2020-06

Juvenile bonefish (Albula vulpes) show a preference to shoal with mojarra (Eucinostomus spp.) in the presence of conspecifics and another gregarious co-occurring species

Szekeres, P

http://hdl.handle.net/10026.1/15684

10.1016/j.jembe.2020.151374
Journal of Experimental Marine Biology and Ecology
Elsevier BV

Juvenile bonefish (*Albula vulpes*) show a preference to shoal with mojarra (*Eucinostomus* spp.) in the presence of conspecifics and morphologically similar species

Petra Szekeres[1], Christopher R. Haak[2], Alexander D.M. Wilson[1,3], Andy J. Danylchuk[2], Jacob W. Brownscombe[1,4*], Aaron D. Shultz[5], and Steven J. Cooke[1]

[1]Fish Ecology and Conservation Physiology Laboratory, Department of Biology, Carleton University, 1125 Colonel By Dr., Ottawa, ON K1S 5B6, Canada

[2]Department of Environmental Conservation, University of Massachusetts Amherst, Amherst, MA, USA

[3]School of Biological and Marine Sciences, University of Plymouth, Plymouth, Devon, PL4 8AA, United Kingdom

[4] Department of Biology, Dalhousie University, 1355 Oxford Street, Halifax, Nova Scotia, Canada B4H 4R2

[5] Flats Ecology and Conservation Program, Cape Eleuthera Institute, Rock Sound, Eleuthera, The Bahamas

*corresponding author email: jakebrownscombe@gmail.com

Declarations of interest: none

Abstract

There are several benefits derived from social behaviour in animals, such as enhanced information transfer, increased foraging opportunities, and predator avoidance. Animal grouping occurs over various taxa, with multi-species grouping taking place across nearly as many taxa as single-species grouping. Fish are commonly used in the study of animal social behaviour, with shoaling or schooling behaviour occurring in approximately 50% of all fish species at some point in their life. The juvenile life stage of bonefish (*Albula vulpes*) is poorly understood, with no experimental evidence of their shoaling associations, but some anecdotal evidence suggests that they tend to be captured in the field alongside mojarra (*Eucinostomus* spp.), but not other nearshore species such as pilchard (*Harengula jaguana*). This study assessed the shoaling preferences of focal juvenile bonefish (n = 25) when given the choice between: (i) conspecifics or mojarra, and (ii) conspecifics or pilchard, in shoal sizes of one, two, four, and eight. In addition, juvenile bonefish shoaling preference was further examined by giving them a choice between a mixed shoal (two conspecifics, two mojarra) as an alternative choice to single species shoals of either: (iii) four conspecifics, or (iv) four mojarra. The results from this study reveal that juvenile bonefish have a strong association with mojarra, spending significantly more time with them than conspecifics, in all but one trial. Additionally, focal fish showed no preference when offered stimulus shoals of conspecifics or pilchard, regardless of shoal size. Lastly, for the two mixed shoal trials, focal fish spent significantly more time wherever there was a higher proportion of mojarra. This study provides ontogenetic evidence regarding the nature of interspecific shoaling preferences in several marine fishes and discusses the possible mechanisms underlying such phenomena; the implications and need for future research into the costs and benefits of such associations in the wild are also discussed.

Keywords: sociality, social behavior, tropical ecology, marine biology

1. Introduction

Sociality is an integral part of animal behaviour across numerous taxa, commonly presenting itself in the form of group living (Krause and Ruxton 2002). Social behaviours of group living aid in enhanced foraging opportunities (Clark and Mangal 1986; Sazima et al. 2007), predator avoidance and vigilance (Turner and Pitcher 1986; Elgar 1989), centralized information transfer (Dall and Johnstone 2002; Couzin et al. 2005), cooperative group hunting (Packer and Ruttan 1988; Pitman and Durban 2012), mate choice and cooperative breeding (Amundsen and Forsgren 2001; Clutton-Brock 2002), and reduce the energetic costs of movement (Weimerskirch et al. 2001; Marras et al. 2015). However, these benefits are often accompanied by various costs, including increased parasite and disease transmission, resource competition (i.e., food, shelter), mate infidelity, and conspicuousness (all reviewed in Krause and Ruxton 2002).

Heretofore, the most widely researched aspects of group living are those focused on the advantages of grouping, with a particular focus on foraging and anti-predator benefits (Székely et al. 1989; Krause and Ruxton 2002; Sridhar et al. 2009). Some associated fitness benefits of grouping are increased foraging success due to the collective food-finding abilities of a group, or by capitalizing and gaining information from individuals within the group that have more local foraging knowledge (Lachlan et al. 1998; Giraldeau and Beauchamp 1999). Furthermore, individuals may experience anti-predator benefits of attack abatement (a combination of predator avoidance and dilution effect), predator confusion, increased vigilance leading to greater information transfer, or a combination of some, or all, of these advantages (Dall and Johnstone 2002). The use of these information sharing systems has a net benefit for individuals in groups, reducing the ecological uncertainty associated with life in the wild (e.g., food acquisition and danger avoidance; Stensland et al. 2003; Dall et al. 2005). In addition to the foraging and anti-predator benefits observed in intraspecific groups, the occurrence of interspecific (i.e., multi-species) groups also mediates some competitive costs of intraspecific group living (Labropoulou and Eleftheriou 1997; Bolnick 2001; Wolf and Weissing 2012).

Multi-species groups exist across nearly as many taxa as do single-species groups (Hoare et al. 2000) and generally receive similar benefits of enhanced food finding, increased vigilance, and social learning through information sharing, which is particularly crucial for animals whose prey have a patchy distribution (a common concern for both avian flocks and fish shoals; Lukoschek and McCormick 2000; Silverman et al. 2004). In addition to the same benefits derived from single-species groups, multi-species groups often have the added benefit of reducing many competitive costs of grouping (Krause and Ruxton 2002). The primary cost of grouping is resource competition; however, in multi-species groups, it is not uncommon for constituents to establish different niches, thereby increasing their fitness while reducing interspecific competition (Labropoulou and Eleftheriou 1997; Stewart et al. 2003; Krajewski et al. 2006). Multi-species grouping advantages may also be present in the form of prey restriction based on morphological differences in feeding apparatus, reducing interspecific competition (e.g., Aguirre et al. 2002), temporally divergent foraging activity (e.g., Albrecht and Gotelli 2001), prey flushing and kleptoparasitism (e.g., Sridhar et al. 2009), and mate choice (e.g., Veen et al. 2001).

Fishes are commonly used in the study of animal social behaviour, with shoaling or schooling behaviour occurring in approximately 50% of all fish species at some point in their development (Radakov 1973; Pavlov and Kasumyan 2000). Multi-species shoaling has been widely documented in tropical marine species (Hoare and Krause 2003), with an emphasis on reef and nearshore systems, likely due to the logistical challenges of observing pelagic species in the wild (Wilson and Krause 2013; Domenici et al. 2014). As tropical nearshore marine habitats often serve as fish nurseries and spawning grounds (Beck et al. 2001; Laegdsgaard and Johnson 2001), it is not unusual for a variety of species to be found using the same habitats (Nagelkerken et al. 2000; Layman and Silliman 2002) to enhance foraging opportunities while reducing predation risk from larger predators (Patterson and Whitfield 2000; Munsch et al. 2016).

Bonefish (*Albula vulpes*), the focal species in this study, are a teleost marine benthivore that reside in the nearshore tropical and sub-tropical waters of the Caribbean (Colborn et al. 2001). As adults, bonefish are an economically important species in the Caribbean through the catch-and-release angling industry that is estimated to generate over $154 billion USD in Florida and $141 million USD annually in The Bahamas (Fedler 2009, 2010). Moreover, because of their benthic feeding mode and relatively high regional abundance, they are thought to be important in structuring nearshore ecosystems (Murchie et al. 2013). Juvenile bonefish are found in nearshore habitats, as are mojarra (*Eucinostomus* spp.) and pilchard (*Harengula jaguana*; Sogard et al. 1989). Mojarra and pilchard are far more abundant in neritic shallow habitats than the juvenile life stage of near-threatened bonefish (Sogard et al. 1989; Adams et al. 2014), with each species occupying distinct regions of the water column and utilizing different foraging techniques (Vega-Cendejas et al. 1994; Layman andSilliman 2002). For example, juvenile bonefish and mojarra are demersal fish that primarily prey on benthic invertebrates found either buried in- or living-on the substrate and remain in water generally less than 2 m depth (Teixeira and Helmer 1998; Reis-Filho et al. 2011). In contrast, pilchard are zooplanktivorous, and as such, their time is primarily spent in the upper reaches of the water column in productive areas of 1 to 5 m total water depth (Modde and Ross 1983; Pierce et al. 2001). These functional group characteristics also align with field observations and co-occurrence indices of mojarra and bonefish, while there is little observational evidence that pilchard also co-occur with these species (Christopher Haak, unpubl. data). Anecdotally, juvenile bonefish are primarily captured with large shoals of mojarra and rarely caught with aggregations of other fish that utilize similar habitat (Christopher Haak, unpubl. data), such as juvenile pilchard. This suggests that there may be more affiliative interactions between juvenile bonefish and mojarra than what might be expected based simply on sharing similar habitat preferences. Here we experimentally test these field observations by quantifying interspecific shoaling preferences for bonefish and several common congeners.

2. Methods

2.1 Capture, Transport, and Holding

The study was conducted in south Eleuthera, The Bahamas (N 24°50′05″ and W 76°20′32″) at the Cape Eleuthera Institute (CEI) during June and July of 2015. Twenty-five juvenile bonefish (mean = 70.2 ± 15 mm SD fork length; range 50-110 mm) were collected from Rock Sound to be the ‘focal fish’ in the shoaling study (Fig. 1). Mojarra (mean = 67.8 ± 7.5 mm SD fork length; range 58-81 mm), juvenile pilchard (mean = 73.2 ± 7.1 mm SD fork length; range 62-90 mm), and additional juvenile bonefish (mean = 70.5 ± 9 mm SD fork length;

range 55-85 mm) were similarly collected; these three species made up the respective 'stimulus shoals'. Juvenile bonefish and mojarra were caught using spot seining techniques, whereby nearshore habitats (< 1 m depth) in Rock Sound were visually assessed, and when the species of interest were identified, a seine net (15.25 m length × 1.22 m height, 0.6 cm mesh size) was used to capture them. Pilchard were caught using a cast net (0.6 cm mesh) on-site at CEI. Captured fish were transferred into flow-through net pens (1.50 m length × 0.7 m width × 1.20 m height) while more fish were collected, before being relocated to coolers (0.9 m length × 0.35 m width × 0.2 m height; 63 L) on the boat for transportation (in the case of juvenile bonefish and mojarra). All fish transfers were done with care to limit exposing fish to air or causing net abrasion (Murchie et al. 2009; Cook et al. 2015). Upon arrival at the wet lab facility at CEI, the juvenile bonefish focal fish (herein referred to as 'focal fish') were held in individual pens (0.35 m length × 0.3 m width × 0.2 m height; 0.3 cm mesh size) in order for researchers to follow the same individuals throughout the entire study without needing to excessively handle or mark these fish. The individual holding pens were set in tanks (1.55 m diameter × 0.25 m height; 472 L) that were aerated and continuously supplied with fresh seawater (10 L/min) at ambient water temperatures (28.6 ± 2.4 °C SD), thus did not induce visual or olfactory isolation (Wright and Krause 2006). The three species of stimulus fish were held in separate tanks with their conspecifics (1.55 m diameter × 0.25 m height; 472 L). All fish were held for a minimum of 48 hr prior to experimentation.

2.2 Shoaling Trials

Each focal fish (n = 25) was observed in four trials, with a total of ten stimulus shoal combinations over the four trials. Focal fish were given the option of shoaling with the following groups of fish(es): (i) conspecifics or mojarra; (ii) conspecifics or pilchard; (iii) conspecifics or a mixed shoal with equal mojarra and bonefish; and (iv) mojarra or a mixed shoal with equal mojarra and bonefish. During the (i) conspecific or mojarra as well as the (ii) conspecific or pilchard trials, focal fish shoaling preference was examined with four stimulus shoal combinations, with either one-, two-, four-, or eight- fish in each stimulus shoal (i.e., 1×1, 2×2, 4×4, 8×8); that is, one mojarra or one bonefish, two mojarra or two bonefish, one pilchard or one bonefish, and so on. Furthermore, this study aimed to determine the shoaling tendencies of focal fish when given the choice of either (iii) four conspecifics or a mixed shoal of two conspecifics and two mojarra (i.e., a 4×4 design); conversely, (iv) four mojarra or a shoal of two conspecifics and two mojarra (herein referred to as a 'mixed shoal').

A Y-maze (0.7 m arm lengths × 0.18 m width × 0.25 m height) was utilized as the experimental arena. Methods were largely modified from Wright and Krause (2006). One arm of the Y-maze was the focal fish release area, with the other two arms housing the two stimulus shoal options. Each stimulus shoal was in a one-way glass transparent bin (18 cm length × 18 cm width × 20 cm height; 6.5 L) at the end of each respective arm, with a daylight emulating light bulb (Lighting Science Group, Satellite Beach, Florida, United States of America; 60 watt) 30 cm above each stimulus fish bin for greater efficacy of the one-way glass (modifications made from Wright and Krause 2006). There was no olfactory exchange between the focal fish and stimulus shoals; due to the one-way glass, focal fish were able to see the stimulus shoals without the opposite occurring (see Wright and Krause 2006). Stimulus shoals were given 1 hr to acclimate to holding bins prior to experimentation. A focal fish was removed from its individual holding pen and first placed in an opaque beaker (14 cm diameter × 15 cm height; 2.3 L) with water from the test tank and left to acclimate for 10 min. After 10 min, the fish was gently poured into a transparent cylinder (15 cm diameter × 30 cm height) in the empty arm of the Y-maze and left to acclimate for another 5 min. Following this final acclimatization period, the focal fish was released and observed via live video feed for 20 min (DVR9-4200 9 Channel 960H Digital Video Recorder and PRO-642 Cameras; Swann Communications U.S.A Inc.; Santa Fe Springs, California, United States of America). The observer recorded seconds spent close-shoaling with either stimulus shoal, quantified as being within approximately two body lengths (20 cm) of the stimulus shoal (Pitcher 1986). After the 20 min trial, the focal fish was moved back to its individual pen and the process was repeated with another randomly selected focal fish. Stimulus shoal position in the Y-maze was changed every five trials, with stimulus shoal individuals also being changed occasionally to prevent shoaling bias (Wright and Krause 2006); the focal fish were tested in a random order at the start of each day.

2.3 Statistical Approach

All analyses were conducted using R version 3.3.1 (R Core Team 2016). For both (i) bonefish or mojarra trials, and (ii) bonefish or pilchard trials, linear mixed effects models

(LME) were fit to square root transformed time (sec) spent with each species to meet the assumptions of normality. Shoal species (bonefish or mojarra; bonefish or pilchard) and shoal size (1×1, 2×2, 4×4, 8×8) were included as predictors, as was the interaction between shoal species and shoal size, and individual focal fish was included as a random effect. A backward model selection approach was used to determine significant predictors by comparing full models to those with reduced terms with log-ratio tests (Zuur et al. 2009). When significant predictors were identified, a Bonferroni post-hoc test was used to determine which stimulus shoal species and shoal sizes were significantly different.

For the mixed shoal experiments, time focal bonefish spent with (iii) conspecifics or a mixed shoal with equal mojarra and bonefish, and (iv) mojarra or a mixed shoal with equal mojarra and bonefish were analyzed using paired t-tests. Parametric assumptions were checked prior to analysis and the data were square root transformed to meet the assumption of normality. For all analyses, data were considered significant at an alpha of 0.05 unless correction applied.

3. Results

3.1 Bonefish or Mojarra Stimulus Shoals

During the trials with bonefish or mojarra as the stimulus shoal choices, focal fish spent more time shoaling with mojarra than conspecifics (Fig. 2a); focal fish spent over three quarters of trial durations engaged in a shoal, with 73% of that time spent shoaling with mojarra. In many instances, focal fish would explore the experimental arena (i.e., investigate both shoal options) and then choose to stay close-shoaling with mojarra. There was a significant interaction between stimulus shoal species and shoal size (LME; $X^2 = 19.3$, $p < 0.001$). Bonefish spent significantly more time with mojarra in shoal sizes of one, four, and eight (Tukey's HSD; $p < 0.001$); however, there was no significant difference in time spent with either species in shoal sizes of two (Tukey's HSD; $p = 1.0$; Fig. 2a).

3.2 Bonefish or Pilchard Stimulus Shoals

Juvenile bonefish generally tended to spend a similar amount of time with both conspecifics and pilchard (Fig. 2b). Focal fish spent nearly the same amount of time shoaling with conspecifics, pilchard, and non-shoaling. It was common for focal fish to swim around the experimental arena to all of the arms several times (i.e., entering and exiting shoaling zones), often without making a discernible choice to shoal with either shoal for a substantial amount of time. When comparing focal fish shoaling tendencies between conspecifics or pilchard, there was no significant interaction between shoal species and shoal size ($X^2 = 2.8$, $p = 0.42$), nor was there a significant effect of shoal species ($X^2 = 0.06$, $p = 0.8$) or shoal size ($X^2 = 0.5$, $p = 0.9$) on juvenile bonefish shoal choice (Fig. 2b).

3.3 Bonefish or Mixed Stimulus Shoals

When given the choice between bonefish or mixed shoals, focal fish preferred to spend more time shoaling with the mixed shoals of bonefish and mojarra than with the conspecific shoal (Fig. 3a); focal fish were engaged with a shoal nearly three quarters of the time, with 66% of that time spent shoaling with the mixed shoal. There was a significant difference between time spent shoaling with bonefish (mean = 263 ± 63 s SE) and time spent shoaling with the mixed shoal (mean = 619 ± 79 s SE). Focal fish spent significantly more time shoaling with the mixed shoal than with conspecifics ($t = -2.6$, $df = 24$, $p = 0.02$).

3.4 Mojarra or Mixed Stimulus Shoals

Contrary to the results of the bonefish or mixed shoal trials, focal fish preferred to shoal with the mojarra stimulus shoal, rather than spending their time with the mixed shoal (Fig. 3b); similarly focal fish spent nearly three quarters of their time engaged with a shoal, with 70% of that time spent shoaling with mojarra. There was a significant difference between the time focal fish spent shoaling with mojarra (mean = 581 ± 62 s SE) and time spent shoaling with the mixed shoal (mean = 291 ± 56 s SE). The focal fish in this trial spent significantly more time with mojarra than with the mixed shoal ($t = 2.8$, $df = 24$, $p = 0.01$).

4. Discussion

The results of this study suggest that juvenile bonefish prefer to actively shoal with mojarra rather than other species options afforded to them throughout the experiment. The four treatments in which focal fish were given a shoaling choice were: (i) bonefish or mojarra (four trials; 1×1, 2×2, 4×4, 8×8), (ii) bonefish or pilchard (four trials; 1×1, 2×2, 4×4, 8×8), (iii) four bonefish or a mixed shoal (two mojarra and two bonefish), and lastly (iv) four mojarra or a mixed shoal (two mojarra and two bonefish). For the (i) bonefish or mojarra treatment, in three of the four trials, juvenile bonefish showed a significant preference for shoaling with mojarra (Fig. 2a). Focal fish showed a strong preference for mojarra during the 1×1, 4×4, and 8×8 treatments, spending substantially more time with mojarra on average than with conspecifics. However, a disparity in the results is in the 2×2 treatment, where focal fish spent approximately the same amount of time with conspecifics and with mojarra, although mean time spent with mojarra was marginally higher. This result is in contrast to the overall trend of our results, and we surmise it may be largely due to a low sample size resulting in low statistical power; with more trials, it is likely the results would have followed the same trend as the other results. Another potential explanation for this disparity may be that there is an ecological implication (i.e., stimulus shoal individuals in the 2×2 were less social; group sizes of two are an unattractive shoal choice; e.g., Cote et al. 2012; Laskowski and Bell 2014). During the treatment where focal fish were given the choice between (ii) conspecifics or pilchard, focal fish showed no preference for shoaling with either stimulus shoal (Fig. 2b). Instead, focal fish appeared to spend their time equally between the conspecific shoal, the pilchard shoal, and non-shoaling. The focal fish were often swimming around the experimental arena and between the stimulus shoals, without spending significant time with either. During both of the two mixed shoal treatments, focal fish had a strong tendency to shoal wherever there was the highest proportion of mojarra (Fig. 3). In the treatment where focal fish were given the opportunity to shoal with either (iii) four conspecifics or a mixed shoal, the focal fish tended to shoal with the mixed shoal that included two mojarra as well as two conspecifics (Fig. 3a). Lastly, when given the option to shoal with (iv) four mojarra or a mixed shoal, focal fish had strong tendencies to shoal with mojarra, abandoning their previous preference for the mixed shoal. The results from the two mixed shoal treatments support the hypothesis that juvenile bonefish have a preference to shoal wherever there is the highest proportion of mojarra.

Anti-predator and foraging benefits are commonly attributed as the key advantages of grouping (Morse 1977; Krause and Ruxton 2002; Sridhar et al. 2009). Anti-predator advantages exist in the context of attack abatement, predator confusion, and increased vigilance (Pitcher and Parrish 1993; Turner and Montgomery 2003). Another consideration in predator-prey models is the ‘oddity effect’, whereby phenotypically dissimilar fish are more easily and readily targeted by predators (Landeau and Terborgh 1986). In the context of this study, the existence of the oddity effect would suggest that juvenile bonefish should prefer to shoal with conspecifics, or to a lesser extent, pilchard (more phenotypically similar than mojarra). Presumably, shoaling with either conspecifics or pilchard would lessen the oddity effect, thereby lowering predation risks for individuals (Landeau and Terborgh 1986); however, this was not the case in this study. Not only did juvenile bonefish show no preference during the treatment with either pilchard or conspecifics, they also showed little preference for conspecifics throughout the entirety of the experiment. Other possible mechanisms may be linked to similarities in foraging modes, microhabitat usage, and spatial niche overlap leading to closer associations between juvenile bonefish and mojarra.

Juvenile bonefish, mojarra, and pilchard all have substantial habitat overlap in tropical and subtropical nearshore habitats (Sogard et al. 1989). However, it can be speculated that the ways in which they are organized in these nearshore habitats differ, resulting in the utilization of different microhabitats. Juvenile bonefish and mojarra are benthivorous fish and belong to the same trophic classification (Reis-Filho et al. 2011), whereas pilchard are zooplanktivorous and remain higher in the water column (Modde and Ross 1983). Therefore, we suggest juvenile bonefish and pilchard are unlikely to have strong associations with one another due to their different foraging modes, likely resulting in little spatial niche overlap. It is also worth noting that although pilchard are arguably more phenotypically similar to juvenile bonefish, mojarra still share superficial similarities with juvenile bonefish; both mojarra and juvenile bonefish have similar dorsal and lateral pigmentation, and are difficult to distinguish in a mixed shoal. Additionally, due to their wide distribution and abundance in nearshore habitats, mojarra may also behave as important information centers for juvenile bonefish, relying on mojarra shoals to inform them of lucrative foraging opportunities (Seppänen et al. 2007).

Evidence of foraging modes and microhabitat usage suggests that mojarra may be an attractive shoal choice for juvenile bonefish. However, these attributes alone are not necessarily sufficient to explain bonefish shoaling preference for mojarra and not conspecifics. In addition to their spatial overlap, mojarra have also demonstrated an auditory specialization which may allow for superior prey-finding (Parmentier et al. 2011). Juvenile bonefish and mojarra may also limit resource competition through differences in the morphology of their feeding apparatuses (Zahorcsak et al. 2000; Snodgrass et al. 2008). Mojarra possess an auditory adaptation whereby their swim bladder has a specialized connection to the inner ear, and a modified cone in their pelvic fin where it sits, all acting to enhance the acoustic amplification provided by the swim bladder (Parmentier et al. 2011). It has been hypothesized that this adaptation is not used for communication, but instead may be used to hear benthic invertebrate prey below the surface of the substrate (Braun and Grande 2008; Parmentier et al. 2011). This auditory specialization would be beneficial to the foraging success of nearby bonefish, thereby making mojarra an advantageous shoal mate.

Mojarra may suffer from the associated cost of increased competition due to their auditory specialization if shoal mates are kleptoparasitic (e.g., Webster and Hart 2006); however, their association with juvenile bonefish may not result in increased competition due to potential trophic resource partitioning. Using isotopic analysis, Haak (unpubl. data) determined that although juvenile bonefish and mojarra utilize similar habitats and are oftentimes caught together, they appear to have minimal dietary overlap, and instead satisfy slightly different trophic niches. Resource niche partitioning is a common occurrence in both avian and fish communities, and has been strongly supported in the literature (e.g., Labropoulou and Eleftheriou 1997; Radford and Du Plessis 2003; Krajewski et al. 2006; Harrison and Whitehouse 2011). Although this was neither explicitly examined in Haak (unpubl. data), nor in the current study, an explanation for the disparity in prey types may be due in part to the morphological differences in their feeding apparatus (Vega-Cendejas et al. 1994). Mojarra have a protractable mouth which is able to extend and protrude into the substrate (Sazima 1986; Zahorcsak et al. 2000), whereas bonefish have a hard palette designed to grind the shells of invertebrates (Alexander 1961). Since bonefish only have a limited ability to protract their mouths and primarily rely on burrowing their snouts into the substrate to capture prey, they may consume prey closer to the surface of the substrate (Snodgrass et al. 2008; Brownscombe et al. 2014), thereby excluding them from mojarra prey types.

There are inherent difficulties associated with studying wild fish populations (Ostrander 2000); it is important to note that juvenile bonefish are present in low densities and are difficult to locate and capture, thus resulting in the current experimental design and limited sample size. Indeed, shoals of mojarra and juvenile bonefish in nature are substantially larger (often 10s to even 100s of individuals) than what was able to test experimentally. Nonetheless, our results reveal that there are strong affiliative interactions between mojarra and bonefish. This study was the first to explore the shoaling preferences of juvenile bonefish, and as such, the plausible behavioural and evolutionary drivers supporting these multi-species associations are still speculative. To begin exploring these possible drivers, future studies should possibly shift to become more 'mojarra-centric', rather than the current model. This shift would allow for further exploration of the notion that mojarra behave as a nuclear species for various nearshore juvenile fish species (an observation of Christopher Haak, unpubl. data), thus driving the foraging activity of interspecific shoal mates (Lukoschek and McCormick 2000). There is a body of evidence within the literature that suggests nuclear species may be more vigilant (e.g., Dolby and Grubb 1998; Ragusa-Netto 2002; Sazima et al. 2006), thereby providing their associate counterparts with the information to reduce predation, and thus their ecological uncertainty (Danchin et al. 2004; Dall et al. 2005). Future behavioural experiments could ascertain whether there is the occurrence of the 'oddity effect' resulting in juvenile bonefish being a preferred prey type, or whether their superficial similarities to mojarra can be attributed to this selective pressure (Landeau and Terborgh 1986; Krause and Ruxton 2002; Sazima 2002). Lastly, future research should consider the possibility of mojarra incurring negative consequences from juvenile bonefish shoaling with them (i.e., kleptoparasitism, increased detection from predators, etc.).

The results of this study provide evidence to suggest that juvenile bonefish preferentially shoal with mojarra over conspecifics and other phenotypically similar nearshore species, likely deriving interspecific benefits from having mojarra as shoal mates. These benefits may manifest in the form of increased foraging opportunities, limiting resource competition, or reduced predation; in all likelihood, the benefits juvenile bonefish derive are a combination of all these benefits. We provide conjecture to explain this observed shoaling preference, but also acknowledge that more research is required to determine the underlying behavioural, ecological, and evolutionary mechanisms driving this relationship. Our study provides experimental validation of the common field observation of juvenile bonefish appearing to prefer heterospecifics (mojarra) to conspecifics, opening various future avenues of study for social behaviour in subtropical nearshore fishes.

Acknowledgements

Financial support was provided by the Natural Sciences and Engineering Research Council of Canada and the Canada Research Chairs Program. Additional support was provided by Bonefish and Tarpon Trust through their BTT Fellows Program. We thank the staff of the Cape Eleuthera Institute for providing logistic support. Research permits were kindly provided by the Bahamas Department of Marine Resources, whereas animal care approvals were secured from the Carleton University Animal Care Committee and conformed with the guidelines of the Canadian Council on Animal Care.

Literature Cited

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.

Aguirre LF, Herrel A, Van Damme R, Matthysen E (2002). Ecomorphological analysis of trophic niche partitioning in a tropical savannah bat community. Proc R Soc Lond B Biol Sci 269(1497): 1271-1278.

Albrecht M, Gotelli NJ (2001) Spatial and temporal niche partitioning in grassland ants. Oecol 126(1): 134-141.

Alexander EC (1961) A contribution to the life history, biology and geographical distribution of the bonefish, *Albula vupes* (Linnaeus).

Amundsen T, Forsgren E (2001) Male mate choice selects for female coloration in a fish. PNAS 98(23): 13155-13160.

Beck MW, Heck Jr KL, Able KW, Childers DL, Eggleston DB, Gillanders BM ... Orth RJ (2001) The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates: a better understanding of the habitats that serve as nurseries for marine species and the factors that create site-specific variability in nursery quality will improve conservation and management of these areas. Bioscience 51(8): 633-641.

Bolnick DI (2001) Intraspecific competition favours niche width expansion in Drosophila melanogaster. Nature 410(6827): 463-466.

Braun CB, Grande T (2008) Evolution of peripheral mechanisms for the enhancement of sound reception. In Springer Handbook of Auditory Research. Fish Bioacoustics, Vol. 32 (ed. AN Popper, RR Fay, JF Webb), pp. 99-144. New York: Springer-Verlag.

Brownscombe JW, Gutowsky LF, Danylchuk AJ, Cooke SJ (2014) Foraging behaviour and activity of a marine benthivorous fish estimated using tri-axial accelerometer biologgers. Mar Ecol Prog Ser 505: 241-251.

Clark CW, Mangel M (1986) The evolutionary advantages of group foraging. Theor Popul Biol 30(1): 45-75.

Clutton-Brock T (2002) Breeding together: kin selection and mutualism in cooperative vertebrates. Science 296(5565): 69-72.

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.

Cook KV, Lennox RJ, Hinch SG, Cooke SJ. 2015. Fish out of water: How much air is too much? Fisheries. 40:452–461.

Couzin ID, Krause J, Franks NR, Levin SA (2005) Effective leadership and decision-making in animal groups on the move. Nature 433(7025): 513-516.

Dall SRX, Johnstone RA (2002) Managing uncertainty: information and insurance under the risk of starvation. Philos. Trans. R. Soc. Lond. Ser. B 357: 1519–1526

Dall SR, Giraldeau LA, Olsson O, McNamara JM, Stephens DW (2005) Information and its use by animals in evolutionary ecology. Trends Ecol Evol 20(4): 187-193.

Danchin É, Giraldeau LA, Valone TJ, Wagner RH (2004) Public information: from nosy neighbors to cultural evolution. Science 305(5683): 487-491.

Dolby AS, Grubb Jr TC (1998) Benefits to satellite members in mixed-species foraging groups: an experimental analysis. Anim Behav 56(2): 501-509.

Domenici P,Wilson ADM, Kurvers RHJM, Marras S, Herbert-Read JE, Steffensen JF, Krause S, Viblanc PE, Couillaud P, Krause J (2014) How sailfish use their bills to capture schooling prey. Proc R Soc Lond [Biol] 281(1784) (DOI: 10.1098/rspb.2014.0444)

Elgar MA (1989) Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. Biol Rev 64(1): 13-33.

Fedler, T (2009) The economic impact of recreational fishing in the Everglades region. Prepared for The Everglades Foundation, Miami, Florida, December.

Giraldeau LA, Beauchamp G (1999) Food exploitation: searching for the optimal joining policy. Trend Ecol Evol 14(3): 102-106.

Harrison NM, Whitehouse MJ (2011) Mixed-species flocks: an example of niche construction?. Anim Behav 81(4): 675-682.

Hoare DJ, Ruxton GD, Godin JGJ, Krause J (2000) The social organization of free-ranging fish shoals. Oikos 89(3): 546-554.

Hoare DJ, Krause J (2003) Social organisation, shoal structure and information transfer. Fish Fish 4(3): 269-279.

Krause J, Ruxton GD (2002) Living in groups. Oxford University Press.

Krajewski JP, Bonaldo RM, Sazima C, Sazima I (2006) Foraging activity and behaviour of two goatfish species (Perciformes: Mullidae) at Fernando de Noronha Archipelago, tropical West Atlantic. Environ Biol Fish 77(1): 1-8.

Lachlan RF, Crooks L, Laland KN (1998) Who follows whom? Shoaling preferences and social learning of foraging information in guppies. Anim Behav 56(1): 181-190.

Laegdsgaard P, Johnson C (2001) Why do juvenile fish utilise mangrove habitats? J Exp Mar Biol Ecol 257(2): 229–253.

Labropoulou M, Eleftheriou A (1997) The foraging ecology of two pairs of congeneric demersal fish species: importance of morphological characteristics in prey selection. J Fish Biol 50(2): 324-340.

Landeau L, Terborgh J (1986) Oddity and the ‘confusion effect’in predation. Anim Behav 34(5): 1372-1380.

Layman CA, Silliman BR (2002) Preliminary survey and diet analysis of juvenile fishes of an estuarine creek on Andros Island, Bahamas. Bull Mar Sci 70(1): 199-210.

Lukoschek V, McCormick MI (2000) A review of multi-species foraging associations in fishes and their ecological significance. In *Proceeding 9th International Coral Reef Symposium (Vol. 1,* *pp. 467-474)*. Ministry of Environment, Indonesian Institute of Sciences and International Society for Reef Studies.

Marras S, Killen SS, Lindström J, McKenzie DJ, Steffensen JF, Domenici P (2015) Fish swimming in schools save energy regardless of their spatial position. Behav Ecol Sociobiol 69(2): 219-226.

Modde T, Ross ST (1983) Trophic relationships of fishes occurring within a surf zone habitat in the northern Gulf of Mexico. NE Gulf Sci 6(2): 109-120.

Morse DH (1977) Feeding behaviour and predator avoidance in heterospecific groups. Biosci 27: 332–339.

Munsch SH, Cordell JR, Toft JD (2016) Fine-scale habitat use and behavior of a nearshore fish community: nursery functions, predation avoidance, and spatiotemporal habitat partitioning. Mar Ecol Prog Ser 557: 1-15.

Murchie KJ, Danylchuk SE, Pullen CE, Brooks E, Shultz AD, Suski CD, Danylchuk AJ, Cooke SJ. (2009) Strategies for the capture and transport of bonefish, *Albula vulpes*, from tidal creeks to a marine research laboratory for long-term holding. Aquac Res. 40(13):1538-1550.

Murchie, KJ, Cooke SJ, Danylchuk AJ, Danylchuk SE, Goldberg TL, Suski CD, Philipp DP. (2013). Movement patterns of bonefish (Albula vulpes) in tidal creeks and coastal waters of Eleuthera, The Bahamas. Fish Res. 147: 404-412.

Nagelkerken I, Van der Velde G, Gorissen MW, Meijer GJ, Van't Hof T, Den Hartog C (2000) Importance of mangroves, seagrass beds and the shallow coral reef as a nursery for important coral reef fishes, using a visual census technique. Estuar Coast Shelf Sci 51(1): 31-44.

Ostrander GK (Ed.) 2000. The Laboratory Fish. San Diego, CA: Academic Press.

Packer C, Ruttan, L (1988) The evolution of cooperative hunting. Am Nat 132(2): 159-198.

Parmentier E, Mann K, Mann D (2011) Hearing and morphological specializations of the mojarra (*Eucinostomus argenteus*). J Exp Biol 214(16): 2697-2701.

Pavlov DS, Kasumyan AO (2000) Patterns and mechanisms of schooling behavior in fish: a review. J Ichthyol 40(2): S163-S231.

Pierce DJ, Mahmoudi B, Wilson RR (2001) Age and growth of the scaled herring, Harengula jaguana, from Florida waters, as indicated by microstructure of the sagittae. Fish Bull Nat Oc At 99(1): 202-209.

Pitcher TJ (1986) Functions of shoaling behaviour in teleosts. In *The behaviour of teleost fishes* (pp. 294-337). Springer US.

Pitman RL, Durban JW (2012) Cooperative hunting behavior, prey selectivity and prey handling by pack ice killer whales (*Orcinus orca*), type B, in Antarctic Peninsula waters. Mar Mam Sci 28(1): 16-36.

Radakov DV (1973) Schooling in the ecology of fish. John Wiley and Sons, New York.

Radford AN, Du Plessis MA (2003) Bill dimorphism and foraging niche partitioning in the green woodhoopoe. J Anim Ecol 72(2): 258-269.

Ragusa-Netto J (2002) Vigilance towards raptors by nuclear species in bird mixed flocks in a Brazilian savannah. Stud Neotrop Fauna E 37(3) 219-226.

Reis-Filho, J. A., Barros, F., Da Costa, J. D. A. C., Sampaio, C. L. S., and De Souza, G. B. G. (2011). Moon and tide effects on fish capture in a tropical tidal flat. J Mar Biol Assoc UK 91(3): 735-743.

Sazima I (1986) Similarities in feeding behaviour between some marine and freshwater fishes in two tropical communities. J Fish Biol 29: 53-65.

Sazima I (2002). Juvenile snooks (Centropomidae) as mimics of mojarras (Gerreidae), with a review of aggressive mimicry in fishes. Enviro Biol Fish 65(1): 37-45.

Sazima C, Krajewski JP, Bonaldo RM, Guimarães PR (2006) The goatfish *Pseudupeneus maculatus* and its follower fishes at an oceanic island in the tropical west Atlantic. J Fish Biol 69(3): 883-891.

Sazima C, Krajewski JP, Bonaldo RM, Sazima I (2007) Nuclear-follower foraging associations of reef fishes and other animals at an oceanic archipelago. Environ Biol Fish 80(4): 351-361.

Seppänen JT, Forsman JT, Mönkkönen M, Thomson RL (2007) Social information use is a process across time, space, and ecology, reaching heterospecifics. Ecology 88(7): 1622-1633.

Silverman ED, Veit RR, Nevitt GA (2004) Nearest neighbors as foraging cues: information transfer in a patchy environment. Mar Ecol Prog Ser 277:25–35.

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

Sogard SM, Powell GV, Holmquist JG (1989) Utilization by fishes of shallow, seagrass-covered banks in Florida Bay: 1. Species composition and spatial heterogeneity. Environ Biol Fish 24(1): 53-65.

Sridhar H, Beauchamp G, Shanker K (2009) Why do birds participate in mixed-species foraging flocks? A large-scale synthesis. Anim Behav 78(2): 337-347.

Stensland EVA, Angerbjörn A, Berggren PER (2003) Mixed species groups in mammals. Mam Rev 33(3-4): 205-223.

Stewart KM, Bowyer RT, Kie J, Dick BL, Ben-David M (2003) Niche partitioning among mule deer, elk, and cattle: do stable isotopes reflect dietary niche? Ecosci 10(3): 297-302.

Székely T, Szép T, Zuhas T (1989) Mixed-species flocking of tits (*Parus* spp.): a field experiment. Oecol 78:490–495.

Teixeira RL, Helmer JL (1998) Ecology of young mojarras (Pisces: Gerreidae) occupying the shallow waters of a tropical estuary. Rev Brasil Biol 57: 637-646.

Turner GF, Pitcher TJ (1986) Attack abatement: a model for group protection by combined avoidance and dilution. Am Nat 128(2): 228-240.

Turner AM, Montgomery SL (2003) Spatial and temporal scales of predator avoidance: experiments with fish and snails. Ecology 84(3): 616-622.

Veen T, Borge T, Griffith SC, Saetre GP, Bures S, Gustafsson L, Sheldon BC (2001) Hybridization and adaptive mate choice in flycatchers. Nature 411(6833): 45-50.

Vega-Cendejas ME, Hernández M, Arreguin-Sanchez F (1994) Trophic interrelations in a beach seine fishery from the northwestern coast of the Yucatan peninsula, Mexico. J Fish Biol 44(4): 647-659.

Weimerskirch H, Martin J, Clerquin Y, Alexandre P, Jiraskova S (2001) Energy saving in flight formation. Nature 413(6857): 697-698.

Wilson ADM, Krause J (2013) Repeated non-agonistic interactions between a bottlenose dolphin (*Tursiops truncatus*) and sperm whales (*Physeter macrocephalus*) in Azorean Waters. Aquat Mamm 39: 89-96.

Webster MM, Hart PJ (2006) Kleptoparasitic prey competition in shoaling fish: effects of familiarity and prey distribution. Behav Ecol 17(6): 959-964.

Wolf M, Weissing FJ (2012) Animal personalities: consequences for ecology and evolution. Trend Ecol Evol 27(8): 452-461.

Wright D, Krause J (2006) Repeated measures of shoaling tendency in zebrafish (*Danio rerio*) and other small teleost fishes. Nat Protoc 1(4): 1828-1831.

Zahorcsak P, Silvano RAM, Sazima I (2000) Feeding biology of a guild of benthivorous fishes in a sandy shore on south-eastern Brazilian coast. Rev Bras Biol 60(3): 511-518.

Figures

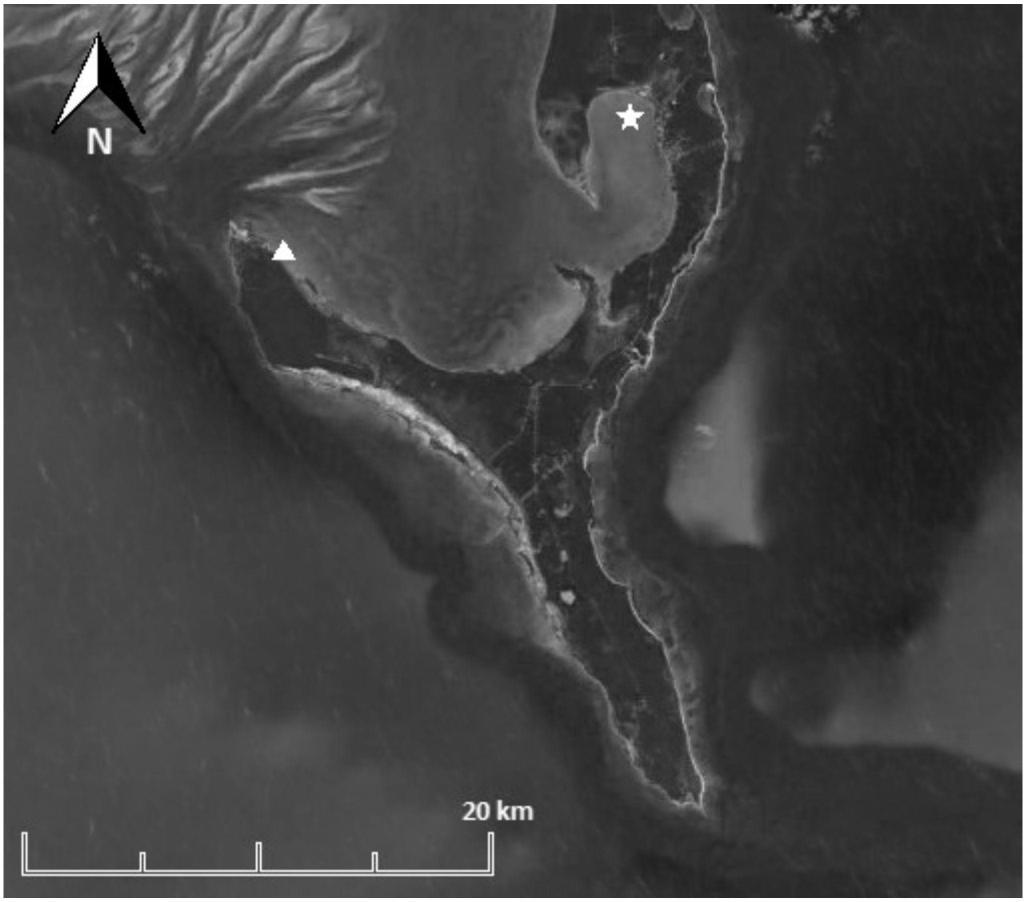

Fig. 1 A map of southern Eleuthera, The Bahamas (developed using Google Earth Pro). The star denotes the capture and collection site of juvenile bonefish and mojarra in Rock Sound, and the triangle denotes the location of the Cape Eleuthera Institute and the location of pilchard capture.

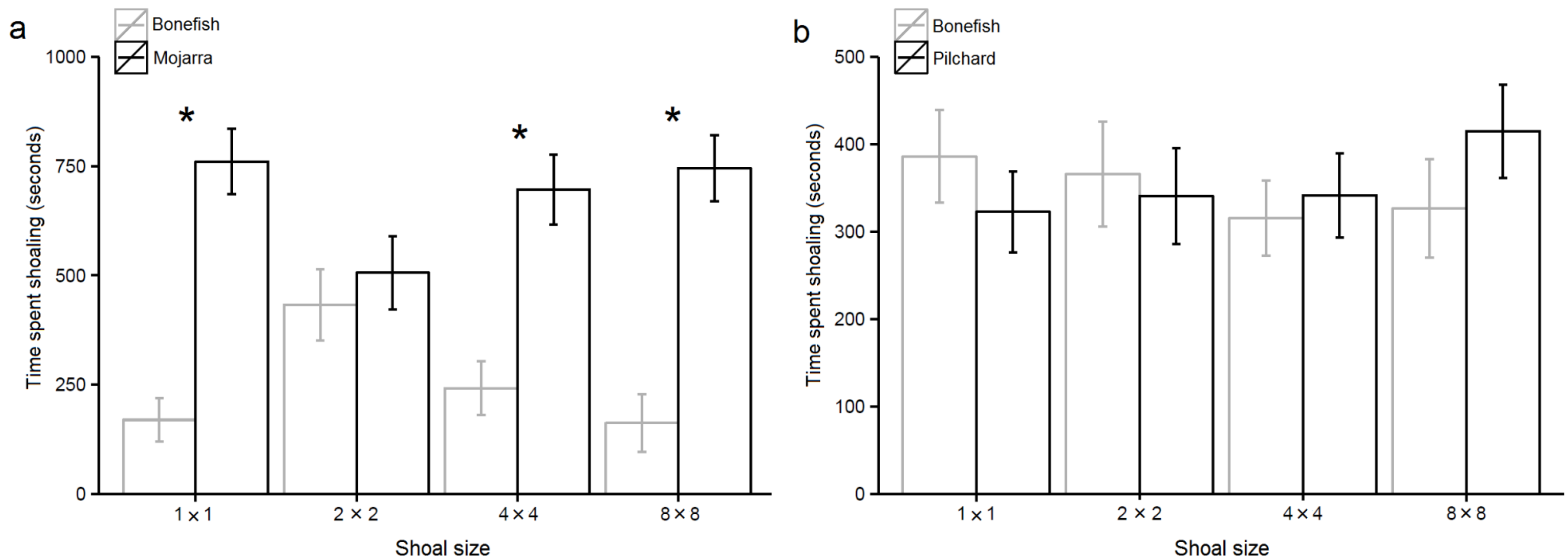

Fig. 2 Mean responses (±SE) of time focal bonefish spent (in seconds) shoaling with other bonefish or mojarra (2a), and time spent (in seconds) shoaling with bonefish or pilchard (2b) in stimulus shoal sizes of 1×1, 2×2, 4×4, 8×8. Asterisks (*) denote significant differences between species in each shoal size.

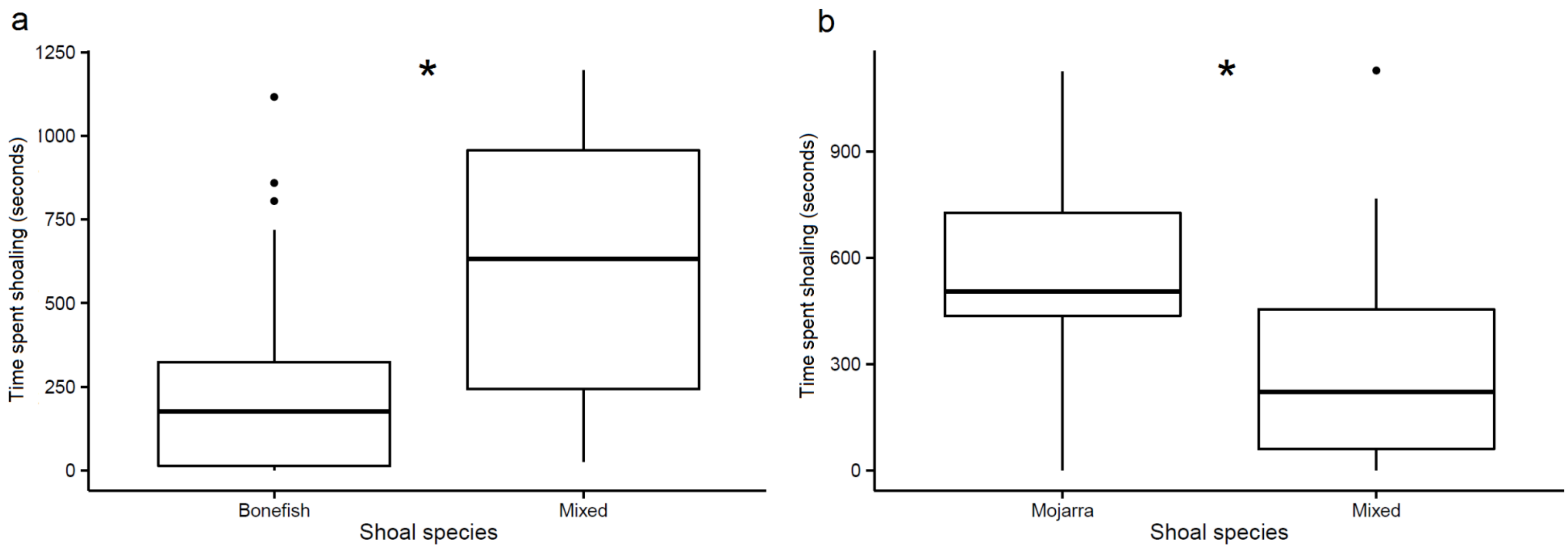

Fig. 3 Box-and-whisker plot of time focal bonefish spent (in seconds) shoaling with four bonefish or a mixed shoal of two bonefish and two mojarra (3a), and time focal bonefish spent (in seconds) shoaling with four mojarra or a mixed shoal of two bonefish and two mojarra(3b). The horizontal bold line within the box indicates the median of the data, while the boundaries of the box indicate the 25th and 75th percentiles, and the whiskers denote upper and lower data points outside the middle 50th percentile. Asterisks (*) denote significant differences between single species and mixed species shoals.