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

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

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26

**27 Abstract**

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

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

## 55 1. Introduction

56 Sociality is an integral part of animal behaviour across numerous taxa, commonly  
57 presenting itself in the form of group living (Krause and Ruxton 2002). Social behaviours of  
58 group living aid in enhanced foraging opportunities (Clark and Mangal 1986; Sazima et al.  
59 2007), predator avoidance and vigilance (Turner and Pitcher 1986; Elgar 1989), centralized  
60 information transfer (Dall and Johnstone 2002; Couzin et al. 2005), cooperative group hunting  
61 (Packer and Ruttan 1988; Pitman and Durban 2012), mate choice and cooperative breeding  
62 (Amundsen and Forsgren 2001; Clutton-Brock 2002), and reduce the energetic costs of  
63 movement (Weimerskirch et al. 2001; Marras et al. 2015). However, these benefits are often  
64 accompanied by various costs, including increased parasite and disease transmission, resource  
65 competition (i.e., food, shelter), mate infidelity, and conspicuousness (all reviewed in Krause and  
66 Ruxton 2002).

67 Heretofore, the most widely researched aspects of group living are those focused on the  
68 advantages of grouping, with a particular focus on foraging and anti-predator benefits (Székely et  
69 al. 1989; Krause and Ruxton 2002; Sridhar et al. 2009). Some associated fitness benefits of  
70 grouping are increased foraging success due to the collective food-finding abilities of a group, or  
71 by capitalizing and gaining information from individuals within the group that have more local  
72 foraging knowledge (Lachlan et al. 1998; Giraldeau and Beauchamp 1999). Furthermore,  
73 individuals may experience anti-predator benefits of attack abatement (a combination of predator  
74 avoidance and dilution effect), predator confusion, increased vigilance leading to greater  
75 information transfer, or a combination of some, or all, of these advantages (Dall and Johnstone  
76 2002). The use of these information sharing systems has a net benefit for individuals in groups,  
77 reducing the ecological uncertainty associated with life in the wild (e.g., food acquisition and  
78 danger avoidance; Stensland et al. 2003; Dall et al. 2005). In addition to the foraging and  
79 anti-predator benefits observed in intraspecific groups, the occurrence of interspecific  
80 (i.e., multi-species) groups also mediates some competitive costs of intraspecific group living  
81 (Labropoulou and Eleftheriou 1997; Bolnick 2001; Wolf and Weissing 2012).

82 Multi-species groups exist across nearly as many taxa as do single-species groups (Hoare  
83 et al. 2000) and generally receive similar benefits of enhanced food finding, increased vigilance,  
84 and social learning through information sharing, which is particularly crucial for animals whose  
85 prey have a patchy distribution (a common concern for both avian flocks and fish shoals;  
86 Lukoschek and McCormick 2000; Silverman et al. 2004). In addition to the same benefits  
87 derived from single-species groups, multi-species groups often have the added benefit of  
88 reducing many competitive costs of grouping (Krause and Ruxton 2002). The primary cost of  
89 grouping is resource competition; however, in multi-species groups, it is not uncommon for  
90 constituents to establish different niches, thereby increasing their fitness while reducing  
91 interspecific competition (Labropoulou and Eleftheriou 1997; Stewart et al. 2003; Krajewski et  
92 al. 2006). Multi-species grouping advantages may also be present in the form of prey restriction  
93 based on morphological differences in feeding apparatus, reducing interspecific competition  
94 (e.g., Aguirre et al. 2002), temporally divergent foraging activity (e.g., Albrecht and Gotelli  
95 2001), prey flushing and kleptoparasitism (e.g., Sridhar et al. 2009), and mate choice (e.g., Veen  
96 et al. 2001).

97 Fishes are commonly used in the study of animal social behaviour, with shoaling or  
98 schooling behaviour occurring in approximately 50% of all fish species at some point in their  
99 development (Radakov 1973; Pavlov and Kasumyan 2000). Multi-species shoaling has been  
100 widely documented in tropical marine species (Hoare and Krause 2003), with an emphasis on  
101 reef and nearshore systems, likely due to the logistical challenges of observing pelagic species in  
102 the wild (Wilson and Krause 2013; Domenici et al. 2014). As tropical nearshore marine habitats  
103 often serve as fish nurseries and spawning grounds (Beck et al. 2001; Laegdsgaard and Johnson  
104 2001), it is not unusual for a variety of species to be found using the same habitats (Nagelkerken  
105 et al. 2000; Layman and Silliman 2002) to enhance foraging opportunities while reducing  
106 predation risk from larger predators (Patterson and Whitfield 2000; Munsch et al. 2016).

107 Bonefish (*Albula vulpes*), the focal species in this study, are a teleost marine benthivore  
108 that reside in the nearshore tropical and sub-tropical waters of the Caribbean (Colborn et al.  
109 2001). As adults, bonefish are an economically important species in the Caribbean through the  
110 catch-and-release angling industry that is estimated to generate over \$154 billion USD in Florida  
111 and \$141 million USD annually in The Bahamas (Fedler 2009, 2010). Moreover, because of

112 their benthic feeding mode and relatively high regional abundance, they are thought to be  
113 important in structuring nearshore ecosystems (Murchie et al. 2013). Juvenile bonefish are found  
114 in nearshore habitats, as are mojarra (*Eucinostomus* spp.) and pilchard (*Harengula jaguana*;  
115 Sogard et al. 1989). Mojarra and pilchard are far more abundant in neritic shallow habitats than  
116 the juvenile life stage of near-threatened bonefish (Sogard et al. 1989; Adams et al. 2014), with  
117 each species occupying distinct regions of the water column and utilizing different foraging  
118 techniques (Vega-Cendejas et al. 1994; Layman and Silliman 2002). For example, juvenile  
119 bonefish and mojarra are demersal fish that primarily prey on benthic invertebrates found either  
120 buried in- or living-on the substrate and remain in water generally less than 2 m depth (Teixeira  
121 and Helmer 1998; Reis-Filho et al. 2011). In contrast, pilchard are zooplanktivorous, and as  
122 such, their time is primarily spent in the upper reaches of the water column in productive areas of  
123 1 to 5 m total water depth (Modde and Ross 1983; Pierce et al. 2001). These functional group  
124 characteristics also align with field observations and co-occurrence indices of mojarra and  
125 bonefish, while there is little observational evidence that pilchard also co-occur with these  
126 species (Christopher Haak, unpubl. data). Anecdotally, juvenile bonefish are primarily captured  
127 with large shoals of mojarra and rarely caught with aggregations of other fish that utilize similar  
128 habitat (Christopher Haak, unpubl. data), such as juvenile pilchard. This suggests that there may  
129 be more affiliative interactions between juvenile bonefish and mojarra than what might be  
130 expected based simply on sharing similar habitat preferences. Here we experimentally test these  
131 field observations by quantifying interspecific shoaling preferences for bonefish and several  
132 common congeners.

## 133 2. Methods

### 134 2.1 Capture, Transport, and Holding

135 The study was conducted in south Eleuthera, The Bahamas (N 24°50'05" and W  
136 76°20'32") at the Cape Eleuthera Institute (CEI) during June and July of 2015. Twenty-five  
137 juvenile bonefish (mean = 70.2 ± 15 mm SD fork length; range 50-110 mm) were collected from  
138 Rock Sound to be the 'focal fish' in the shoaling study (Fig. 1). Mojarra (mean = 67.8 ± 7.5 mm  
139 SD fork length; range 58-81 mm), juvenile pilchard (mean = 73.2 ± 7.1 mm SD fork length;  
140 range 62-90 mm), and additional juvenile bonefish (mean = 70.5 ± 9 mm SD fork length;

141 range 55-85 mm) were similarly collected; these three species made up the respective 'stimulus  
142 shoals'. Juvenile bonefish and mojarra were caught using spot seining techniques, whereby  
143 nearshore habitats (< 1 m depth) in Rock Sound were visually assessed, and when the species of  
144 interest were identified, a seine net (15.25 m length × 1.22 m height, 0.6 cm mesh size) was used  
145 to capture them. Pilchard were caught using a cast net (0.6 cm mesh) on-site at CEI. Captured  
146 fish were transferred into flow-through net pens (1.50 m length × 0.7 m width × 1.20 m height)  
147 while more fish were collected, before being relocated to coolers (0.9 m length × 0.35 m width ×  
148 0.2 m height; 63 L) on the boat for transportation (in the case of juvenile bonefish and mojarra).  
149 All fish transfers were done with care to limit exposing fish to air or causing net abrasion  
150 (Murchie et al. 2009; Cook et al. 2015). Upon arrival at the wet lab facility at CEI, the juvenile  
151 bonefish focal fish (herein referred to as 'focal fish') were held in individual pens  
152 (0.35 m length × 0.3 m width × 0.2 m height; 0.3 cm mesh size) in order for researchers to  
153 follow the same individuals throughout the entire study without needing to excessively handle or  
154 mark these fish. The individual holding pens were set in tanks (1.55 m diameter × 0.25 m height;  
155 472 L) that were aerated and continuously supplied with fresh seawater (10 L/min) at ambient  
156 water temperatures ( $28.6 \pm 2.4$  °C SD), thus did not induce visual or olfactory isolation (Wright  
157 and Krause 2006). The three species of stimulus fish were held in separate tanks with their  
158 conspecifics (1.55 m diameter × 0.25 m height; 472 L). All fish were held for a minimum of  
159 48 hr prior to experimentation.

## 160 *2.2 Shoaling Trials*

161 Each focal fish ( $n = 25$ ) was observed in four trials, with a total of ten stimulus shoal  
162 combinations over the four trials. Focal fish were given the option of shoaling with the following  
163 groups of fish(es): (i) conspecifics or mojarra; (ii) conspecifics or pilchard; (iii) conspecifics or a  
164 mixed shoal with equal mojarra and bonefish; and (iv) mojarra or a mixed shoal with equal  
165 mojarra and bonefish. During the (i) conspecific or mojarra as well as the (ii) conspecific or  
166 pilchard trials, focal fish shoaling preference was examined with four stimulus shoal  
167 combinations, with either one-, two-, four-, or eight- fish in each stimulus shoal (i.e.,  $1 \times 1$ ,  $2 \times 2$ ,  
168  $4 \times 4$ ,  $8 \times 8$ ); that is, one mojarra or one bonefish, two mojarra or two bonefish, one pilchard or one  
169 bonefish, and so on. Furthermore, this study aimed to determine the shoaling tendencies of focal  
170 fish when given the choice of either (iii) four conspecifics or a mixed shoal of two conspecifics

171 and two mojarra (i.e., a 4×4 design); conversely, (iv) four mojarra or a shoal of two conspecifics  
172 and two mojarra (herein referred to as a ‘mixed shoal’).

173 A Y-maze (0.7 m arm lengths × 0.18 m width × 0.25 m height) was utilized as the  
174 experimental arena. Methods were largely modified from Wright and Krause (2006). One arm of  
175 the Y-maze was the focal fish release area, with the other two arms housing the two stimulus  
176 shoal options. Each stimulus shoal was in a one-way glass transparent bin (18 cm length × 18 cm  
177 width × 20 cm height; 6.5 L) at the end of each respective arm, with a daylight emulating light  
178 bulb (Lighting Science Group, Satellite Beach, Florida, United States of America; 60 watt)  
179 30 cm above each stimulus fish bin for greater efficacy of the one-way glass (modifications  
180 made from Wright and Krause 2006). There was no olfactory exchange between the focal fish  
181 and stimulus shoals; due to the one-way glass, focal fish were able to see the stimulus shoals  
182 without the opposite occurring (see Wright and Krause 2006). Stimulus shoals were given 1 hr to  
183 acclimate to holding bins prior to experimentation. A focal fish was removed from its individual  
184 holding pen and first placed in an opaque beaker (14 cm diameter × 15 cm height; 2.3 L) with  
185 water from the test tank and left to acclimate for 10 min. After 10 min, the fish was gently  
186 poured into a transparent cylinder (15 cm diameter × 30 cm height) in the empty arm of the Y-  
187 maze and left to acclimate for another 5 min. Following this final acclimatization period, the  
188 focal fish was released and observed via live video feed for 20 min (DVR9-4200 9 Channel  
189 960H Digital Video Recorder and PRO-642 Cameras; Swann Communications U.S.A Inc.; Santa  
190 Fe Springs, California, United States of America). The observer recorded seconds spent close-  
191 shoaling with either stimulus shoal, quantified as being within approximately two body lengths  
192 (20 cm) of the stimulus shoal (Pitcher 1986). After the 20 min trial, the focal fish was moved  
193 back to its individual pen and the process was repeated with another randomly selected focal  
194 fish. Stimulus shoal position in the Y-maze was changed every five trials, with stimulus shoal  
195 individuals also being changed occasionally to prevent shoaling bias (Wright and Krause 2006);  
196 the focal fish were tested in a random order at the start of each day.

### 197 *2.3 Statistical Approach*

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

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

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

### 213 3. Results

#### 214 *3.1 Bonefish or Mojarra Stimulus Shoals*

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

#### 224 *3.2 Bonefish or Pilchard Stimulus Shoals*

225 Juvenile bonefish generally tended to spend a similar amount of time with both  
226 conspecifics and pilchard (Fig. 2b). Focal fish spent nearly the same amount of time shoaling  
227 with conspecifics, pilchard, and non-shoaling. It was common for focal fish to swim around the

228 experimental arena to all of the arms several times (i.e., entering and exiting shoaling zones),  
229 often without making a discernible choice to shoal with either shoal for a substantial amount of  
230 time. When comparing focal fish shoaling tendencies between conspecifics or pilchard, there was  
231 no significant interaction between shoal species and shoal size ( $X^2 = 2.8$ ,  $p = 0.42$ ), nor was there  
232 a significant effect of shoal species ( $X^2 = 0.06$ ,  $p = 0.8$ ) or shoal size ( $X^2 = 0.5$ ,  $p = 0.9$ ) on  
233 juvenile bonefish shoal choice (Fig. 2b).

### 234 *3.3 Bonefish or Mixed Stimulus Shoals*

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

### 242 *3.4 Mojarra or Mixed Stimulus Shoals*

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

## 250 4. Discussion

251 The results of this study suggest that juvenile bonefish prefer to actively shoal with  
252 mojarra rather than other species options afforded to them throughout the experiment. The four  
253 treatments in which focal fish were given a shoaling choice were: (i) bonefish or mojarra (four  
254 trials;  $1 \times 1$ ,  $2 \times 2$ ,  $4 \times 4$ ,  $8 \times 8$ ), (ii) bonefish or pilchard (four trials;  $1 \times 1$ ,  $2 \times 2$ ,  $4 \times 4$ ,  $8 \times 8$ ), (iii) four  
255 bonefish or a mixed shoal (two mojarra and two bonefish), and lastly (iv) four mojarra or a

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

281         Anti-predator and foraging benefits are commonly attributed as the key advantages of  
282 grouping (Morse 1977; Krause and Ruxton 2002; Sridhar et al. 2009). Anti-predator advantages  
283 exist in the context of attack abatement, predator confusion, and increased vigilance (Pitcher and  
284 Parrish 1993; Turner and Montgomery 2003). Another consideration in predator-prey models is  
285 the ‘oddity effect’, whereby phenotypically dissimilar fish are more easily and readily targeted  
286 by predators (Landeau and Terborgh 1986). In the context of this study, the existence of the

287 oddity effect would suggest that juvenile bonefish should prefer to shoal with conspecifics, or to  
288 a lesser extent, pilchard (more phenotypically similar than mojarra). Presumably, shoaling with  
289 either conspecifics or pilchard would lessen the oddity effect, thereby lowering predation risks  
290 for individuals (Landeau and Terborgh 1986); however, this was not the case in this study. Not  
291 only did juvenile bonefish show no preference during the treatment with either pilchard or  
292 conspecifics, they also showed little preference for conspecifics throughout the entirety of the  
293 experiment. Other possible mechanisms may be linked to similarities in foraging modes,  
294 microhabitat usage, and spatial niche overlap leading to closer associations between juvenile  
295 bonefish and mojarra.

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

310 Evidence of foraging modes and microhabitat usage suggests that mojarra may be an  
311 attractive shoal choice for juvenile bonefish. However, these attributes alone are not necessarily  
312 sufficient to explain bonefish shoaling preference for mojarra and not conspecifics. In addition to  
313 their spatial overlap, mojarra have also demonstrated an auditory specialization which may allow  
314 for superior prey-finding (Parmentier et al. 2011). Juvenile bonefish and mojarra may also limit  
315 resource competition through differences in the morphology of their feeding apparatuses  
316 (Zahorcsak et al. 2000; Snodgrass et al. 2008). Mojarra possess an auditory adaptation whereby

317 their swim bladder has a specialized connection to the inner ear, and a modified cone in their  
318 pelvic fin where it sits, all acting to enhance the acoustic amplification provided by the swim  
319 bladder (Parmentier et al. 2011). It has been hypothesized that this adaptation is not used for  
320 communication, but instead may be used to hear benthic invertebrate prey below the surface of  
321 the substrate (Braun and Grande 2008; Parmentier et al. 2011). This auditory specialization  
322 would be beneficial to the foraging success of nearby bonefish, thereby making mojarra an  
323 advantageous shoal mate.

324           Mojarra may suffer from the associated cost of increased competition due to their  
325 auditory specialization if shoal mates are kleptoparasitic (e.g., Webster and Hart 2006); however,  
326 their association with juvenile bonefish may not result in increased competition due to potential  
327 trophic resource partitioning. Using isotopic analysis, Haak (unpubl. data) determined that  
328 although juvenile bonefish and mojarra utilize similar habitats and are oftentimes caught  
329 together, they appear to have minimal dietary overlap, and instead satisfy slightly different  
330 trophic niches. Resource niche partitioning is a common occurrence in both avian and fish  
331 communities, and has been strongly supported in the literature (e.g., Labropoulou and  
332 Eleftheriou 1997; Radford and Du Plessis 2003; Krajewski et al. 2006; Harrison and Whitehouse  
333 2011). Although this was neither explicitly examined in Haak (unpubl. data), nor in the current  
334 study, an explanation for the disparity in prey types may be due in part to the morphological  
335 differences in their feeding apparatus (Vega-Cendejas et al. 1994). Mojarra have a protractable  
336 mouth which is able to extend and protrude into the substrate (Sazima 1986; Zahorcsak et al.  
337 2000), whereas bonefish have a hard palette designed to grind the shells of invertebrates  
338 (Alexander 1961). Since bonefish only have a limited ability to protract their mouths and  
339 primarily rely on burrowing their snouts into the substrate to capture prey, they may consume  
340 prey closer to the surface of the substrate (Snodgrass et al. 2008; Brownscombe et al. 2014),  
341 thereby excluding them from mojarra prey types.

342           There are inherent difficulties associated with studying wild fish populations (Ostrander  
343 2000); it is important to note that juvenile bonefish are present in low densities and are difficult  
344 to locate and capture, thus resulting in the current experimental design and limited sample size.  
345 Indeed, shoals of mojarra and juvenile bonefish in nature are substantially larger (often 10s to  
346 even 100s of individuals) than what was able to test experimentally. Nonetheless, our results

347 reveal that there are strong affiliative interactions between mojarra and bonefish. This study was  
348 the first to explore the shoaling preferences of juvenile bonefish, and as such, the plausible  
349 behavioural and evolutionary drivers supporting these multi-species associations are still  
350 speculative. To begin exploring these possible drivers, future studies should possibly shift to  
351 become more ‘mojarra-centric’, rather than the current model. This shift would allow for further  
352 exploration of the notion that mojarra behave as a nuclear species for various nearshore juvenile  
353 fish species (an observation of Christopher Haak, unpubl. data), thus driving the foraging activity  
354 of interspecific shoal mates (Lukoschek and McCormick 2000). There is a body of evidence  
355 within the literature that suggests nuclear species may be more vigilant (e.g., Dolby and Grubb  
356 1998; Ragusa-Netto 2002; Sazima et al. 2006), thereby providing their associate counterparts  
357 with the information to reduce predation, and thus their ecological uncertainty (Danchin et al.  
358 2004; Dall et al. 2005). Future behavioural experiments could ascertain whether there is the  
359 occurrence of the ‘oddity effect’ resulting in juvenile bonefish being a preferred prey type, or  
360 whether their superficial similarities to mojarra can be attributed to this selective pressure  
361 (Landeau and Terborgh 1986; Krause and Ruxton 2002; Sazima 2002). Lastly, future research  
362 should consider the possibility of mojarra incurring negative consequences from juvenile  
363 bonefish shoaling with them (i.e., kleptoparasitism, increased detection from predators, etc.).

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

375

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384

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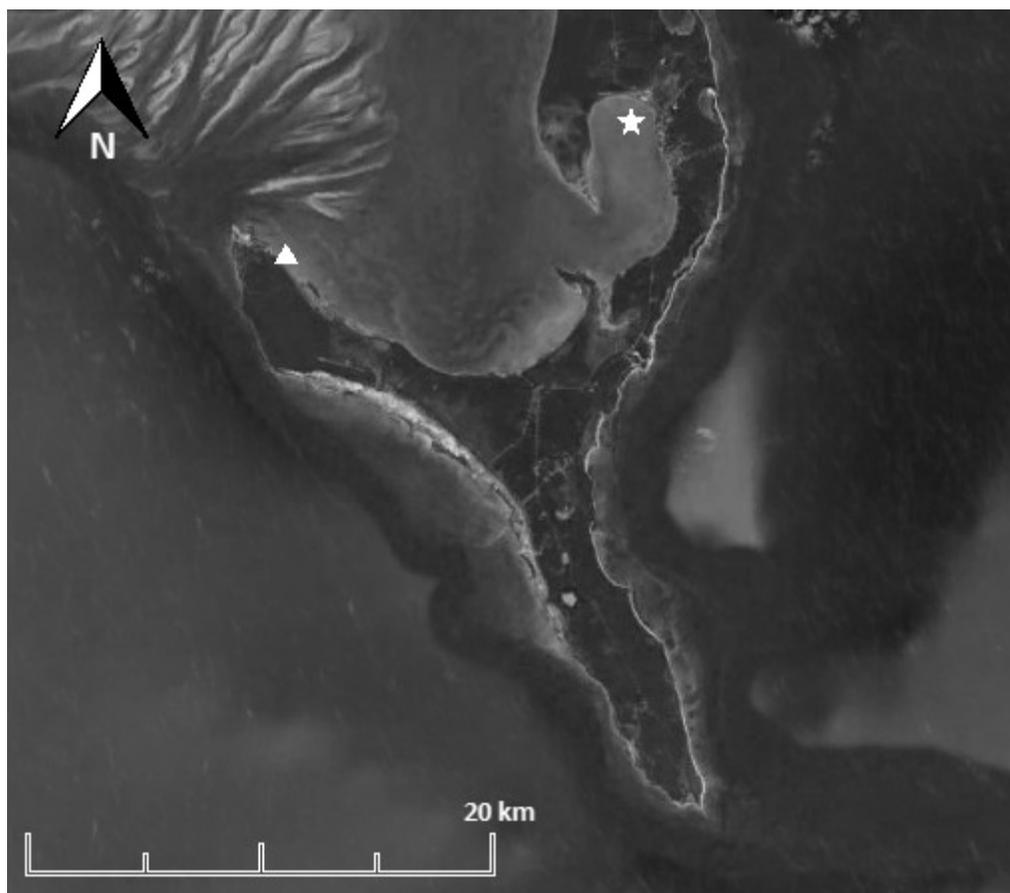
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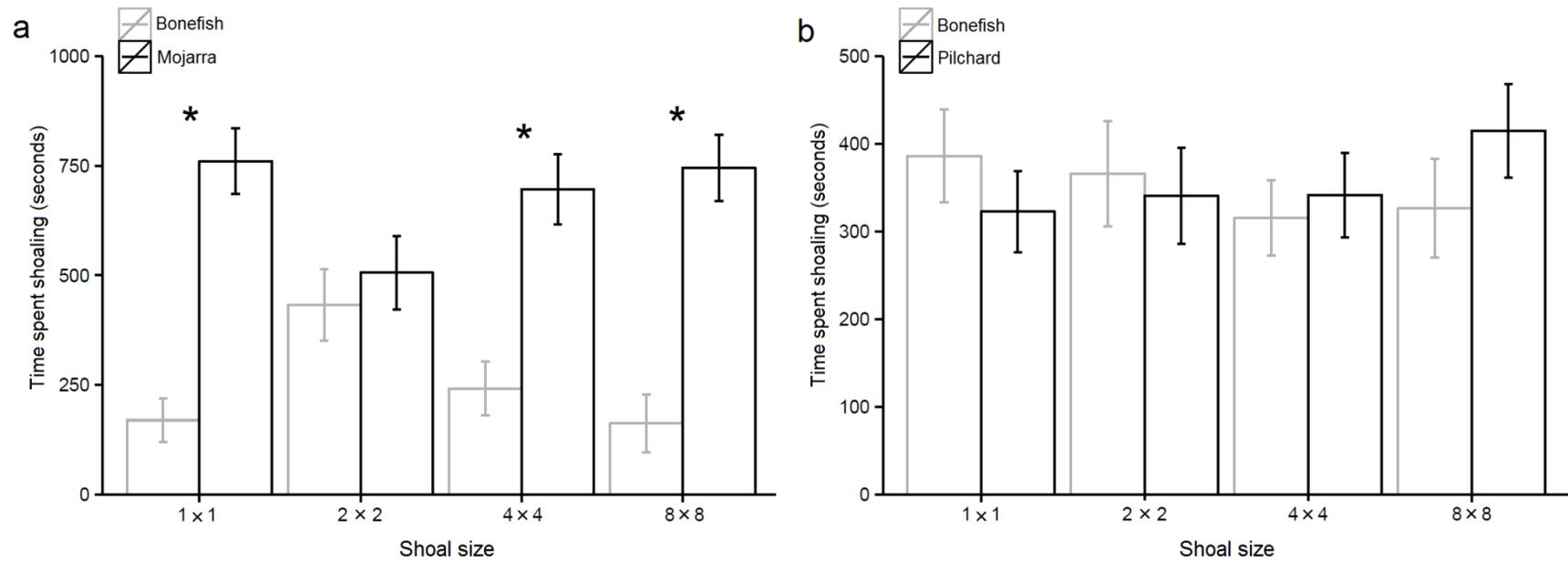
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556 Figures

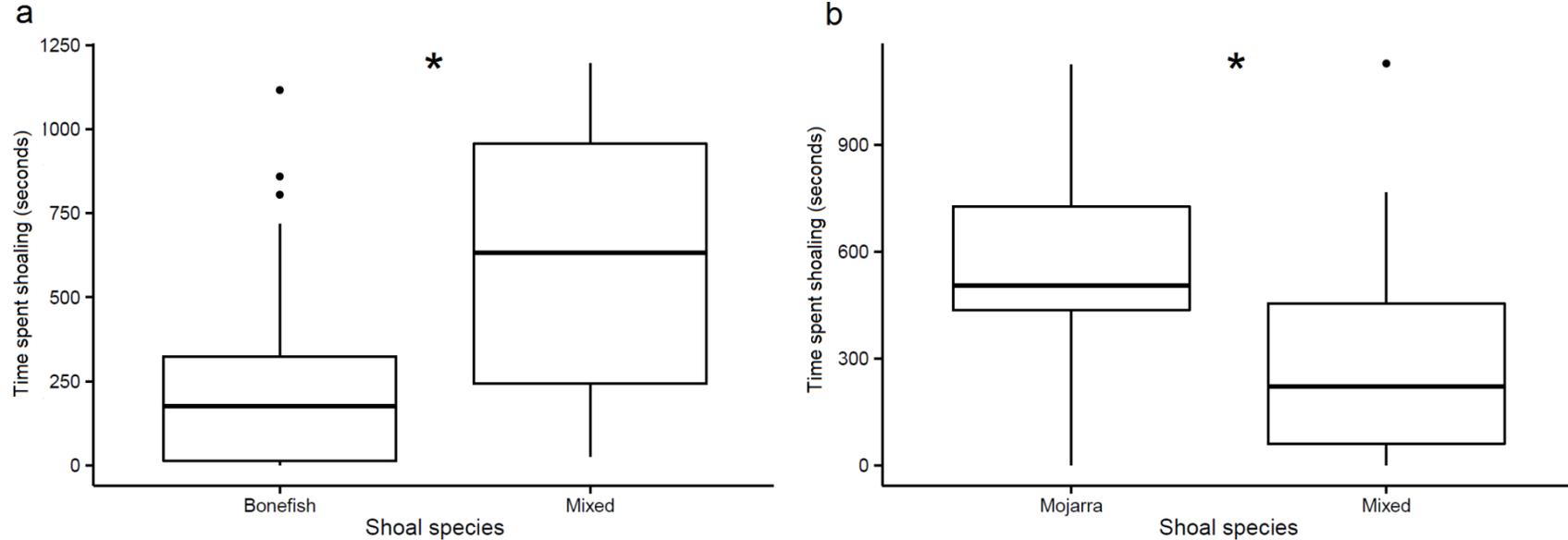


557

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



**Fig. 2** Mean responses ( $\pm$ 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 1x1, 2x2, 4x4, 8x8. 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 25<sup>th</sup> and 75<sup>th</sup> percentiles, and the whiskers denote upper and lower data points outside the middle 50<sup>th</sup> percentile. Asterisks (\*) denote significant differences between single species and mixed species shoals.