



Stable isotopes and foraging behaviors support the role of antipredator benefits in driving the association between two marine fishes

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Abstract

Research from terrestrial communities shows that diminished predation risk is a principal driver of heterospecific grouping behavior, with foraging ecology predicting the roles that species play in groups, as more vulnerable foragers preferentially join more vigilant ones from whom they can benefit. Meanwhile, field studies examining the adaptive significance of heterospecific shoaling among marine fish have focused disproportionately on feeding advantages such as scrounging or prey-flushing. Juvenile bonefish (*Albula vulpes*) occur almost exclusively among mojarras (*Eucinostomus* spp.) and even elect to join them over conspecifics, suggesting they benefit from doing so. We evaluated the roles of risk-related and food-related factors in motivating this pattern of affiliation, estimating: (1) the relative levels of risk associated with each species' search and prey capture activities, via behavioral vulnerability traits discerned from in situ video of heterospecific shoals, and (2) resource use redundancy, using stable isotopes ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$) to quantify niche overlap. Across four distinct metrics, bonefish behaviors implied a markedly greater level of risk than those of mojarras, typified by higher activity levels and a reduced capacity for overt vigilance; consistent with expectations if their association conformed to patterns of joining observed in terrestrial habitats. Resource use overlap inferred from stable isotopes was low, indicating that the two species partitioned resources and making it unlikely that bonefish derived substantive food-related benefits. Collectively, these findings suggest that the attraction of juvenile bonefish to mojarras is motivated primarily by antipredator advantages, which may include the exploitation of risk-related social cues.

Keywords Heterospecific shoals · Mixed species groups · Antipredator vigilance · Eavesdropping · Niche partitioning

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Introduction

The physical activities, sensory demands, and habitats associated with the search for and capture of prey are often incompatible or at odds with those that facilitate the detection and avoidance of predators, so that most animals face a heightened risk of predation while foraging and must weigh the need to feed against the risk of becoming food themselves (Lima and Dill 1990; Houston et al. 1993; Brown and Kotler 2004). Group foraging is a common behavioral strategy that is theorized to help balance the basic tradeoff between energy gain and the threat of predation by reducing an individual's level of risk and/or enhancing its uptake of resources, albeit at the potential cost of intensified competition (reviewed in Ward and Webster 2016). While several adaptive benefits of social foraging emerge through basic statistical or physical consequences of grouping (Foster and Treherne 1981; Landeau and Terborgh 1986), they can also

arise through information related processes such as collective threat detection (Ward et al. 2011) and social learning about food (reviewed in Galef and Giraldeau 2001), as animals exploit cues or signals produced by others to inform their own decisions about shared resources and predators (Schmidt et al. 2010; Gil et al. 2017).

Mixed-species groups are widespread across terrestrial and aquatic communities and represent a special case of social foraging (reviewed in Goodale et al. 2017). While many of the fundamental mechanisms that underly the advantages of group participation operate similarly in a heterospecific context, the inherently greater diversity of mixed species groups has important implications for the costs and benefits of joining. For instance, the diminished niche redundancy between members of different species may mitigate costs of competition, possibly making heterospecifics more lucrative partners than conspecifics (Seppänen et al. 2007; Goodale et al. 2010). Interspecific trait heterogeneity can also act to promote asymmetries not only in the extent to which individuals profit from joining, but in the basic nature of benefits that are derived or exchanged via group participation, so that species function in altogether distinct roles, gaining access to advantages that could not be obtained from conspecifics (reviewed in Sridhar and Guttal 2018; Goodale et al. 2020). Such “complementary” benefits, which can range from the uncovering or flushing of prey (Aronson and Sanderson 1987; Satischandra et al. 2007) to early warning of approaching predators (Fitzgibbon 1990; Templeton and Greene 2007), are often provisioned by a relatively small subset of species, making them uniquely attractive partners that exert a disproportionately large influence on the formation of mixed species assemblages.

In terrestrial communities where field-based research and hypothesis testing on the drivers of grouping behavior have been the most rigorous, foraging ecology has been established as a key determinant of species’ varying roles in heterospecific groups. Animals with more vulnerable or “riskier” foraging behaviors (e.g., those that feed in more open habitats, myopically from substrates, or in a head-down position) exhibit a greater dependence on risk-related cues produced by heterospecifics and a higher propensity for joining them (Martínez et al. 2016; Jones and Sieving 2019; Meise et al. 2020). Conversely, animals whose foraging-related adaptations confer an elevated capacity for threat detection (e.g., those with high sensory acuity, or that forage from a position that facilitates antipredator scanning) often function as cue producers, and are preferentially joined by more vulnerable species (Goodale and Kotagama 2008; Sridhar et al. 2009; Schmitt et al. 2016). Accordingly, several recent studies have concluded that access to risk-related social information is the principal driver of heterospecific association in avian (Sridhar and Shanker 2014; Hua et al. 2016) and terrestrial mammalian assemblages (Schmitt et al. 2014; Meise et al.

2020), enabling associates to reduce their own vigilance and increase food intake (Sridhar et al. 2009; Stears et al. 2020).

Heterospecific foraging groups are ubiquitous among tropical marine fishes, taking forms from pairwise collaborative hunting (Vail et al. 2013) to opportunistic and loosely organized multispecies shoals (Sazima et al. 2006). Like their analogs in terrestrial habitats, interspecific fish foraging associations are frequently structured around attractive “nuclear” species, in whose company “followers” display elevated rates of feeding (Aronson and Sanderson 1987; Lukoschek and McCormick 2000; Sabino et al. 2017). Foraging ecology has also been cited as a predictor of species’ function in these groups, with gregarious substrate-disturbing benthivores, whose activities result in the uncovering or flushing of prey, playing a central role in shoal formation (Strand 1988; Sazima et al. 2006; Krajewski 2009). Consequently, the adaptive significance of these associations (and the magnetism of nuclear species) is generally attributed to direct food-related (instead of risk-related) complementary benefits, contrasting with findings in terrestrial communities. Even so, recent work has demonstrated that coral reef fish use social cues from both conspecifics and heterospecifics to assess risk and maximize their uptake of resources (Brandl and Bellwood 2015; Gil and Hein 2017; Kent et al. 2019).

A recently identified relationship between two tropical shallow water benthivores, bonefish (*Albula vulpes*) and mojarras (*Eucinostomus* spp.) presents an opportunity for exploring the apparent inconsistency between terrestrial and marine mixed species groups. In littoral zone habitats, juvenile bonefish (typically 30–100 mm fork length) occur almost exclusively in the presence of similarly sized mojarras, at a rate far exceeding that predicted by chance even when controlling for the species’ similar environmental preferences (Haak et al. 2020). Furthermore, subsequent shoal choice experiments have demonstrated that juvenile bonefish are attracted to mojarras and even elect to join them over conspecifics, an anomalous pattern of behavior which also hints that participation in mojarras shoals may offer significant fitness benefits (Szekeres et al. 2020).

Still, the nature of any benefits derived by bonefish is not clear. Mojarras are in fact gregarious substrate-disturbing benthivores from whom associated taxa may obtain increased access to resources via prey flushing or kleptoparasitism (Zahorcsak et al. 2000; Sazima 2002). Yet despite their common benthivorous foraging mode and mutual reliance on invertebrate prey (Layman and Silliman 2002), mojarras and bonefish feeding together in the wild display little outward evidence of competitive interactions or behaviors that might signal scrounging or the exploitation of flushed prey (Haak et al. 2020). Meanwhile, juveniles of the two taxa share a common suite of predators in lemon sharks (*Negaprion brevirostris*), barracudas (Sphyraenidae) and snappers (Lutjanidae) that can impose high

levels of mortality in the fringing mangrove habitats where mojarras and bonefish reside (Rypel et al. 2007; Hamerschlag et al. 2010), making risk-related cues reciprocally relevant. Moreover, basic similarities in the fishes' outward appearances, with both being characterized by reflective camouflage and similar patterns of dorsolateral pigmentation (Online Resource 1: Fig. ESM1), suggest that mojarras may be particularly well suited for conveying a variety of antipredator benefits to juvenile bonefish (Haak et al. 2020; Szekeres et al. 2020).

To reveal the ecological underpinnings of the association between juvenile bonefish and mojarras, the present study coupled field-based behavioral observations and trophic ecology to evaluate the alternate hypotheses that: (1) direct food-related benefits, or (2) antipredator benefits, were at the core of this relationship. We reasoned that direct food-related benefits obtained by bonefish through area-copying or scrounging would be evidenced by high resource use overlap with mojarras. Alternatively, if the procurement of risk-related benefits was the primary motivation behind bonefish's affinity for mojarras, we expected that (following patterns described in terrestrial systems) the two taxa would exhibit divergent foraging behaviors, with those displayed by bonefish implying a diminished capacity for the detection of threats and heightened vulnerability to predation compared to the behaviors of the mojarras that they join.

Predation risk is dynamic and context dependent, however, for prey of similar sizes and degrees of crypsis that share the same habitat, foraging strategy, and a common suite of predators (as is the case for bonefish and mojarras), vulnerability is in large part determined by behavioral traits that affect the likelihood of encountering or attracting the attention of predators, and/or the ability to detect or evade them (Scharf et al. 2003; Boukal 2014; Schmitz 2017). Accordingly, to address the hypotheses outlined above, we used *in situ* video surveys of heterospecific shoals to quantify interspecific differences in search and prey capture behaviors that have proven to be consistent correlates of predation susceptibility or antipredator awareness across an array of aquatic species and circumstances; specifically: (1) activity levels (Strobbe et al. 2011; Almeda et al. 2017; Saenz et al. 2020), and (2) body posture (Krause and Godin 1996; Foam et al. 2005; Brandl and Bellwood 2015). Concurrently, to evaluate redundancy in resource use between bonefish and mojarras over extended timescales (i.e., weeks to months; Vander Zanden et al. 2015), we inferred trophic niche overlap using stable isotope analysis (SIA; Jackson et al. 2012; Layman et al. 2012) of $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$ in white muscle tissue, employing a tri-variate framework to facilitate discrimination between resources that might otherwise be indistinguishable using the traditional dual-element ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) approach (Peterson et al. 1985; Connolly et al. 2004).

Methods

Stable isotopes and niche overlap

Sampling and laboratory protocols

Juvenile bonefish ($n=46$, FL [mean \pm SD] = 72 ± 31 mm) and mojarras ($n=30$, FL = 60 ± 14 mm) were collected together in 19 seine hauls conducted in two distinct embayments (labeled A and B, respectively, in Fig. 1) on the west and east coasts of Eleuthera island in The Bahamas between February 2012 and November 2015, using methods described in Haak et al. (2019). Due to close physical resemblances and unresolved taxonomic questions within the genus *Eucinostomus* (Matheson and McEachran 1984; Jacobina et al. 2020), mojarras were not identified to species, but may include *E. argenteus*, *E. gula*, and *E. jonesii*. Full specimens were frozen and stored at -20°C for subsequent processing, which involved thawing, weighing, measurement

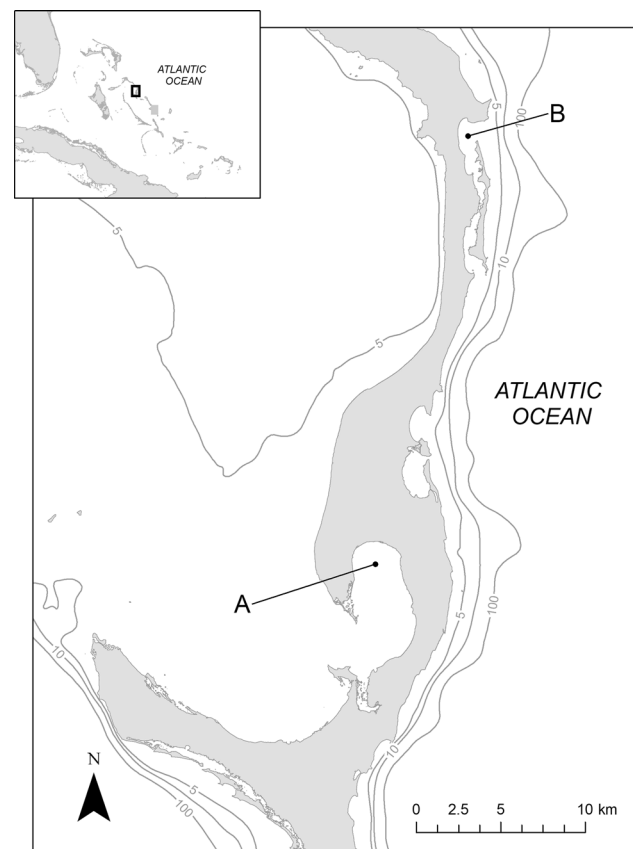


Fig. 1 Map of the study area on the island of Eleuthera, The Bahamas, depicting the locations of west-facing (labeled “A”) and east-facing (labeled “B”) embayments where juvenile bonefish (*Albula vulpes*) and mojarras (*Eucinostomus* spp.) were collected for stable isotope analyses. Remote underwater video surveys for behavioral analyses were conducted in embayment A

to the nearest 1 mm fork length (FL), and the extraction of white muscle tissue from the dorsal region. Tissue samples were then dried, homogenized and prepared for SIA as described in Murchie et al. (2018). Analyses of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were carried out as outlined in Murchie et al. (2018) on a Delta Plus Continuous Flow Stable Isotope Ratio Mass Spectrometer (Thermo Finnigan, Bremen, Germany) coupled to a Carlo Erba elemental analyzer (CHNS-O EA1108, Carlo Erba, Milan, Italy). Analyses of $\delta^{34}\text{S}$ were completed on an Isochrom Continuous Flow Stable Isotope Ratio Mass Spectrometer (GV Instruments, Micromass, Manchester, UK) paired with a Costech Elemental Analyzer (CNSO 4010, Costech Analytical Technologies Inc., Valencia, USA). Internal laboratory standards were calibrated against the International Atomic Energy Agency standards CH6 for $\delta^{13}\text{C}$, N1 and N2 for $\delta^{15}\text{N}$, and SO-5, S1 and S2 for $\delta^{34}\text{S}$ and were run as controls to ensure the continued accuracy of all measurements ($\pm 0.2\text{‰}$ for $\delta^{13}\text{C}$, $\pm 0.3\text{‰}$ for $\delta^{15}\text{N}$, and $\pm 0.5\text{‰}$ for $\delta^{34}\text{S}$ in organic material). Stable isotope ratios are presented using delta notation (δ), expressed as the permil deviation (‰) relative to the standards of Vienna Pee Dee Belemnite (VPDB), atmospheric nitrogen, and Vienna-Canyon Diablo Troilite (VCDT) for $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$, respectively.

Statistical analyses

Isotopic contrasts and estimates of niche overlap were conducted independently for individuals taken from each embayment, an approach deemed necessary by baseline differences in the isotopic composition of fishes from the two locations, as identified by previous work (Murchie et al. 2018). Given the nearly 100 km swimming distance separating sampling sites, inter-embayment connectivity was highly unlikely for the small juveniles studied here.

To estimate niche overlap between taxa considering the full suite of isotopes simultaneously, we used the techniques developed in the R package nicheROVER (Swanson et al. 2015), which integrates uncertainty through a Bayesian framework to approximate the niche region encompassing a specified proportion of a given population in isotopic space. In the present case, this corresponded to three-dimensional ellipsoids within which any individual had a 40% (core niche, sensu Jackson et al. 2012) or 95% (total niche) probability of occurring. The overlap between each taxon's niche was then estimated using a probabilistic approach, by obtaining the likelihood that a randomly selected individual of one species fell within the respective niche region (i.e., 40% or 95% ellipsoid) of the other species, and vice-versa. As such, nicheROVER generates asymmetric or directional (i.e., species-specific) estimates of niche overlap that include error via credible intervals and are likewise robust to variation in sample size. For these analyses, we used the default

(uninformative) prior, and 10,000 samples drawn from the posterior distribution.

For distinct elemental comparisons between taxa, we used linear-mixed models describing observed isotope ratios as a function of Species. To control for the influence of fish size on isotopic composition, we considered Fork Length (FL) as an explanatory covariate in all models, also including a Species:Length interaction to allow the effect of length to vary across species. Furthermore, to account for the possibility of interdependence among individuals collected together (i.e., cluster sampling bias; see Nelson 2014), we included a random intercept term at the level of seine haul. Models were reduced via backward stepwise selection, comparing nested models using likelihood ratio tests with single-term deletions of fixed effects, and *P* values for coefficients were obtained based on Satterthwaite-approximated degrees of freedom using the R packages lme4 (Bates et al. 2015) and lmerTest (Kuznetsova et al. 2017). Confidence intervals were estimated via nonparametric bootstrapping with 10,000 replicates.

Foraging behavior and vulnerability traits

Behavioral observations

Behavioral data were obtained by reviewing high-definition imagery acquired by remote underwater video surveys. Video was captured using GoPro™ Hero 3 (San Mateo, California) digital video cameras with a spatial resolution of 1920×1080 pixels recording at a rate of 24 frames per second (fps) and sampling an effective area of approximately 4 m^2 of seabed. On each of 3 days in February 2014, three recording units were deployed concurrently in shallow ($< 0.3\text{ m}$), sparsely vegetated littoral zone habitats within embayment B (Fig. 1), separated by a horizontal distance of at least 100 m. Cameras were oriented level to the horizon and left in place to record for a minimum of 1 h before they were recovered. Additional details on video capture methodology can be found in Haak et al. (2020). Video recordings obtained from the surveys were then screened and analyzed using Adobe (Adobe Systems, San Jose, CA) After Effects™ image processing software.

Behavioral analyses were limited to recordings where at least one individual of both bonefish and mojarra was observed to engage in a feeding event. Because the invertebrate prey consumed by these fishes are typically small, cryptic, and unlikely to be resolved by video recordings, feeding events were identified via “strikes” on benthic substrates (i.e., sediment or vegetation), evidenced in both taxa by conspicuous and clearly discernable actions which are described in detail below. Due to the relative rarity of bonefish compared to mojarras in recordings, instances of bonefish feeding were identified first, followed by the feeding

of mojarras that occurred in close temporal proximity (i.e., typically within several seconds).

Foraging individuals were then screened against a set of criteria designed to minimize inaccuracies or ambiguities arising due to the limitations of inferring motion from monoscopic video. For example, due to obvious shortcomings in the utility of 2-D (i.e., x , y) imagery to accurately measure movement along the z axis (i.e., parallel with the principal axis of the lens), we limited consideration to individuals whose movement occurred primarily along the x and y axes, where it could be reliably measured. Likewise, to minimize the effects of camera-subject distance and perspective on apparent velocity as measured at the image plane (i.e., in x , y pixel space), we limited evaluation to individuals who spent the majority of their recorded time within a relatively narrow range of distances from camera (i.e., z depths), omitting those in very close proximity to ($< \approx 0.25$ m), or distant from ($> \approx 1$ m) the lens. Subjects that were obscured from view by other fish or benthic vegetation for extended periods (> 5 s) were omitted. Due to the nature of the habitats and species studied, it is unlikely that any individuals selected for analysis were sampled by more than a single survey. Nevertheless, within the context of each unique camera deployment, we took precautions to limit the likelihood that subjects were sampled repeatedly, using features such as size and/or pigmentation, and screen entry and/or exit points to distinguish and track individuals. When conspecifics could not be differentiated based on the above factors, only those individuals that were on-screen simultaneously or temporally separated by at least several minutes were included in analyses.

Of the individuals meeting the above constraints, the foraging behaviors of all bonefish and a randomly selected subset of mojarras were evaluated using motion analysis. In After Effects, a path depicting the movement of each individual was generated by marking a series of “keyframes”, or coordinates in (x , y) pixel space for sequential frames of video, using the fish’s eyeball as a reference point whenever it was within the camera’s field of view (FOV). Keyframes were spaced adaptively in time, at intervals not exceeding 12 frames (0.5 s) and as short as a single frame (0.042 s), to ensure that rapid or complex movements were well-resolved. When individuals were briefly occluded (for < 5 s) when passing behind objects such as other fish or benthic vegetation, their position at intermediate keyframes was linearly interpolated. From the resulting motion paths or time-series of 2-D coordinates, the distance (in pixels) traveled by an individual between every two consecutive keyframes was approximated and then divided by the length of the corresponding time interval, producing a time series of velocity magnitudes (measured in pixels s^{-1}). Finally, two additional time series were generated for each fish, recording: (1) the moment of each discrete strike or prey capture attempt, to the nearest frame of video (i.e., within 0.042 s), and (2) the

postural orientation of each individual relative to the underlying benthic substrate, where (following Brandl and Bellwood 2015) angles of 90° or greater equated to an upright or “heads up” orientation and values below 90° denoted a “head down” posture associated with feeding.

Four complementary metrics were produced from the resulting data, capturing distinct aspects of foraging behavior that also bore inherent consequences for predation risk via their effects on encounter rate, conspicuity, and the potential for overt vigilance. The faster or more frequent movements characteristic of an active search for prey should equate with a larger area covered per unit time (Eklöv 1992; Colléter and Brown 2011), and by the same token a more active or widely searching forager should spend less time within a predefined area than a comparatively passive one (Fauchald and Tveraa 2003). Therefore, as a proxy for search activity and its corresponding effect on predator encounter probability (Gerritsen and Strickler 1977; Norberg 1977; Huey and Pianka 1981), we calculated the total amount of time that a fish was present within the region defined by the camera’s FOV, (i.e., from frame entry to exit, in seconds), which we termed “Transit-time”. Importantly, this metric integrates the forward speed at which an individual travels as well as the tortuosity of its path.

Activity level can alternatively be expressed as the proportion of time that an individual spends in motion or unmoving (Huey and Pianka 1981; Halperin et al. 2018; Levell and Travis 2018). Accordingly, as a second measure of activity that captured the frequency or continuity of motion exhibited by a fish, and the impacts thereof on its conspicuousness to predators (Howick and O’Brien 1983; Skelly 1994; Martel and Dill 1995), we estimated the percentage of Transit-time during which an individual was stationary, termed “Time-at-rest”. A fish was considered to be at rest when its mean velocity magnitude for a given time interval (i.e., between two consecutive keyframes) did not exceed 1 pixel $frame^{-1}$, or roughly 1% of the camera’s horizontal FOV every 1 s.

A fish’s ability to detect and respond to threats can be affected by the intensity of its feeding activities (Milinski 1984; Godin and Smith 1988; Bohórquez-Herrera et al. 2013) and also by its body posture (Krause and Godin 1996; Foam et al. 2005; Brandl and Bellwood 2015). Thus, we determined the Strike-rate for each fish by dividing their total observed number of prey capture attempts (i.e., strikes at the substrate) by their total Transit-time, and likewise calculated the proportion of Transit-time that each individual spent in a head-down orientation (i.e., “Time-head-down”).

Statistical analyses

Behavioral characteristics were compared between species using regression models. In the case of the continuous

responses Transit-time and Strike-rate, we used linear regression models fit in R to describe log-transformed dependent variables as a function of Species. When dependent variables took the form of proportional data with values between 0 and 1 (i.e., Time-at-rest or Time-head-down), beta regression models with a variable (species-specific) dispersion component were employed, using the R package betareg (Cribari-Neto and Zeileis 2010). Additionally, to elucidate basic differences in the way that the two species integrated locomotion in the act of foraging, we modeled the relationship between Strike-rate and Time-at-rest across the two species. For all models, we considered Survey as a supplemental fixed covariate to account for any differences in environmental conditions that may have introduced dependency in the behaviors displayed by individuals at the level of each recording. Furthermore, to allow for species-specific differences in reaction to environmental variation, a Species:Survey interaction term was included. Reduced models were selected using backward elimination via likelihood ratio tests with single-term deletions. Confidence intervals (95%) were obtained via nonparametric bootstrapping using 10,000 samples.

Results

Isotopic analyses

Overall, SIA indicated limited redundancy in resource use between bonefish and mojarras (Table 1, Fig. 2), with estimated niche overlaps rarely exceeding 40%, and always falling below the 60% threshold that is conventionally taken to denote ecological significance (Guzzo et al. 2013; Vaslet et al. 2015; Kingsbury et al. 2020). In embayment A, the mean directional total niche overlap of bonefish on mojarras (i.e., the probability that a randomly selected bonefish fell within the 95% niche region of mojarras) was 40.42% (95% credible interval [CI] = 20.45–63.75%), nearly equivalent to the estimated overlap of mojarras on bonefish (37.83%, CI = 18.70–60.12). Total niche volumes were generally smaller, and overlaps less symmetrical, in embayment B, where the probability of overlap for bonefish on mojarras (22.04%, CI = 7.48–43.80) was less than half the probability of overlap in the opposite direction (56.14%, CI = 23.90–84.87).

Corresponding probabilities of core (i.e., 40%) niche redundancy were universally low, reflecting the fact that most overlap was confined to the outer margins of the species respective niche volumes (Fig. 2). In embayment A, the mean core overlap of bonefish on mojarras was just 5.59% (CI = 0.61–15.72), similar to that of mojarras on bonefish (9.62%, CI = 2.83–19.88). Core overlaps in embayment B were also small, with the mean of 4.60% (CI = 0.94–11.61)

Table 1 Summary of fork lengths (FL) and stable isotope ratios ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, $\delta^{34}\text{S}$) recorded in white muscle tissue of juvenile bonefish and mojarras collected from two distinct embayments on the west (A) and east-facing (B) coasts of Eleuthera, The Bahamas

Species	Embayment	n	FL (mm)	$\delta^{13}\text{C}$ (‰)		$\delta^{15}\text{N}$ (‰)		$\delta^{34}\text{S}$ (‰)		
				Mean \pm SD	Min–max	Mean \pm SD	Min–max	Mean \pm SD	Min–max	
<i>A. vulpes</i>	A	26	72 \pm 24	35–117	–8.66 \pm 1.75	–11.79 to –6.75	8.4 \pm 0.57	7.02–9.16	12.88 \pm 1.65	9.35–16.15
	B	20	74 \pm 40	38–134	–12.06 \pm 0.8	–13.71 to –10.53	7.06 \pm 0.4	6.19–7.86	8.55 \pm 2.96	3.26–12.37
<i>Eucinostomus</i> spp.	A	15	60 \pm 15	40–82	–7.63 \pm 1.33	–9.89 to –5.52	8.48 \pm 0.53	7.74–9.38	8.11 \pm 3.94	1.69–14.21
	B	15	59 \pm 13	39–90	–10.71 \pm 0.48	–11.36 to –9.75	7.42 \pm 0.52	6.55–8.23	4.63 \pm 1.63	2.59–7.06

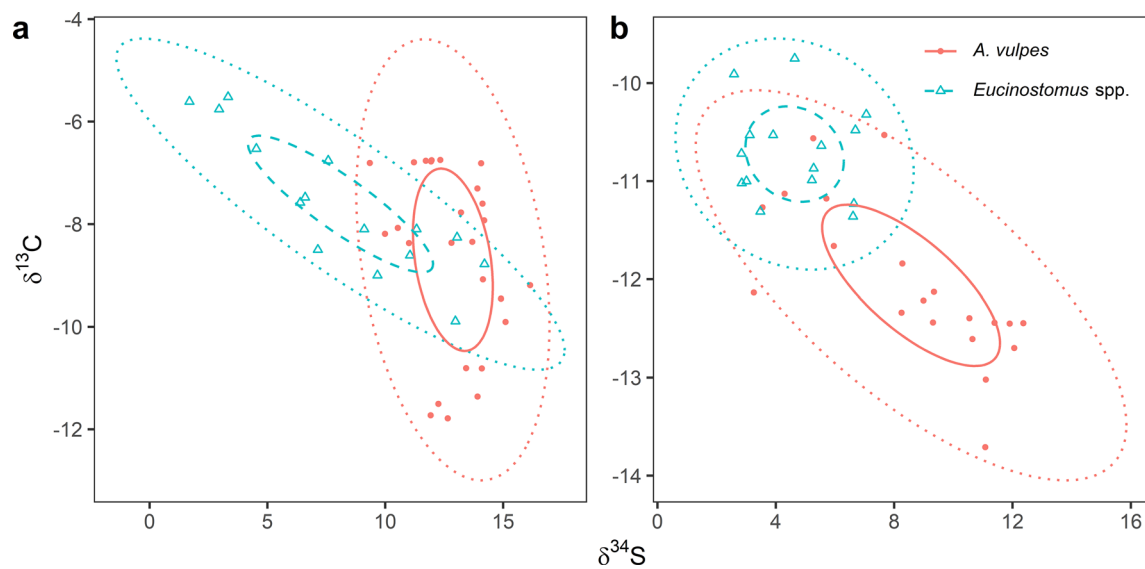


Fig. 2 Plots depicting the isotopic niches (in $\delta^{34}\text{S}$, $\delta^{13}\text{C}$ space) occupied by juvenile bonefish (in red) and mojarras (in blue) collected from **a** west-facing ($n=26$ bonefish; $n=15$ mojarras) and **b** east-facing ($n=20$ bonefish; $n=15$ mojarras) embayments on Eleuthera.

Points (solid circles or open triangles) represent individual observations, while the smaller (solid or dashed) and larger (dotted) ellipses represent core (40%) and total (95%) niche regions, respectively

for bonefish on mojarras comparable to the reciprocal overlap of mojarras on bonefish (3.70%, $\text{CI}=0.05\text{--}16.6$).

Resource use (as inferred from isotopic composition) varied between embayments; however, some species-specific contrasts were consistent across sites (Table 1, Online Resource 1: Table ESM1). Controlling for FL and random haul effects, muscle tissue from mojarras was significantly more depleted in ^{34}S than that of bonefish, with mean differences of -4.76‰ (95% bootstrapped confidence interval [BCI] = -6.5 to -2.9 , $F_{1,39}=29.50$, $P<0.00001$) in embayment A, and -3.02‰ (BCI = -4.86 to -1.16 , $F_{1,30}=11.05$, $P=0.00232$) in embayment B, likely evidencing divergent inputs of isotopically-lighter sulfides produced by bacterial reduction in benthic sediments (Peterson et al. 1986; Fry and Chumchal 2011). Conversely, the muscle of mojarras was enriched in ^{13}C compared to that of bonefish in both embayments, although this disparity was only statistically significant in embayment A (mean difference = 1.5‰ , BCI = $1.21\text{--}1.86$, $F_{1,9}=75.14$, $P<0.0001$), likely signaling differential inputs of carbon from isotopically heavy benthic primary producers. No significant interspecific discrepancies were detected for $\delta^{15}\text{N}$ in either embayment, suggesting that both taxa occupied similar trophic levels.

Behavioral analyses

Examples of joint foraging behavior were discernable in six of the nine recordings, comprising all three survey dates. However, high levels of wave-induced turbulence during one of the days introduced large involuntary excursions to

the position of individuals, precluding reliable inferences about activity based on motion paths (although species-specific differences in behavior remained consistent). As such, recordings from this day were omitted from consideration and quantitative analyses were based on bonefish and mojarras present in recordings obtained from three distinct cameras during the two remaining survey days. Of these, a total of 20 bonefish and 33 mojarras met the criteria established above and were employed in detailed motion analyses (Online Resource 1: Table ESM2).

From a qualitative perspective, the locomotor patterns displayed by foraging mojarras and bonefish were manifestly different (see Online Resource 2 for video). Mojarras moved in an intermittent manner, remaining stationary in an upright posture for long periods (typically 5–10 s or more) that were punctuated by occasional, isolated strikes at the substrate or short repositioning movements. Prey capture in mojarras was characterized by a swift forward pitch rotation that oriented the head toward the substrate, followed immediately by a single rapid protrusion of the mouthparts into the benthic sediments and a subsequent return to an upright position, where sediment was promptly expelled from the mouth and/or gills in a pattern that has been described by others (Sazima 1986, 2002; Parmentier et al. 2011), before moving to a new location. In contrast, foraging bonefish swam continuously in an often tortuous and seemingly random search pattern, slowing or pausing only when they appeared to sense the presence of a potential prey item. The presumable detection of prey by bonefish elicited a transition to a notably more head-down posture, with the fish's

snout nearly contacting the sediment, suggesting a narrowed focus on benthic substrates that was sustained until the prey was located and/or captured, often via several consecutive nearby strikes.

Highlighting these behavioral differences, quantitative analyses revealed pronounced interspecific contrasts across all activity metrics (Fig. 3) and a significant effect of Species in all regression models (Online Resource 1: Tables ESM3–5). The fixed covariate Survey did not contribute appreciably to explaining variation in any of the responses, nor did its interaction with Species, indicating

that observed patterns of behavior were relatively insensitive to changes in environmental conditions across distinct camera deployments. The mean Transit-time, or time required to traverse the camera's FOV for mojarra was 64.5 s (BCI = 52.0–78.5), roughly three times that of bonefish (21.9 s, BCI = 17.0–27.1), suggesting that bonefish searched a larger area per unit time than mojarra. Species was closely related to (\log_{10}) Transit-time ($\chi^2 = 29.18$, $P < 0.00001$), accounting for 41% of variance explained by the model. Interspecific differences in Time-at-rest were of a similar magnitude; the mean for mojarra (69.5%,

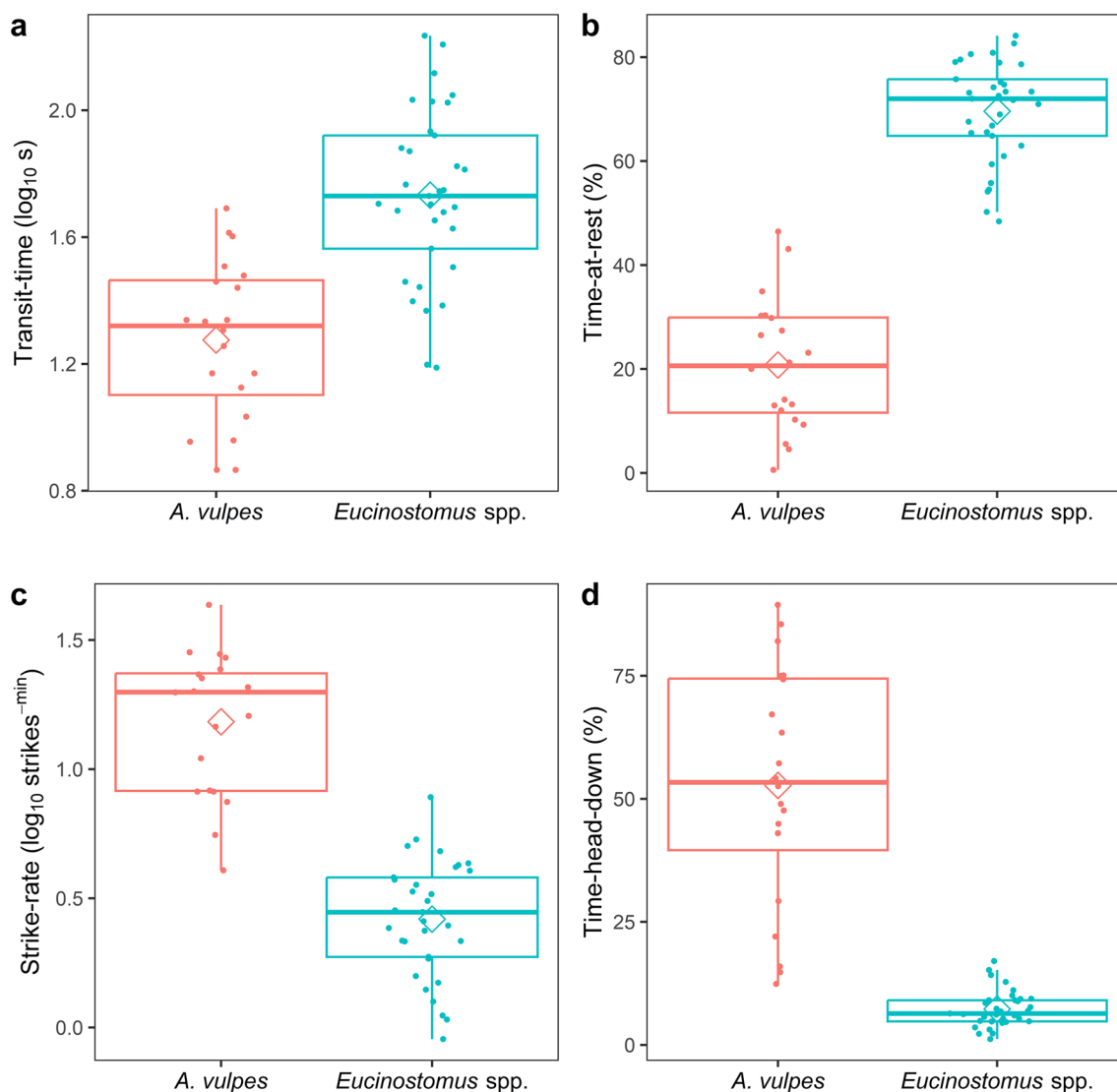


Fig. 3 Boxplots highlighting interspecific contrasts in the foraging behaviors of juvenile bonefish ($n=20$) and mojarra ($n=33$), as quantified through three different activity metrics: **a** Transit-time, the time (in s) required for an individual to traverse the camera's horizontal field of view; **b** time-at-rest, or the proportion (%) of Transit-time during which an individual was not detectably moving or at near-zero velocities; **c** strike-rate, or the number of strikes made by an indi-

vidual while within view (expressed $^{-min}$); and **d** Time-head-down, or the proportion (%) of Transit-time during which an individual maintained a head-down body posture. Boxes depict the interquartile range and median value, while diamonds indicate the mean. Whiskers denote the full range of observed values, and points (solid circles) represent individual observations

BCI=66.2–72.7) was more than three times that of bonefish (20.8%, BCI=15.4–26.3), and the effect of Species explained over 70% of variation in this metric ($\chi^2=50.78$, $P<0.00001$).

Strike-rate also differed greatly between species, with bonefish engaging in a prey capture attempt roughly every 3 s on average (or 18 strikes^{-min}, BCI=13.8–22.3), more than six times as often as mojarras, which struck approximately once every 20 s (2.97 strikes^{-min}, BCI=2.49–3.48). Species was again a close correlate of (log₁₀) Strike-rate ($\chi^2=64.99$, $P<0.00001$), responsible for 70% of explained variance. Species-specific disparities in strike rate were accompanied by corresponding differences in posture; the proportion of time that bonefish spent in a head-down orientation (52.7%, BCI=42.2–62.8) was on average more than sevenfold that of mojarras (7.3% (BCI=6.07–8.59), with 71% of observed variation attributable to the effect of Species ($\chi^2=72.98$, $P<0.00001$).

Strike-rate was a strong predictor of Time-at-rest for both bonefish and mojarras ($\chi^2=70.64$, $P<0.00001$), together with Species explaining 80% of variation in this activity metric; yet a significant Species:Strike rate interaction ($\chi^2=18.75$, $P<0.0001$) showed that the nature of the relationship differed markedly across taxa (Fig. 4). In the case of mojarras, increased Strike-rates were linked to reductions in Time-at-rest, a correspondence one might intuitively expect. However, the correlation was reversed in the case of bonefish, for whom higher Strike-rates were associated with increased Time-at-rest; such that bonefish engaging in more frequent prey capture attempts spent a greater proportion of time at near-zero velocities. The cause of this unexpected relationship became evident upon inspection of representative velocity profiles for the two taxa (Fig. 5). For mojarras, which spent most of their time hovering (i.e., immobile),

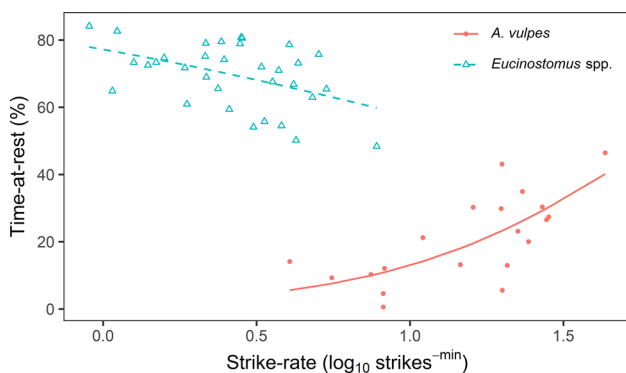


Fig. 4 Scatterplots of the relationship between Strike-rate and Time-at-rest for juvenile bonefish ($n=20$, solid red circles) and mojarras ($n=33$, open blue triangles) observed in underwater video surveys. Lines (solid or dashed) represent the predictions of a beta regression model describing Time-at-rest as a function of Strike-rate, Species, and a Strike-Rate:Species interaction

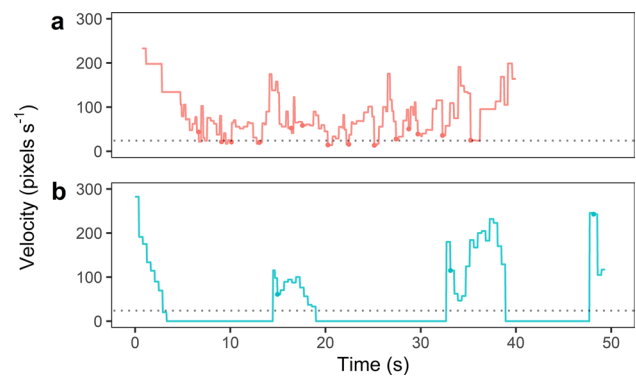


Fig. 5 Time-series plots of representative velocity profiles (in pixels s⁻¹) for **a** a foraging juvenile bonefish and **b** a foraging mojarra as estimated by motion analysis of remote underwater video surveys. Solid circles represent strikes (i.e., feeding attempts). The gray dotted line (parallel to the x axis) delineates the velocity below which individuals were considered to be “at-rest”

prey capture attempts generally comprised the periods of most intense activity; however, relative to the steady swimming that characterized bonefishes’ more active search for prey, the moments surrounding a strike amounted to a notable decline in velocity, constituting intervals of the least movement for this species.

Discussion

Niche overlap and resource utilization

While a small degree of isotopic niche overlap (principally in $\delta^{15}\text{N}$) was observed, the modest and largely peripheral nature of redundancies revealed by SIA imply that overlap in trophic resource use between bonefish and mojarras is limited, and that the likelihood of significant competition between these fish is similarly low. Directional niche overlaps were similar for both taxa when considered at the level of interacting individuals; however, when one takes into account the small proportion of bonefish (relative to mojarras) in heterospecific shoals ($\approx 1\%$ on average, as described by Haak et al. 2019), the competitive costs imposed by bonefish on mojarras at the population level should be inconsequential compared to pressure exerted by much more abundant conspecifics.

Contrasts in isotopic composition offer insights on the functional distinctions that underly niche partitioning between bonefish and mojarras. Since both taxa display a high level of overlap in habitat utilization and forage in the same locations, species-specific differences in $\delta^{34}\text{S}$, and to a lesser degree $\delta^{13}\text{C}$, are almost certainly indicative of fine-scale differences in foraging microhabitat or prey preference. The relatively enriched ^{13}C values of mojarras may reflect a

greater dependence on prey that assimilate carbon from isotopically heavier seagrass habitats (Fry et al. 1982), which are used more readily by mojarras than by juvenile bonefish (Haak et al. 2020). Meanwhile, the more depleted ^{34}S values of mojarras evidence larger inputs of sulfur from sedimentary detrital food webs, pointing to a reliance upon infaunal prey that occupy deeper benthic substrata (Croiseti re et al. 2009); a premise that aligns well with established interspecific differences in functional morphology, sensory physiology, and dietary makeup.

The terminally located tubular mouth and highly protrusible maxillae of mojarras facilitate the capture of more deeply buried organisms by digging or “excavating” deep into substrates and extracting sediment, which is subsequently sifted to extract prey and then expelled from the mouth and gills (Cyrus and Blaber 1982; Sazima 1986); a process known as “winnowing”. In contrast, the subterminal inferior mouth of bonefish is an adaptation consistent with the more selective capture of epifaunal or infaunal prey near the surface of substrates via suction feeding. Differences in the sensory systems employed by the two taxa for prey detection may also promote the capture of benthic fauna from different depths within sediments; while bonefish are thought to be primarily visual predators (Hannan et al. 2015; Grace and Taylor 2017), mojarras are believed to locate prey acoustically, through a specialized auditory adaptation that permits the identification of buried organisms that are completely obscured from view (Green 1971; Parmentier et al. 2011). Indeed, trophic data inferred from gut content analyses concur with the notion that these taxa utilize prey from different depths of burial in sediments, with largely epifaunal gammarid amphipods and caridean shrimp dominating the diet of juvenile bonefish from our study sites (Griffin et al. 2018), while infaunal polychaete worms, copepods (primarily harpacticoid), and bivalve mollusks comprised the majority of prey consumed by equivalently sized mojarras from similar habitats in Florida (Kerschner et al. 1985).

Foraging behavior and species-specific vulnerabilities

Large interspecific disparities in all four behavioral metrics evidenced fundamentally distinct search and prey capture tactics in bonefish and mojarras and provided additional support for the differences in prey utilization inferred from SIA. Following foraging theory, the optimal rate of movement while searching for prey reflects a tradeoff between encounter rate and detection probability; while a faster search speed increases the rate of prey encounter, it has the inverse effect on detection probability, since less time is devoted to inspecting a given area (Gendron and Staddon 1983, 1984). Because the “base” probability of detection for hidden or cryptic prey is low relative to that of conspicuous prey,

the optimal search speed should decline as prey become increasingly hidden or cryptic, permitting increased inspection time (Gendron and Staddon 1983, 1984; O’Brien et al. 1990). Hence, the extended Transit-times and large proportion of time spent at rest (presumably listening for prey) documented for mojarras are in keeping with the hypothesis that this taxon exploits relatively hidden or hard-to-find prey items, such as those concealed within sediments. Likewise, the higher search speeds displayed by bonefish are consistent with the utilization of more conspicuous, exposed, or dispersed epifaunal prey.

Contradictory relationships between Strike-rate and Time-at-rest for bonefish and mojarras highlight a key divergence in the ways that the two taxa integrate locomotion in the act of prey capture (Higham 2007; Rice and Hale 2010). A notable deceleration prior to consuming prey and correspondingly limited strike speeds displayed by bonefish are consistent with behaviors described for suction feeders (a group to which bonefish belongs), for whom high ram speeds can diminish the strength and effectiveness of suction (Higham et al. 2005, 2006). This discrepancy in prey capture tactics is also in keeping with morphological differences between the taxa; the comparatively small gape of bonefish is thought to demand more adaptive and precise mouth positioning with respect to prey, made possible by prolonged approach times associated with a lower closing speed (Higham et al. 2007). Conversely, the faster strike speeds exhibited by mojarras are consistent with a larger gape which requires less exacting precision, as is demonstrated by this taxon’s habit of “excavating”, ingesting, and sifting through sediments to filter out prey (Cyrus and Blaber 1982; Sazima 1986).

Collectively, pronounced differences in the foraging behaviors of bonefish and mojarras imply a stark divide in the overall level of risk associated with their foraging activities. The more expansive area searched per unit time and nearly continuous locomotion ($\approx 80\%$ of their Transit-time) of bonefish should act not only to elevate rates of encounter with predators (Gerritsen and Strickler 1977; Norberg 1977; Huey and Pianka 1981), but also to draw their attention, eliciting more frequent attacks (Howick and O’Brien 1983; Skelly 1994; Martel and Dill 1995). On the contrary, the extended pauses that comprised nearly 70% of mojarras’ Transit-time should have the opposite effect, limiting predator encounter rates and reducing visual conspicuity, while also enhancing sensory perception and processing to facilitate the detection of threats (McAdam and Kramer 1998; Trouilloud et al. 2004). For these reasons, less active foragers that move in an intermittent or “saltatory” manner are thought to maintain relatively high levels of antipredator awareness and face diminished risk while foraging (O’Brien et al. 1990; Kramer and McLaughlin 2001) compared to more active behavioral phenotypes, which often experience

heightened rates of attack, capture, and predation mortality (Biro et al. 2003; Scharf et al. 2003; Strobbe et al. 2011).

Concurrently, when juxtaposed with the swift, isolated strikes that were characteristic of mojarras, the much higher Strike-rates displayed by bonefish (commonly in the form of several consecutive, closely spaced capture attempts) entail greater cognitive demands that can limit the resources available for vigilance, leading to reduced detection efficiency, increased response latency, and a heightened risk of predation mortality (Milinski 1984; Godin and Smith 1988; Bohórquez-Herrera et al. 2013). Moreover, the “head-down” posture that was maintained by bonefish for more than half of their Transit-time (versus less than a tenth of mojarras’) implies a prolonged focus on benthic substrates, which can hinder visual scanning and further degrade responsiveness, resulting in shorter reaction distances and elevated vulnerability to capture (Krause and Godin 1996; Foam et al. 2005; Brandl and Bellwood 2015).

Pauses in the movement of foraging animals are typically presumed to correlate with periods of relatively high antipredator awareness (Kramer and McLaughlin 2001; Trouilloud et al. 2004), and this likely applies in the case of mojarras, for whom Time-at-rest was characterized by hovering in an upright posture well above the seabed, conducive to visual antipredator scanning. However, the assumption did not appear to hold in the case of bonefish, for whom pauses corresponded with prey capture or handling behaviors that involved a sustained head-down posture, connoting a reduced capacity for threat detection. As such, while Time-at-rest may express the prevalence of vigilance-related activities for mojarras, it may capture the inverse for bonefish, reflecting periods of heightened vulnerability.

Beyond the behavioral factors that we quantified here, species-specific differences in morphological and physiological traits may affect predation risk by influencing an individual’s attractiveness to predators or its ability to evade capture (Boukal 2014; Schmitz 2017). The deeper body and robust bony dorsal fin spines of mojarras function as antipredator defenses that can reduce capture success and/or extend handling times (Scharf et al. 2003; Hodge et al. 2018), possibly making them a less desirable target than the more easily ingested fusiform and soft fin-rayed bonefish. Whilst both taxa share deeply forked caudal fins, the more streamlined body form of bonefish may be taken to imply quicker escapes (Blake 2004). However, for juvenile fish of the sizes studied here, interspecific differences in locomotor performance tend to be small and have little impact on susceptibility to capture by larger predators, which is instead determined by response latency and/or flight initiation distance (Scharf et al. 2003; Fuiman et al. 2006; Nannini and Belk 2006). Although the observational nature of our study precluded the direct measurement of these variables (an obvious direction for future work), the more frequent prey

capture attempts and protracted periods of head-down orientation exhibited by bonefish connote a more limited capacity for overt vigilance and the detection of stimuli, upon which the initiation of an escape response depends.

A central concept underlying the theorized tradeoff between foraging and predation risk is the notion of limited attention (Dukas and Kamil 2000; Dukas 2002; Dadda and Bisazza 2006); specifically, it is assumed that the performance of a task (i.e., predator detection) is degraded by the coincident performance of a second task (i.e., prey detection). However, when tasks involve different sensory modalities or parts of the nervous system (e.g., one task is visual and one is auditory), the presumed performance deficit is mostly abated (Duncan et al. 1997; Dadda and Bisazza 2006; Martens et al. 2010). Accordingly, the aforementioned auditory specializations of mojarras may provide this taxon with the unique capability of searching for food and scanning for predators simultaneously via two distinct sensory systems, alleviating the attention deficits associated with multitasking and enabling them to maintain an unusually high level of vigilance while foraging.

Likely drivers of association

It is widely accepted that: (1) enhanced access to resources, and (2) reduced risk of predation, are the principal adaptive benefits derived from group foraging. The procurement of direct food-related benefits via area-copying or scrounging tactics is largely contingent upon the utilization of shared trophic resources (Goodale et al. 2020); however, SIA indicated only marginal niche overlap between bonefish and mojarras. Instead, our work suggests that the two taxa partition resources in a manner explained by differences in their sensory physiology and functional morphology, so that direct food-related advantages are unlikely to be the main driver of their relationship. In contrast, differences in the level of risk associated with their foraging activities conformed closely with patterns observed in terrestrial habitats, with the search and prey capture behaviors (and other vulnerability traits) of bonefish implying a markedly greater susceptibility to predation than those of the mojarras they preferentially join, providing support for the hypothesis that antipredator benefits are an important motivation for doing so.

As gregarious substrate-disturbing benthivores, the foraging ecology of mojarras is broadly consistent with that of other “nuclear” fishes that provide complementary feeding benefits. However, the degree of disturbance caused by mojarras (as discerned from video surveys) was minor and produced little evidence of conspicuous sediment clouds that serve as important cues to attract followers (Strand 1988; Sazima et al. 2006; Krajewski 2009), which may limit the function of mojarras in this role. Alternatively, the primary

feeding advantage derived by piscivorous juvenile snooks (*Centropomus mexicanus*), which exploit mojarras (*Eucinostomus melanopterus*) as a form of camouflage to prey upon unsuspecting benthic fishes (Sazima 2002), is dependent upon their occupying altogether distinct trophic guilds, precluding aforesaid benefits in the case of bonefish and mojarras. While bonefish may opportunistically consume prey flushed (but not targeted) by mojarras, the absence of any such behavior in our video surveys suggests it is not prevalent enough to explain the strength of the species' affiliation.

The results of SIA and behavioral analyses point strongly to risk-related benefits as the main motivation behind bonefishes' attraction to mojarras, yet the means through which they arise are less clear, and can be difficult to disentangle (Beauchamp 2017). Given the fishes' basic physical resemblance (Online Resource 1: Fig. ESM1) and common benthivorous foraging mode, juvenile bonefish joining mojarras may capitalize on risk dilution or predator confusion effects with presumably limited costs of conspicuity (Foster and Treherne 1981; Landeau and Terborgh 1986), and subtle phenotypic differences may even increase the efficacy of these mechanisms in some circumstances (Ruxton et al. 2007; Tosh et al. 2007). If numerical processes are at work, then the value of mojarras as partners may arise simply because their much greater abundances and/or densities make them more readily available partners than conspecifics, while their larger group sizes serve to maximize statistical advantages.

Nonetheless, bonefish opt to join mojarras over conspecifics even when both taxa are equally available and in identically sized groups (Szekeres et al. 2020), suggesting that mojarras offer benefits that extend beyond basic numerical mechanisms. Insights on the likely nature of these "complementary" advantages may be gathered from patterns of association in well-studied terrestrial ungulate and avian communities, where access to heterospecifically produced social information about shared predation threats drives interspecific attraction, leading relatively vulnerable species to join more vigilant ones whose cues or signals they can utilize. (Sridhar et al. 2009; Meise et al. 2020).

Indeed, given their comparatively risky search and prey capture tactics and respective lack of morphological defenses, juvenile bonefish may experience greater selective pressures to exploit the antipredator benefits of group foraging, including socially acquired cues about threats (Thiollay and Jullien 1998; Sridhar et al. 2009; Hodge et al. 2018). Meanwhile, the feeding-related behaviors and unusual sensory abilities of mojarras imply a superior capacity for vigilance, and this taxon's potential for information production may be further augmented by their characteristically large groups, which not only increase the probability of identifying threats through collective

detection (Ward et al. 2011), but also reinforce or amplify the transmission of their cues or signals (Goodale et al. 2010). As such, when considered together, the biological and ecological traits of mojarras appear to make them singularly well qualified for the role of antipredator informants.

By joining mojarras, juvenile bonefish may gain access to fitness-enhancing social information via "eavesdropping" on risk-related cues or signals such as changes in activity (i.e., freeze or dash responses) or modifications to fin or body posture that can provide early warning of predation threats (Xia et al. 2018). In fact, video surveys revealed several instances of coordinated flight behavior among mojarras and bonefish shoalmates. In this way, mojarras may serve a function similar to giraffes in terrestrial habitats (Schmitt et al. 2016), or perhaps in light of their gregariousness, more akin to that of parids in avian communities (Jones and Sieving 2019) by enhancing the fitness and/or survival of other juvenile fishes; a phenomenon which may explain their key influence in structuring juvenile fish assemblages (Haak et al. 2020).

Whatever the nature of benefits acquired by bonefish, the small niche overlap indicated by SIA implies that they carry reduced costs of competition compared to joining conspecifics. It is also worth noting that even in the absence of direct food-related gains, increased resource uptake may still be among the means through which bonefish profit from their association with mojarras, as individuals in groups generally perceive reduced levels of risk and adjust their behaviors accordingly (Beauchamp 2017). Therefore, despite exploiting largely disparate resource pools, bonefish joining mojarras may obtain indirect trophic advantages by reducing the amount of time they devote to vigilance or by feeding in circumstances where they otherwise might not (Sridhar et al. 2009; Gil and Hein 2017; Stears et al. 2020).

Are the relatively risky or non-vigilant behaviors exhibited by bonefish representative of this species across all social contexts, or do they reflect diminished risk perceived by individuals associating with mojarras? Addressing this question is complicated by the fact that juvenile bonefish occur almost solely in the presence of mojarras, preventing the establishment of "baseline" behaviors in situ. An experimental setting could permit the assessment of vigilance behavior across different social contexts, while also allowing more direct measurements of species-specific vulnerabilities and presents a logical next step in corroborating the observations presented here. Nevertheless, the more rapid growth and much larger maximum sizes achieved by bonefish correspond with greater metabolic demands, which are typically associated with less risk-averse behavior (Biro et al. 2003).

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00442-023-05390-1>.

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Author contribution statements CRH developed the idea, methodology, and conducted fieldwork, with inputs from all authors. MP conducted stable isotope analyses and aided in interpretation. CRH analyzed the data and wrote the manuscript, with editorial advice from MP, ADMW, and AJD.

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Availability of data and materials The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Code availability All R-code used for analyses is available from the corresponding author on reasonable request.

Declarations

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

Ethics approval All applicable institutional and/or national guidelines for the care and use of animals were followed and fish sampling was approved by the University of Massachusetts Amherst Institutional Animal Care and Use Committee (protocol 2010–0005).

Consent to participate Not applicable.

Consent for publication Not applicable.

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