave-bottom orbital velocities at capture locations averaged over a 4-year timeframe encompassing the study period (U_{mean}) and the 24-h period preceding a given seine haul (U_{24}). Reef distance reflects the minimum swimming distance from a given capture location to the nearest coral reef habitat

Species	*n hauls*	U_{mean} ± SD (cm s^{-1})	U_{mean} min/max (cm s^{-1})	U_{24} ± SD (cm s^{-1})	U_{24} min/max (cm s^{-1})	Reef distance ± SD (m)	Reef distance min/max (m)
A. goreensis	13	21.7 ± 8.4	6.2/33.8	22.1 ± 11.5	1.4/46.7	400 ± 600	100/2300
A. vulpes	26	7.5 ± 6.3	1.9/25.1	6.8 ± 6.5	0.0/24.2	1900 ± 900	100/2500

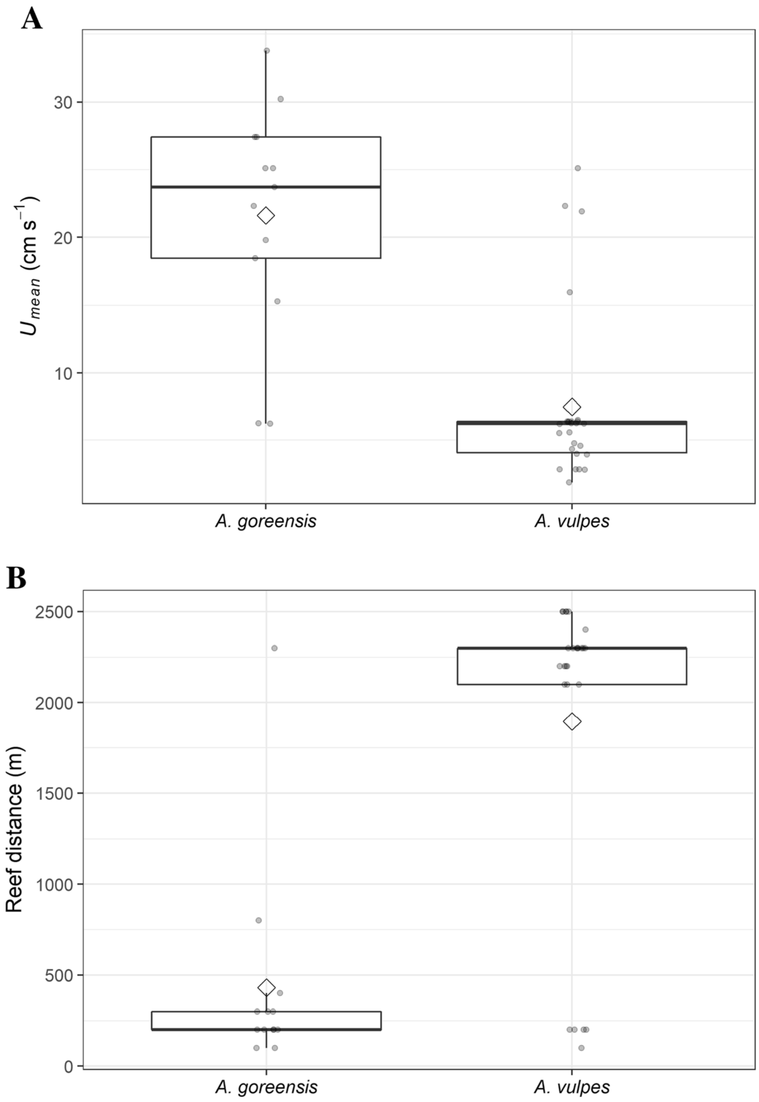

Fig. 3 Boxplots depicting the distribution of: **a** long-term (4-year) mean wave bottom orbital velocities (U_{mean} [cm s^{-1}]), and **b** swimming distance to coral reef habitats (to the nearest 100 m), at the locations of seine hauls capturing *A. goreensis* ($n = 13$) and *A. vulpes* ($n = 26$) juveniles. Solid grey dots represent individual observations, and diamonds denote the mean

Discussion

Albula goreensis juveniles were present in habitats subject to substantially greater bottom orbital velocities than those of *A. vulpes*, supporting the notion that the two species occupy distinct positions along a gradient in the strength of wave-driven flow. Flow intensity was closely correlated with proximity to coral reef habitats, which likewise differed greatly between locations where the species occurred, further underpinning interspecific divergence in habitat use. The broader range of locations and water velocities inhabited by *A. goreensis* suggests that this species may display a greater degree of adaptability to variation in incident flow. Contrasts (or the lack thereof) in otolith isotopic composition between the species were consistent with variation in the environmental conditions in which they occurred. The absence of interspecific differences in otolith $\delta^{18}O$ is congruent with the comparable ambient water temperatures that *A. goreensis* and *A. vulpes* were collected in, suggesting that both species share similar temperature-dependent fractionation relationships and that water temperature is not among the factors that differentiate their respective niches. Moreover, the clear disparity in $\delta^{13}C_{oto}$ between *A. goreensis* and *A. vulpes* juveniles suggests distinctions in habitat and/or resource utilization linked to gradients in flow velocity and/or reef proximity.

Table 3 Summary of sizes and bulk-otolith stable isotope ratios ($\delta^{13}C$ and $\delta^{18}O$) for a subset of juvenile bonefishes (*A. goreensis* and *A. vulpes*) collected from six stations along the Atlantic coast of Eleuthera, The Bahamas. Lengths are reported as fork length (FL)

Species	*n*	*n* hauls	Length ± SD (mm)	Length min/max (mm)	$\delta^{13}C$ ± SD (‰)	$\delta^{13}C$ min/max (‰)	$\delta^{18}O$ ± SD (‰)	$\delta^{18}O$ min/max (‰)
A. goreensis	18	12	54 ± 9	39/77	−2.04 ± 0.51	−3.10/−1.08	−0.29 ± 0.57	−1.33/0.77
A. vulpes	23	12	55 ± 13	40/88	−1.14 ± 0.53	−2.03/−0.15	−0.38 ± 0.54	−1.52/0.65

The differential resource use revealed here implies the existence of niche partitioning and habitat segregation between *A. goreensis* and *A. vulpes* with respect to the intensity of wave-driven water movement. Differences in flow-related habitat use among fishes are most commonly attributed to interspecific discrepancies in locomotor performance, typically associated with phylogenetic variation in morphological characteristics, such as body form or fin shape, that influence the ability of fishes to negotiate fast, unsteady or turbulent flows (Bellwood and Wainwright 2001; Fulton et al. 2001; Fulton and Bellwood 2005). However, the adaptive distinctions that accompany niche partitioning are not necessarily reflected in outward anatomical form. Behavioral differences, commonly paired with divergent physiological adaptations, can also have implications for resource use, constituting important niche determinants among morphologically and functionally-similar organisms (Schmitt and Coyer 1982; Hartney 1989; Clarke et al. 2009). The conspicuous absence of any defining morphological characters between the species studied here seems to suggest that the disparate flow environments exploited by *A. goreensis* and *A. vulpes* may thus be related to differences in behavior and/or internal physiology.

Examples of niche partitioning or habitat segregation with respect to ambient flow can be found among several other sympatric, closely related fishes (Hyndes et al. 1997; Clarke et al. 2005; Davis and Wing 2012). For example, distinctions in feeding behavior and metabolic rate between congeneric blennies (*Acanthemblemaria* spp.) have been linked with fine-scale habitat partitioning along a vertical gradient in wave-driven water velocity (Clarke et al. 2009; Finelli et al. 2009). Such seemingly small differences in foraging microhabitat use can also give rise to segregation at much broader spatial scales (Hixon 1980; Holbrook and Schmitt 1989; Hyndes et al. 1997). For example, Hyndes et al. (1997) determined that trophic niche differentiation and landscape-scale habitat partitioning among juveniles of several sympatric, morphologically-similar members of the genus *Sillago* was attributable to relatively fine-scale differences in the use of foraging microhabitats, with *S. baseensis*, a species associated with exposed high-energy environments, exploiting invertebrate epifauna from detached macrophytes (drift algae), while its

Fig. 4 Boxplots depicting the distribution of $\delta^{13}C$ values (‰) of bulk otolith material from *A. goreensis* (*n* = 18) and *A. vulpes* (*n* = 23) juveniles. Solid grey dots represent individual observations, and diamonds denote the mean

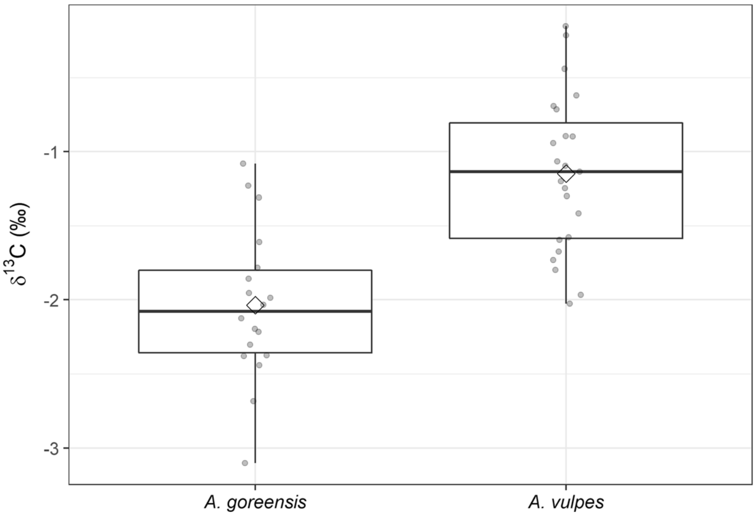

Table 4 Summary of reduced Linear Model Results for fixed predictors U_{mean} + Species

Parameter	Estimate	SE	*t*-value	*p* value
Intercept	−1.601	0.277	−5.779	<0.001
U_{mean}	−1.803	1.036	−1.740	0.090
Species	0.605	0.228	2.646	0.011

counterparts in more sheltered low-energy habitats foraged primarily on invertebrate prey from benthic sediments. Accordingly, if broad-scale environmental gradients in flow intensity are correlated with similar shifts in the abundance of distinct microhabitats or prey taxa upon which *A. goreensis* and *A. vulpes* differentially rely, one might expect to observe interspecific contrasts in habitat utilization (spatial segregation) analogous to those observed here.

Wave energy is among the most fundamental factors structuring littoral zones (Brind'Amour et al. 2005), shaping the distributions of benthic sediments and primary producers (Keddy 1982; Fonseca et al. 1983), as well as the structure of invertebrate communities which inhabit them (Fenwick 1976; Snelgrove and Butman 1994; Boström et al. 2006). It is thus logical that gradients in wave-driven flow should be associated with shifts in the structure of plant and animal communities, and consequently the isotopic composition of the fishes which forage within them (Davis and Wing 2012). The higher energy habitats typically occupied by *A. goreensis* exhibited closer proximity and greater connectivity to pelagic and coral-reef environments, which are characterized by isotopically-lighter carbon sources such as phytoplankton (De la Morinière et al. 2003; Crawley et al. 2009; McMahon et al. 2016). In contrast, the more sheltered and enclosed flats habitats utilized by *A. vulpes* likely received greater inputs from isotopically heavier, neritic sources of carbon such as seagrasses (Fry et al. 1982; De la Morinière et al. 2003; Nagelkerken and van der Velde 2004), potentially contributing to the observed interspecific disparity.

Table 5 Summary of reduced Linear Model Results for fixed predictors Reef distance + Species

Parameter	Estimate	SE	*t*-value	*p* value
Intercept	−3.295	0.470	−7.075	<0.001
log(Reef distance)	0.526	0.186	2.832	0.007
Species	0.552	0.192	2.871	0.006

Furthermore, variation in the strength of ambient flow can influence carbon uptake for primary producers, leading to ^{13}C depletion of plant tissues in high-flow environments (Trudeau and Rasmussen 2003; Cornelisen et al. 2007; McPherson et al. 2015), which in turn can be reflected in the isotopic composition of organisms at higher trophic levels (Finlay et al. 1999; Rasmussen and Trudeau 2010). Accordingly, the higher water velocities in habitats where *A. goreensis* occurred should be correlated with ^{13}C depletion in algae or seagrasses relative to their analogs in the low-energy habitats occupied by *A. vulpes*, in agreement with observed trends. Whether a result of broad-scale changes in community structure and shifts in the dominance of distinct primary producers along a wave-energy gradient, or of flow-related intraspecific variation in δ^{13}C within similar communities of primary producers, the comparatively low δ^{13}C values observed in the otoliths of *A. goreensis* are consistent with the utilization of more open, pelagically-connected habitats exposed to greater wave energy.

Alternatively, the observed differences in δ^{13}C may be related to distinctions in resource exploitation occurring at much finer scales. In habitats akin to those surveyed in the present study, the isotopic composition of both producers and consumers can vary markedly over very small distances (Higgs et al. 2016; Tue et al. 2017). As such, species-specific discrepancies in prey selection and foraging microhabitat utilization (e.g., consumption of pelagic vs. epibenthic vs. infaunal invertebrate prey), may give rise to contrasts in the isotopic makeup of *A. goreensis* and *A. vulpes* even despite their functional similarity and broad-scale overlap in habitat use. In this event, variation in isotopic signatures between the species may reflect greater inputs from pelagic carbon sources in the diet of *A. goreensis*, possibly indicating increased utilization of prey from the water column or from detached macrophytes (Robertson and Lenanton 1984; Crawley et al. 2006), which can be the primary source of organic carbon for consumers in surf-zone habitats (Crawley et al. 2009).

Interspecific differences in metabolism may also have contributed to observed interspecific contrasts in otolith δ^{13}C. Assuming the species display equivalent δ^{13}C fractionation and have analogous dietary inputs, the isotopically-lighter otolith δ^{13}C values of *A. goreensis* may be interpreted to suggest that this

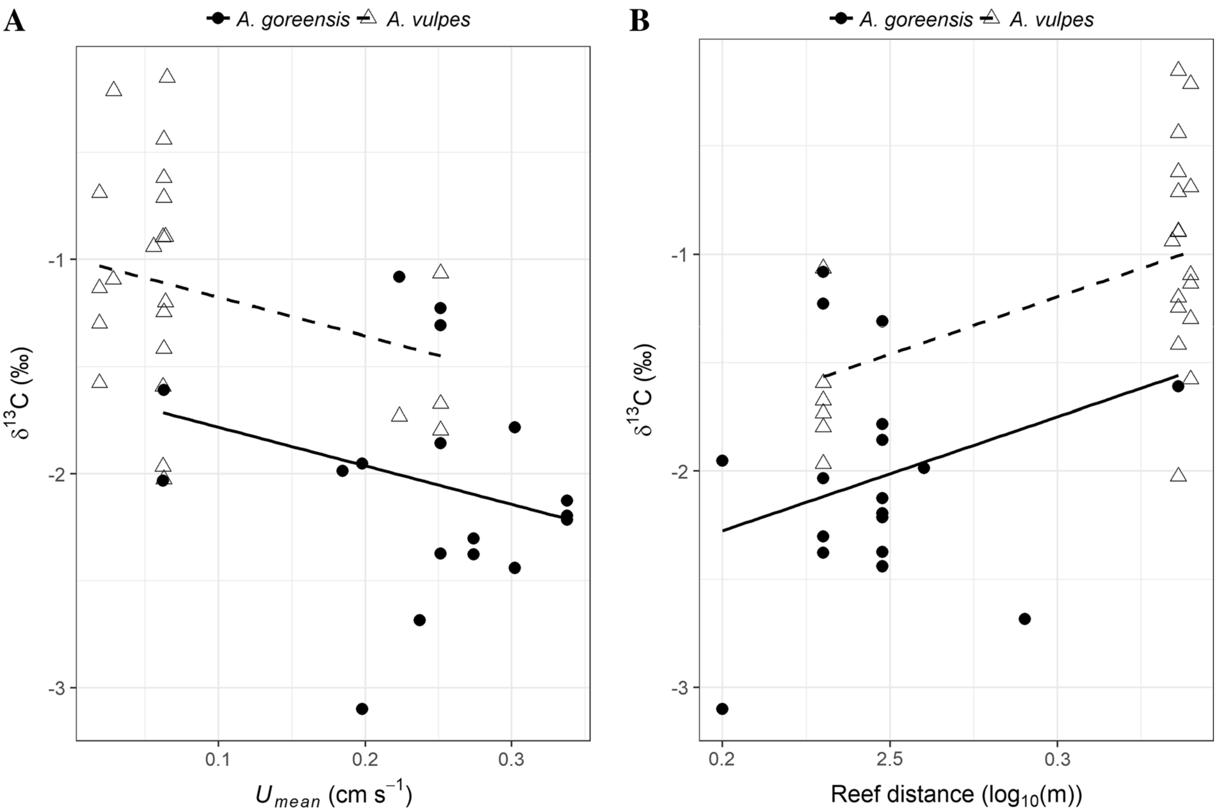

Fig. 5 Scatterplots depicting observed values and the predictions of linear regression models relating bulk otolith δ^{13}C for *A. vulpes* and *A. goreensis* juveniles to: **a** long-term mean wave bottom orbital velocity (U_{mean} [cm s^{-1}]) at capture locations, and **b** swimming distance to coral reef habitats (to the nearest 100 m) from capture locations

species maintains a higher metabolic rate (Kalish 1991; Høie et al. 2003), consistent with the greater energetic demands required by the comparatively high-flow or turbulent habitats it occupies (Enders et al. 2003; Roche et al. 2014). Similar discrepancies in species-specific metabolism or activity level have been linked with differential microhabitat and resource use among other sympatric congeners, and may represent adaptations that help to balance habitat-specific energetic costs and resource availability (Hartney 1989; Clarke et al. 2005, 2009).

The more widely ranging $\delta^{13}C_{oto}$ values observed for *A. goreensis* suggest that this species exploits a greater assortment of resources or microhabitats, in accordance with its broader distribution among sampling stations and the notably more heterogenous hydrodynamic regimes it occurred in. The seemingly more generalist nature of *A. goreensis* may reflect interspecific distinctions in sensory capability, which often accompany differences in resource use between closely related fishes (Lombarte et al. 2000; Cummings and J 2001; Schwalbe and Webb 2014), perhaps indicating that this species exploits alternative or more diverse sensory mechanisms than its counterpart, facilitating the detection of prey in a wider variety of habitats or sensory environments (Deary et al. 2016).

Collectively, our observations suggest that *A. goreensis* and *A. vulpes* exhibit divergent behavioral and/or physiological adaptations, likely linked to foraging and microhabitat use, that influence their relative abilities to compete over a range of flow conditions leading to differential distributions with respect to incident wave energy (Pekcan-Hekim et al. 2016). The much more constrained range of flow environments inhabited by *A. vulpes*, and consequently its more limited spatial distribution, indicate that this species may be more of a habitat specialist compared to *A. goreensis*, a supposition that appears compatible with the dietary habits of the two species (Griffin et al. this issue). As such, *A. vulpes* may out-compete *A. goreensis* in hydrodynamically stable low-flow habitats, possibly explaining the relative absence of *A. goreensis* from the more sheltered stations (2 & 4) where *A. vulpes* predominated. Concurrently, however, the greater specialization of *A. vulpes* may come at the cost of reduced adaptability, limiting the species' capacity to compete in more variable flow environments (Poff and Allan 1995) such as those occupied by *A. goreensis*, for which greater plasticity in foraging mode or microhabitat utilization may permit the exploitation of more diverse flow and resource regimes.

While this work focuses on the role of wave-driven flow in shaping differential habitat use, it is possible that unmeasured environmental factors that covaried with wave exposure also contributed to producing the observed distributional patterns. Although salinity and turbidity are important drivers of habitat use in estuarine waters (Blaber and Blaber 1980; Cyrus and Blaber 1992; Akin et al. 2005), background levels of these parameters vary comparatively little across the habitats surveyed here due to negligible freshwater inputs and the generally oligotrophic nature of the study area (Buchan 2000). Nonetheless, wave forcing can precipitate sediment resuspension in shallow coastal zones (Arfi et al. 1993; Lawson et al. 2007), and the greater susceptibility of more exposed sites to fluctuations in flow-related turbidity may have influenced habitat use. Likewise, benthic microhabitat features that are affected by wave exposure may have acted, perhaps more directly than wave-driven flow itself, to shape species distributions (Santin and Willis 2007). We did not detect interspecific differences with respect to benthic vegetation cover; nevertheless, the composition of benthic flora communities may have varied at scales finer than were assessed here. Similarly, whilst there were no obvious differences in substrate composition across sampling stations (all of which were dominated by fine sand), subtle differences in the characteristics of benthic sediments may also have existed.

Our study did not explicitly evaluate variation in the presence or relative density of allochthonous algae or detached macrophytes across seine haul locations; yet the more exposed windward habitats where *A. goreensis* occurred certainly received greater inputs of drifting *sargassum* spp. than the more sheltered habitats used by *A. vulpes*. Given the interspecific differences elucidated here, and the observations of others with regard to the importance of drift algae as a source of invertebrate prey and organic carbon in surf-zone habitats similar to those occupied by *A. goreensis* (Robertson and Lenanton 1984; Crawley et al. 2006; Crawley et al. 2009), future studies should consider including this as an environmental predictor.

While divergence in habitat and resource utilization was clearly discernable between the species, the underlying mechanisms giving rise to these differences were less transparent. Although disparities in the resource use of *A. goreensis* and *A. vulpes* were correlated with gradients in ambient flow and connectivity to coral reef habitats, it is unclear whether these contrasts arose due to distinctions in fine-scale microhabitat utilization and/or prey selection, or as a result of exploiting similar microhabitats or prey taxa but from distinct locations within broader-scale isotopic gradients (i.e., isoscapes). More detailed dietary analyses, optimally from the same region and with greater taxonomic resolution, may help resolve these questions by identifying the habitat associations of prey taxa (e.g., benthic or pelagic). Likewise, more comprehensive stable isotope studies, employing muscle tissue and including the analysis of $\delta^{34}S$ may help reveal the relative importance of benthic vs. pelagic food webs between species, and emerging methods, such as compound-specific SIA of amino acids (McMahon et al. 2016) may provide even greater ability to distinguish between carbon sources. Measurements of species-specific metabolic rates, exercise capacity, and swimming performance may help to identify whether differential physiological adaptation plays a role in generating the observed contrasts, as may comparative anatomical studies of the species' sensory systems.

This work was the first to quantitatively examine interspecific distinctions in the habitat and resource utilization patterns of sympatric bonefishes of any ontogenetic stage in the Atlantic region. In doing so, we revealed fundamental differences in the basic ecological requirements of *A. vulpes* and *A. goreensis* during a critical and poorly understood life stage. From the perspective of conservation this information should prove particularly valuable, offering guidance for habitat preservation efforts, while also providing a practical, field-applicable method for discriminating between species based on observable associations with the physical environment.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

References

Adams AJ, Wolfe RK, Tringali MD, Wallace EM, Kellison GT (2007) Rethinking the status of Albula spp. biology in the Caribbean and western Atlantic. In: Ault J (ed) Biology and management of the world tarpon and bonefish fisheries. CRC Press, Boca Raton, pp p203–p215

Adams AJ, Horodysky AZ, McBride RS, Guindon K, Shenker J, MacDonald TC, Harwell HD, Ward R, Carpenter K (2014) Global conservation status and research needs for tarpons (Megalopidae), ladyfishes (Elopidae) and bonefishes (Albulidae). Fish Fish 15(2):280–311. https://doi.org/10.1111/faf.12017

Akin S, Buhan E, Winemiller KO, Yilmaz H (2005) Fish assemblage structure of Koycegiz lagoon–estuary, Turkey: spatial and temporal distribution patterns in relation to environmental variation. Estuar Coast Shelf Sci 64(4):671–684. https://doi.org/10.1016/j.ecss.2005.03.019

Anton A, Simpson MS, Vu I (2014) Environmental and biotic correlates to lionfish invasion success in Bahamian coral reefs. PLoS One 9(9):e106229. https://doi.org/10.1371/journal.pone.0106229

Arfi R, Guiral D, Bouvy M (1993) Wind induced resuspension in a shallow tropical lagoon. Estuar Coast Shelf Sci 36(6):587–604. https://doi.org/10.1006/ecss.1993.1036

Arlettaz R (1999) Habitat selection as a major resource partitioning mechanism between the two sympatric sibling bat species Myotis myotis and Myotis blythii. J Anim Ecol 68(3):460–471. https://doi.org/10.1046/j.1365-2656.1999.00293.x

Bellwood D, Wainwright P (2001) Locomotion in labrid fishes: implications for habitat use and cross-shelf biogeography on the great barrier reef. Coral Reefs 20(2):139–150. https://doi.org/10.1007/s003380100156

Blaber SJM, Blaber TG (1980) Factors affecting the distribution of juvenile estuarine and inshore fish. J Fish Biol 17(2):143–162. https://doi.org/10.1111/j.1095-8649.1980.tb02749.x

Booij NR, Ris RC, Holthuijsen LH (1999) A third-generation wave model for coastal regions: 1. Model description and validation. J Geophys Res Oceans 104(C4):7649–7666. https://doi.org/10.1029/98JC02622

Boström C, O'Brien K, Roos C, Ekebom J (2006) Environmental variables explaining structural and functional diversity of seagrass macrofauna in an archipelago landscape. J Exp Mar Biol Ecol 335(1):52–73. https://doi.org/10.1016/j.jembe.2006.02.015

Bowen BW, Karl SA, Pfeiler E (2007) Resolving evolutionary lineages and taxonomy of bonefishes (Albula spp.). In: Ault J (ed) Biology and management of the world tarpon and bonefish fisheries. CRC Press, Boca Raton, pp 147–153

Box GEP, Draper NR (1987) Empirical model-building and response surfaces. John Wiley & Sons

Brind'Amour A, Boisclair D, Legendre P, Borcard D (2005) Multiscale spatial distribution of a littoral fish community in relation to environmental variables. Limnol Oceanogr 50(2):465–479. https://doi.org/10.4319/lo.2005.50.2.0465

Bruger GE (1974) Age, growth, food habits, and reproduction of bonefish, *Albula vulpes*, in south Florida waters. Florida Marine Research Publications, No 3. Florida Department of Natural Resources, St Petersburg, FL

Buchan KC (2000) The Bahamas. Mar Pollut Bull 41(1):94–111. https://doi.org/10.1016/S0025-326X(00)00104-1

Campana SE (1999) Chemistry and composition of fish otoliths: pathways, mechanisms and applications. Mar Ecol Prog Ser 188:263–297

Clarke RD, Buskey EJ, Marsden KC (2005) Effects of water motion and prey behavior on zooplankton capture by two coral reef fishes. Mar Biol 146(6):1145–1155. https://doi.org/10.1007/s00227-004-1528-y

Clarke RD, Finelli CM, Buskey EJ (2009) Water flow controls distribution and feeding behavior of two co-occurring coral reef fishes: II. Laboratory experiments. Coral Reefs 28(2):475–488. https://doi.org/10.1007/s00338-009-0479-7

Colborn J, Crabtree RE, Shaklee JB, Pfeiler E, Bowen BW (2001) The evolutionary enigma of bonefishes (Albula spp.): cryptic species and ancient separations in a globally distributed shorefish. Evolution 55(4):807–820. https://doi.org/10.1554/0014-3820(2001)055[0807:TEEOBA]2.0.CO;2

Cornelisen CD, Wing SR, Clark KL, Hamish BM, Frew RD, Hurd CL (2007) Patterns in the δ^{13}C and δ^{15}N signature of Ulva pertusa: interaction between physical gradients and nutrient source pools. Limnol Oceanogr 52(2):820–832. https://doi.org/10.4319/lo.2007.52.2.0820

Correia AT, Barros F, Sial AN (2011) Stock discrimination of European conger eel (Conger conger L.) using otolith stable isotope ratios. Fish Res 108(1):88–94. https://doi.org/10.1016/j.fishres.2010.12.002

Crabtree RE, Snodgrass DJ, Stengard FJ (2003) Bonefish species differentiation and delineation of critical juvenile habitat in the Florida Keys. In: Barbieri LR, Crabtree RE (eds) Five-year performance report to the US Department of Interior Fish and Wildlife Service from the Florida Fish and Wildlife Conservation Commission Florida Marine Research Institute, Investigations into nearshore and estuarine gamefish behavior, ecology, and life history in Florida. p 7–13

Crawley KR, Hyndes GA, Ayvazian SG (2006) Influence of different volumes and types of detached macrophytes on fish community structure in surf zones of sandy beaches. Mar Ecol Prog Ser 307:233–246

Crawley KR, Hyndes GA, Vanderklift MA, Revill AT, Nichols PD (2009) Allochthonous brown algae are the primary food source for consumers in a temperate, coastal environment. Mar Ecol Prog Ser 376:33–44. https://doi.org/10.3354/meps07810

Cummings M, J P (2001) Visual pigments and optical habitats of surfperch (Embiotocidae) in the California kelp forest. J Comp Physiol A 187(11):875–889. https://doi.org/10.1007/s00359-001-0258-6

Currey LM, Heupel MR, Simpfendorfer CA, Williams AJ (2014) Inferring movement patterns of a coral reef fish using oxygen and carbon isotopes in otolith carbonate. J Exp Mar Biol Ecol 456:18–25. https://doi.org/10.1016/j.jembe.2014.03.004

Cyrus D, Blaber S (1992) Turbidity and salinity in a tropical northern Australian estuary and their influence on fish distribution. Estuar Coast Shelf Sci 35:545–563

Davis JP, Wing SR (2012) Niche partitioning in the Fiordland wrasse guild. Mar Ecol Prog Ser 446:207–220. https://doi.org/10.3354/meps09452

De la Morinière EC, Pollux BJA, Nagelkerken I, Hemminga MA, Huiskes AHL, van der Velde G (2003) Ontogenetic dietary changes of coral reef fishes in the mangrove-seagrass-reef continuum: stable isotopes and gut-content analysis. Mar Ecol Prog Ser 246:279–289

Deary AL, Metscher B, Brill RW, Hilton EJ (2016) Shifts of sensory modalities in early life history stage estuarine fishes (Sciaenidae) from the Chesapeake Bay using X-ray micro computed tomography. Environ Biol Fish 99(4):361–375. https://doi.org/10.1007/s10641-016-0479-8

Donovan MK, Friedlander AM, Harding KK, Schemmel EM, Filous A, Kamikawa K, Torkelson N (2015) Ecology and niche specialization of two bonefish species in Hawai'i. Environ Biol Fish 98(11):2159–2171. https://doi.org/10.1007/s10641-015-0427-z

Dufour E, Gerdeaux D, Wurster CM (2007) Whitefish (Coregonus lavaretus) respiration rate governs intra-otolith variation of δ^{13}C values in Lake Annecy. Can J Fish Aquat Sci 64(12): 1736–1746. https://doi.org/10.1139/f07-132

Edmonds JS, Fletcher WJ (1997) Stock discrimination of pilchards Sardinops sagax by stable isotope ratio analysis of otolith carbonate. Mar Ecol Prog Ser 152(1/3):241–247

Elsdon TS, Ayvazian S, McMahon KW, Thorrold SR (2010) Experimental evaluation of stable isotope fractionation in fish muscle and otoliths. Mar Ecol Prog Ser 408:195–205. https://doi.org/10.3354/meps08518

Enders EC, Boisclair D, Roy AG (2003) The effect of turbulence on the cost of swimming for juvenile Atlantic salmon (Salmo salar). Can J Fish Aquat Sci 60(9):1149–1160. https://doi.org/10.1139/f03-101

Fedler T (2010) The economic impact of flats fishing in the Bahamas. The Bahamian flats fishing alliance. Gainesville, Florida

Fedler T (2013) Economic impact of the Florida keys flats fishery. The bonefish and tarpon trust. Gainesville, Florida

Fenwick GD (1976) The effect of wave exposure on the amphipod fauna of the alga Caulerpa brownii. J Exp Mar Biol Ecol 25(1):1–18. https://doi.org/10.1016/0022-0981(76)90072-1

Finelli CM, Clarke RD, Robinson HE, Buskey EJ (2009) Water flow controls distribution and feeding behavior of two co-occurring coral reef fishes: I. Field measurements. Coral Reefs 28(2):461–473. https://doi.org/10.1007/s00338-009-0481-0

Finlay JC, Power ME, Cabana G (1999) Effects of water velocity on algal carbon isotope ratios: implications for river food web studies. Limnol Oceanogr 44(5):1198–1203. https://doi.org/10.4319/lo.1999.44.5.1198

Fonseca MS, Zieman JC, Thayer GW, Fisher JS (1983) The role of current velocity in structuring eelgrass (Zostera marina L.) meadows. Estuar Coast Shelf Sci 17(4):367–380. https://doi.org/10.1016/0272-7714(83)90123-3

Frezza PE, Clem SE (2015) Using local fishers' knowledge to characterize historical trends in the Florida bay bonefish population and fishery. Environ Biol Fish 98(11):2187–2202. https://doi.org/10.1007/s10641-015-0442-0

Friedlander AM, Parrish JD (1998) Temporal dynamics of fish communities on an exposed shoreline in Hawaii. Environ Biol Fish 53(1):1–18. https://doi.org/10.1023/a:1007497210998

Fry B, Sherr EB δ^{13}C Measurements as Indicators of Carbon Flow in Marine and Freshwater Ecosystems. In, New York, 1989. Stable Isotopes in Ecological Research. Springer New York, p 196–229

Fry B, Lutes R, Northam M, Parker PL, Ogden J (1982) A ^{13}C/^{12}C comparison of food webs in Caribbean seagrass meadows and coral reefs. Aquat Bot 14:389–398. https://doi.org/10.1016/0304-3770(82)90112-7

Fulton CJ, Bellwood DR (2005) Wave-induced water motion and the functional implications for coral reef fish assemblages. Limnol Oceanogr 50(1):255–264. https://doi.org/10.4319/lo.2005.50.1.0255

Fulton CJ, Bellwood DR, Wainwright PC (2001) The relationship between swimming ability and habitat use in wrasses (Labridae). Mar Biol 139(1):25–33. https://doi.org/10.1007/s002270100565

Gabel F, Stoll S, Fischer P, Pusch MT, Garcia XF (2011) Waves affect predator-prey interactions between fish and benthic invertebrates. Oecologia 165(1):101–109. https://doi.org/10.1007/s00442-010-1841-8

Gao Y, Joner SH, Svec RA, Weinberg KL (2004) Stable isotopic comparison in otoliths of juvenile sablefish (Anoplopoma fimbria) from waters off the Washington and Oregon coast. Fish Res 68(1–3):351–360. https://doi.org/10.1016/j.fishres.2003.11.002

Godiksen JA, Svenning M-A, Dempson JB, Marttila M, Storm-Suke A, Power M (2010) Development of a species-specific fractionation equation for Arctic charr (Salvelinus alpinus (L.)): an experimental approach. Hydrobiologia 650(1):67–77. https://doi.org/10.1007/s10750-009-0056-7

Guiguer KRRA, Drimmie R, Power M (2003) Validating methods for measuring δ^{18}O and δ^{13}C in otoliths from freshwater fish. Rapid Commun Mass Spectrom 17(5):463–471. https://doi.org/10.1002/rcm.935

Haak CR, Cowles GW, Danylchuk AJ (2018) Wave and tide-driven flow act on multiple scales to shape the distribution of a juvenile fish (*Albula vulpes*) in shallow nearshore habitats. Limnol Oceanogr. https://doi.org/10.1002/lno.11063

Harborne AR et al (2008) Tropical coastal habitats as surrogates of fish community structure, grazing, and fisheries value. Ecol Appl 18(7):1689–1701. https://doi.org/10.1890/07-0454.1

Hartney KB (1989) The foraging ecology of two sympatric gobiid fishes: importance of behavior in prey type selection. Environ Biol Fish 26(2):105–118. https://doi.org/10.1007/bf00001027

Hidalgo M, Tomás J, Høie H, Morales-Nin B, Ninnemann US (2008) Environmental influences on the recruitment process inferred from otolith stable isotopes in Merluccius merluccius off the Balearic Islands. Aquat Biol 3:195–207. https://doi.org/10.3354/ab00081

Higgs ND, Newton J, Attrill MJ (2016) Caribbean spiny lobster fishery is underpinned by trophic subsidies from chemosynthetic primary production. Curr Biol 26(24):3393–3398. https://doi.org/10.1016/j.cub.2016.10.034

Hixon MA (1980) Competitive interactions between California reef fishes of the genus Embiotoca. Ecology 61(4):918–931. https://doi.org/10.2307/1936761

Hobson KA (1999) Tracing origins and migration of wildlife using stable isotopes: a review. Oecologia 120(3):314–326. https://doi.org/10.1007/s004420050865

Høie H, Folkvord A, Otterlei E (2003) Effect of somatic and otolith growth rate on stable isotopic composition of early juvenile cod (Gadus morhua L) otoliths. J Exp Mar Biol Ecol 289(1):41–58. https://doi.org/10.1016/s0022-0981(03)00034-0

Høie H, Otterlei E, Folkvord A (2004) Temperature-dependent fractionation of stable oxygen isotopes in otoliths of juvenile cod (Gadus morhua L.). ICES J Mar Sci 61(2):243–251. https://doi.org/10.1016/j.icesjms.2003.11.006

Holbrook SJ, Schmitt RJ (1989) Resource overlap, prey dynamics, and the strength of competition. Ecology 70(6):1943–1953. https://doi.org/10.2307/1938124

Hu X, Burdige DJ (2007) Enriched stable carbon isotopes in the pore waters of carbonate sediments dominated by seagrasses: evidence for coupled carbonate dissolution and reprecipitation. Geochim Cosmochim Acta 71(1):129–144. https://doi.org/10.1016/j.gca.2006.08.043

Hyndes GA, Platell ME, Potter IC (1997) Relationships between diet and body size, mouth morphology, habitat and movements of six sillaginid species in coastal waters: implications for resource partitioning. Mar Biol 128(4):585–598. https://doi.org/10.1007/s002270050125

Jamieson RE, Schwarcz HP, Brattey J (2004) Carbon isotopic records from the otoliths of Atlantic cod (Gadus morhua) from eastern Newfoundland, Canada. Fish Res 68(1–3):83–97. https://doi.org/10.1016/j.fishres.2004.02.009

Kalish JM (1991) ^{13}C and ^{18}O isotopic disequilibria in fish otoliths: metabolic and kinetic effects. Mar Ecol Prog Ser 75(2/3):191–203

Keddy PA (1982) Quantifying within-Lake gradients of wave energy: interrelationships of wave energy, substrate particle size and shoreline plants in axe lake, Ontario. Aquat Bot 14:41–58

Kieckbusch DK, Koch MS, Serafy JE, Anderson WT (2004) Trophic linkages among primary producers and consumers in fringing mangroves of subtropical lagoons. Bull Mar Sci 74(2):271–285

Lasiak T (1984) Structural aspects of the surf-zone fish assemblage at King's beach, Algoa Bay, South Africa: long-term fluctuations. Estuar Coast Shelf Sci 18(4):459–483

Lawson SE, Wiberg PL, McGlathery KJ, Fugate DC (2007) Wind-driven sediment suspension controls light availability in a shallow coastal lagoon. Estuar Coasts 30(1):102–112. https://doi.org/10.1007/bf02782971

Levin PS, Stunz GW (2005) Habitat triage for exploited fishes: can we identify essential "essential fish habitat?". Estuar Coast Shelf Sci 64(1):70–78. https://doi.org/10.1016/j.ecss.2005.02.007

Lombarte A, Recasens L, Gonzalez M, de Sola LG (2000) Spatial segregation of two species of Mullidae (Mullus surmuletus and M. Barbatus) in relation to habitat. Mar Ecol Prog Ser 206:239–249

Lugendo BR, Nagelkerken I, van der Velde G, Mgaya YD (2006) The importance of mangroves, mud and sand flats, and seagrass beds as feeding areas for juvenile fishes in Chwaka Bay, Zanzibar: gut content and stable isotope analyses. J Fish Biol 69(6):1639–1661. https://doi.org/10.1111/j.1095-8649.2006.01231.x

McMahon KW, Berumen ML, Mateo I, Elsdon TS, Thorrold SR (2011a) Carbon isotopes in otolith amino acids identify residency of juvenile snapper (family: Lutjanidae) in coastal nurseries. Coral Reefs 30(4):1135–1145. https://doi.org/10.1007/s00338-011-0816-5

McMahon KW, Fogel ML, Johnson BJ, Houghton LA, Thorrold SR, Gillanders B (2011b) A new method to reconstruct fish diet and movement patterns from δ^{13}C values in otolith amino acids. Can J Fish Aquat Sci 68(8):1330–1340. https://doi.org/10.1139/f2011-070

McMahon KW, Hamady LL, Thorrold SR (2013) A review of ecogeochemistry approaches to estimating movements of marine animals. Limnol Oceanogr 58(2):697–714. https://doi.org/10.4319/lo.2013.58.2.0697

McMahon KW, Thorrold SR, Houghton LA, Berumen ML (2016) Tracing carbon flow through coral reef food webs using a compound-specific stable isotope approach. Oecologia 180(3):809–821. https://doi.org/10.1007/s00442-015-3475-3

McPherson ML, Zimmerman RC, Hill VJ (2015) Predicting carbon isotope discrimination in eelgrass (Zostera marinaL.) from the environmental parameters-light, flow, and [DIC]. Limnol Oceanogr 60(6):1875–1889. https://doi.org/10.1002/lno.10142

Minello TJ (1999) Nekton densities in shallow estuarine habitats of Texas and Louisiana and the identification of essential fish habitat in: Benaka L (ed) fish habitat: essential fish habitat and rehabilitation. American fisheries society. In: Symposium, vol 22. Bethesda, Maryland, pp 43–75

Nagelkerken I, van der Velde G (2004) Are Caribbean mangroves important feeding grounds for juvenile reef fish from adjacent seagrass beds? Mar Ecol Prog Ser 274:143–151

Nelson GA (2014) Cluster sampling: a pervasive, yet little recognized survey Design in Fisheries Research. Trans Am Fish Soc 143(4):926–938. https://doi.org/10.1080/00028487.2014.901252

Nelson J, Hanson CW, Koenig C, Chanton J (2011) Influence of diet on stable carbon isotope composition in otoliths of juvenile red drum Sciaenops ocellatus. Aquat Biol 13(1):89–95. https://doi.org/10.3354/ab00354

Pekcan-Hekim Z, Hellen N, Harkonen L, Nilsson PA, Nurminen L, Horppila J (2016) Bridge under troubled water: turbulence and niche partitioning in fish foraging. Ecol Evol 6(24):8919–8930. https://doi.org/10.1002/ece3.2593

Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. Annu Rev Ecol Syst 18:293–320

Pfeiler E (1996) Allozyme differences in Caribbean and gulf of California populations of bonefishes (Albula). Copeia 1996(1):181–183. https://doi.org/10.2307/1446953

Poff NL, Allan JD (1995) Functional organization of stream fish assemblages in relation to hydrological variability. Ecology 76(2):606–627

Post DM (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83(3):703–718. https://doi.org/10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2

Radtke RL, Lenz P, Showers W, Moksness E (1996) Environmental information stored in otoliths: insights from stable isotopes. Mar Biol 127(1):161–170. https://doi.org/10.1007/bf00993656

Rasmussen JB, Trudeau V (2010) How well are velocity effects on δ ^{13}C signatures transmitted up the food web from algae to fish? Freshw Biol 55(6):1303–1314. https://doi.org/10.1111/j.1365-2427.2009.02354.x

Robertson AI, Lenanton RCJ (1984) Fish community structure and food chain dynamics in the surf-zone of sandy beaches: the role of detached macrophyte detritus. J Exp Mar Biol Ecol 84(3):265–283. https://doi.org/10.1016/0022-0981(84)90185-0

Roche DG, Taylor MK, Binning SA, Johansen JL, Domenici P, Steffensen JF (2014) Unsteady flow affects swimming energetics in a labriform fish (Cymatogaster aggregata). J Exp Biol 217(Pt 3):414–422. https://doi.org/10.1242/jeb.085811

Rubenstein DR, Hobson KA (2004) From birds to butterflies: animal movement patterns and stable isotopes. Trends Ecol Evol 19(5): 256–263. https://doi.org/10.1016/j.tree.2004.03.017

Santin S, Willis TJ (2007) Direct versus indirect effects of wave exposure as a structuring force on temperate cryptobenthic fish assemblages. Mar Biol 151(5):1683–1694. https://doi.org/10.1007/s00227-006-0586-8

Santos RO, Rehage JS, Adams AJ, Black BD, Osborne J, Kroloff EKN (2017) Quantitative assessment of a data-limited recreational bonefish fishery using a time-series of fishing guides reports. PLoS One 12(9):e0184776. https://doi.org/10.1371/journal.pone.0184776

Sattler T, Bontadina F, Hirzel AH, Arlettaz R (2007) Ecological niche modelling of two cryptic bat species calls for a reassessment of their conservation status. J Appl Ecol 44(6): 1188–1199. https://doi.org/10.1111/j.1365-2664.2007.01328.x

Schmitt RJ, Coyer JA (1982) The foraging ecology of sympatric marine fish in the genus Embiotoca (Embiotocidae): importance of foraging behavior in prey size selection. Oecologia 55(3):369–378. https://doi.org/10.1007/bf00376925

Schwalbe MAB, Webb JF (2014) Sensory basis for detection of benthic prey in two Lake Malawi cichlids. Zoology 117(2): 112–121. https://doi.org/10.1016/j.zool.2013.09.003

Schwarcz HP, Gao Y, Campana S, Browne D, Knyf M, Brand U (1998) Stable carbon isotope variations in otoliths of Atlantic cod (Gadus morhua). Can J Fish Aquat Sci 55(8):1798–1806. https://doi.org/10.1139/f98-053

Seyoum S, Wallace EM, Tringali MD (2008) Permanent genetic resources: twelve polymorphic microsatellite markers for the bonefish, Albula vulpes and two congeners. Mol Ecol Resour 8(2):354–356. https://doi.org/10.1111/j.1471-8286.2007.01954.x

Snelgrove PVR, Butman CA (1994) Animal-sediment relationships revisited: cause versus effect. Oceanogr Mar Biol Annu Rev 32:111–177

Snodgrass D, Crabtree RE, Serafy JE (2008) Abundance, growth, and diet of young-of-the-year bonefish (Albula spp.) off the Florida keys, USA. Bull Mar Sci 82(2):185–193

Solomon CT, Weber PK, Cech JJ Jr, Ingram BL, Conrad ME, Machavaram MV, Pogodina AR, Franklin RL (2006) Experimental determination of the sources of otolith carbon and associated isotopic fractionation. Can J Fish Aquat Sci 63(1):79–89. https://doi.org/10.1139/f05-200

Storm-Suke A, Dempson JB, Reist JD, Power M (2007) A field-derived oxygen isotope fractionation equation for Salvelinus species. Rapid Commun Mass Spectrom 21(24):4109–4116. https://doi.org/10.1002/rcm.3320

Thorrold SR, Campana SE, Jones CM, Swart PK (1997) Factors determining δ13C and δ18O fractionation in aragonitic otoliths of marine fish. Geochim Cosmochim Acta 61(14):2909–2919. https://doi.org/10.1016/S0016-7037(97)00141-5

Tohse H, Mugiya Y (2008) Sources of otolith carbonate: experimental determination of carbon incorporation rates from water and metabolic CO2, and their diel variations. Aquat Biol 1:259–268. https://doi.org/10.3354/ab00029

Trudeau V, Rasmussen JB (2003) The effect of water velocity on stable carbon and nitrogen isotope signatures of periphyton. Limnol Oceanogr 48(6):2194–2199. https://doi.org/10.4319/lo.2003.48.6.2194

Tue NT, Quy TD, Nhuan MT, Dung LV, Thai ND (2017) Tracing carbon transfer and assimilation by invertebrates and fish across a tropical mangrove ecosystem using stable isotopes. Mar Ecol 38(5). https://doi.org/10.1111/maec.12460

UNEP-WCMC, WorldFish Centre, WRI, TNC (2010) Global distribution of warm-water coral reefs, compiled from multiple sources including the Millennium Coral Reef Mapping Project. Version 1.3. Includes contributions from IMaRS-USF and IRD (2005), IMaRS-USF (2005) And Spalding et al. (2001). UNEP World Conservation Monitoring Centre, Cambridge

Wallace EM (2014) Assessing biodiversity, evolution, and biogeography in bonefishes (Albuliformes): resolving relationships and aiding management. University of Minnesota, Dissertation

Wallace EM, Tringali MD (2010) Identification of a novel member in the family Albulidae (bonefishes). J Fish Biol 76(8):1972–1983. https://doi.org/10.1111/j.1095-8649.2010.02639.x

Wallace EM, Tringali MD (2016) Fishery composition and evidence of population structure and hybridization in the Atlantic bonefish species complex (Albula spp.). Mar Biol 163(6). https://doi.org/10.1007/s00227-016-2915-x