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1 **A meta-analysis of fish behavioural reaction to underwater human presence**

2

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24 **Running Title: Fish flight distance toward humans**

25

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28

29 **Abstract**

30 In an increasingly anthropic world, humans have profound impacts on the distribution
31 and behaviour of marine fishes. The increased human presence has modified fishes'
32 antipredator behavioural responses, and consequently flight decisions, as a function of
33 their changed perceptions of risk. Understanding how fish react to human presence can
34 help identify the most vulnerable functional groups/species and estimate impacts caused
35 by human disturbance. Shoal and body size are known to influence fish flight initiation
36 distance (FID; the distance between the predator and prey when the prey begins to
37 escape), however few studies attempt to test the moderators of these relationships. Here
38 we present a comprehensive meta-analysis evaluating FID of fish in response to human
39 presence. Specifically, we investigated six candidate moderators that could influence the
40 relationship between FID with shoal and body size. Our results showed that individual
41 fish size was strongly and positively correlated with FID and the most important
42 moderator that explained the variance in individual body size-FID relationship was
43 shoaling behaviour. However, and somehow surprisingly, we detected no significant
44 relationship between shoal size and FID. We discuss how these results can inform the
45 development of fish conservation strategies and ultimately assist in the management of
46 marine protected areas.

47

48 **Keywords:** antipredator behaviour; economic escape theory; fish size; flight initiation
49 distance; shoal size

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71 **1. INTRODUCTION**

72 Avoiding predators is an important part of an animal's life that has profound influences
73 on morphology, metabolism and behaviour (Ferrari et al., 2015; Arnett & Kinnison, 2017;
74 Dalton, Tracy, Hairston Jr, & Flecker, 2018). Avoiding predators may involves
75 camouflage or other physiological mechanisms (e.g., toxicity), but it commonly occurs
76 by escaping (Langridge, Broom, & Osorio, 2007). While often effective, fleeing a
77 predator is not without costs because fleeing interrupts the current activity of the animal,
78 and has both energetic and time costs (Ydenberg & Dill, 1986; Blanchard, Blanchard,
79 Rodgers, & Weiss, 1990).

80

81 The decision when to flee is based on a cost-benefit trade-off. Prey should have a greater
82 flight initiation distance (FID—the distance between the predator and prey when the prey
83 begins to escape) if they face increased risk or if energetic or opportunity costs of leaving
84 is low (Ydenberg and Dill 1986; Cooper Jr and Frederick 2007). FID is one of the most
85 commonly-studied variables in the animal anti-predatory literature (Cooper Jr &
86 Blumstein, 2015; Samia, Blumstein, et al. 2016; Geffroy, Sadoul, & Ellenberg, 2017) and
87 sheds light on species' cognitive abilities and the evolutionary history of predator-prey
88 interactions (Blumstein 2006; Cooper Jr *et al.* 2014; Møller and Erritzøe 2014; Samia *et*
89 *al.* 2015a). Additionally, due to its ease-of-use and conceptual clarity, FID is an attractive
90 metric to routinely and straightforwardly evaluate the capacity of prey animals to avoid
91 predators. Consequently, it has recently become used to evaluate anthropogenic impacts
92 on fishes (Januchowski-Hartley, Graham, Cinner, & Russ, 2015; Bergseth, Williamson,
93 et al., 2017; Geffroy, Sadoul, et al., 2018; Sbragaglia et al., 2018) .

94

95 In fishes, FID was first quantified in Atlantic Salmon (*Salmo salar*, Salmonidae) and

96 brook trout (*Salvelinus fontinalis*, Salmonidae) based on underwater observations
97 (Keenleyside, 1962). About 10 years later, the first experimental FID study in controlled
98 conditions was performed on zebrafish (*Danio rerio*, Cyprinidae) (Dill, 1974). Since then,
99 a plethora of studies have been conducted to investigate FID in fishes and assess the
100 influence of different factors on fishes' response to threats, most notably group (shoal)
101 size and body size.

102

103 An important intrinsic driver of FID of fish is body size. Several studies have identified
104 the positive link between individual fish size and FID in exploited populations (Gotanda,
105 Turgeon, & Kramer, 2009; Januchowski-Hartley, Graham, Feary, Morove, & Cinner,
106 2011; Benevides, Nunes, Costa, & Sampaio, 2016; Sbragaglia et al., 2018). A seemingly
107 reasonable assumption to explain this correlation involves fish fitness-related traits (i.e.,
108 age and size; Uusi-Heikkilä et al., 2015). First, larger fish are often the preferential target
109 of fisherman, thus they are more responsive to the threat (Johnston *et al.* 2013; Tsikliras
110 & Polymeros 2014). Second, larger fish are generally older, so assuming a learning
111 mechanism, they have more experience with threats (Samia et al., 2016). Third, the
112 relative fitness (in terms of reproductive output) is much higher in larger individuals than
113 smaller ones. For example, a large female produces disproportionately more offspring than
114 the same body mass' worth of smaller females (Barneche, Robertson, White, & Marshall,
115 2018), and also produces larvae with a greater chance of survival (Birkeland & Dayton,
116 2005). Thus, the correlation between FID and body size is of paramount importance in
117 characterizing fish response towards humans. Protecting old and big fishes has become a
118 priority for fisheries management and conservation policies (Jørgensen et al., 2007;
119 Collette et al., 2011; Gwinn et al., 2015).

120

121 In social animals, the accuracy of a decision is expected to increase with number of
122 individuals within a group. It happens because individuals in groups have a higher ability
123 to gather and integrate information than individuals alone (Couzin, 2009). In fishes, the
124 “many eyes” hypothesis (Lima, 1995) predicts that fishes in larger groups/shoals would
125 escape sooner (have a larger FID) since having more eyes should increase the probability
126 of detecting threats (Seghers, 1981; Domenici & Batty, 1997; Semeniuk & Dill, 2005).
127 Indeed, collective vigilance in fish shoals has been shown to significantly improve
128 detection (Ward, Herbert-Read, Sumpter, & Krause, 2011a). However, the evidence of
129 this occurring *in situ* is mixed (e.g., Januchowski-Hartley et al., 2011) and a previous
130 meta-analysis identified a weak negative effect of shoal size on FID in fishes (Stankowich
131 & Blumstein, 2005). Therefore, the extent to which FID correlates with shoal size and
132 how it generalizes across fish species remains unclear.

133

134 In addition to the negative impacts of harvesting activities some fish populations are
135 constantly exposed to a massive presence of tourists which may create a suite of
136 physiological and behavioural consequences (Geffroy et al., 2015; Geffroy, Sadoul, et al.,
137 2018). Indeed, the popularity of both snorkelling and diving activities has massively
138 increased over the past several decades, and there are an estimated 22 million divers
139 worldwide (Dimmock & Cummins, 2013). Recent studies demonstrate that SCUBA
140 diving has impacted fish for the past 60 years (Rowe & Santos, 2016) and spear-fishing
141 has also increased, often preferentially targeting the largest individuals (Giglio, Bender,
142 Zapelini, & Ferreira, 2017). With increasing anthropogenic impacts, coastal ecosystems,
143 particularly rocky and coral reef, are arguably the most impacted by both divers and
144 fishers. Traditional methods employed to quantify the human “footprint” on fish
145 populations focuses on fish biomass assessment at both global (Cinner et al., 2018) and

146 local (e.g., Goetze et al., 2017) scales. However, biomass estimates are often highly
147 variable (McClanahan, Graham, Calnan, & MacNeil, 2007), which can mask both
148 positive effects of management and lack of effect or compliance. Nevertheless, if FID
149 varies consistently with both individual size and shoal size in different fish species, it has
150 the potential to be a good proxy for the management status or intensity of human
151 disturbance of a focal population (Goetze et al., 2017; Benevides, Pinto, Nunes, &
152 Sampaio, 2018).

153

154 Thus, an understanding of how fish react to human presence can be valuable information
155 to help manage fish populations. Here we present a comprehensive meta-analysis
156 evaluating FID of fish in response to humans, taking advantage of the surge of recent
157 studies on this topic. We aimed to understand the body-size and the shoal-size effect on
158 fish escape behaviour. Based on existing literature, we predicted that both body size and
159 shoal size would have positive relationships with FID (i.e., larger individual fish would
160 have longer FIDs and fish occurring in larger shoals will have longer FIDs). We also
161 investigated key traits related to species' morphology, ecology, life history and natural
162 history that should modulate these relationships (see hypotheses in Table 1). Finally, we
163 discuss our findings in a context of increased human presence on marine coastal
164 ecosystems, focusing on identifying fishes that are most vulnerable.

165

166 **2. METHODS**

167 2.1 Literature survey

168 We used the Web of Science and Google Scholar databases to search for papers published
169 before 1 April 2016. We used the following terms in our search in these databases: “fish*”
170 AND (“flight initiation distance” OR “flight distance” OR “escape distance” OR

171 “approach distance” OR “flushing distance” OR “response distance”). We checked all
172 references of the retained papers to identify studies not located by our key-words survey.
173 We also searched for relevant papers cited by the main reviews about escape theory
174 (Ydenberg and Dill 1986; Stankowich and Blumstein 2005; Cooper Jr and Blumstein
175 2015). Non-published data were also included in the meta-analysis (see Appendix S1).
176 The inclusion criterium was that studies must have tested the effect of body size and/or
177 group/shoal size on FID of fishes approached by humans. A PRISMA diagram describing
178 our literature search is available in Appendix S2. The data set of the fish individual body
179 size-FID meta-analysis consisted of 131 effect-sizes from 11 studies across 31 species
180 distributed across 12 families (Appendix S1). The group size-FID meta-analysis consisted
181 of 62 effect-sizes from 5 studies across 22 species distributed across 7 families (Appendix
182 S1).

183

184 2.2 Estimating effect sizes

185 We used Pearson’s product-moment correlation coefficient, r , as our measure of effect
186 size. Here, r represents the magnitude of the fish individual body size-FID relationship
187 and the fish shoal size-FID relationship. Positive r values represent a positive body size-
188 FID relationship (i.e., that larger individuals flee sooner from humans than small
189 individuals) and a positive shoal size-FID relationship (i.e., that individuals in larger
190 shoals flee sooner from humans than solitary individuals or those in smaller shoals).
191 Conversely, negative r values represent a negative individual body size-FID relationship
192 (i.e., that smaller individuals flee sooner from humans than larger individuals) and a
193 negative shoal size-FID relationship (i.e., that solitary individuals or those in smaller
194 shoals flee sooner from humans than individuals in larger shoals). When raw data were
195 not available to directly calculate r , we calculated r in the following order of preference

196 from published statistical results: 1) published correlation coefficients; 2) *t* or *F* statistics;
197 or 3) the exact *P*-values reported with sample sizes (Koricheva, Gurevitch, & Mengersen,
198 2013). We contacted authors directly for missing data (see Acknowledgements for
199 details). In the ecological literature *r*-values of 0.1, 0.3, and 0.5 are usually considered to
200 reflect small, medium, and large effect sizes, respectively (J. Cohen, 1992; Jennions &
201 Møller, 2002). For analysis, *r*-values were transformed to Fisher's *z* to improve normality
202 of data (Koricheva, Gurevitch, & Mengersen, 2013).

203

204 We used the raw data to calculate the effect sizes from Januchowski-Hartley's studies
205 (Januchowski-Hartley et al., 2011; Januchowski-Hartley, Nash, & Lawton, 2012;
206 Januchowski-Hartley, Graham, Cinner, & Russ, 2013). We therefore opted to include
207 only those effect sizes with $N \geq 10$ to avoid incorporating into the meta-analysis effect
208 sizes that were not well supported. Unlike fixed-effect meta-analysis, random-effect
209 meta-analysis (like the one performed here; see below) tend to homogenise the weight of
210 individual effect sizes on the overall mean effect size independently of their sample size
211 (Borenstein, Hedges, Higgins, & Rothstein, 2009; Koricheva, Gurevitch, & Mengersen,
212 2013). By excluding observations with $N < 10$ we avoid incorporating noise into the
213 analysis, and thus our results should be viewed as conservative.

214

215 2.3 Meta-analysis

216 We used multilevel mixed-effects meta-analysis to test for both overall effect sizes and
217 the importance of our predictors (Nakagawa & Santos, 2012). The overall effect sizes
218 (i.e., mean of the effect sizes weighted by the inverse of their variance) were considered
219 significant if their 95% confidence intervals (CI) did not include zero (Koricheva et al.,
220 2013).

221

222 We used model selection to determine which random factors should be included in each
223 meta-analysis (Nakagawa & Santos, 2012). We controlled for non-independence of effect
224 sizes within studies by including “study identity” as a random-factor in the body size-FID
225 model (Appendix 3). Data could exhibit non-independence caused either by phylogenetic
226 inertia or by multiple estimates per species, the model selection showed that inclusion of
227 “phylogeny” and/or “species identity” as additional random-effects did not improve the
228 model (Appendix 3). Indeed, a model without random factors was the most parsimonious
229 for the group size-FID meta-analysis (Appendix 3).

230

231 The phylogenetic tree of the species was implemented using
232 <http://phylot.biobyte.de/index.html> based on the most recent taxonomy available in NCBI
233 (<https://www.ncbi.nlm.nih.gov/guide/taxonomy/>). When a species in our data set was not
234 included in this broad phylogeny, we used a closely related (congeneric) species as a
235 substitute (Garamszegi, 2014). Species were included into a polytomic clade when the
236 relationship among species was unknown (Garamszegi, 2014). The trees were pruned
237 using the R package *picante* 1.6-2 (Kembel et al., 2010). The phylogenetic tree of the taxa
238 included in the study is provided in Appendix 4.

239

240 We used I^2 index as a measure of heterogeneity in the effect sizes in which the value
241 represents the proportion of total variation in data that is not due to sampling error (0%--
242 all sampling error; 100%--no sampling error) (Higgins, Thompson, Deeks, & Altman,
243 2003). We used an extended version of I^2 that partitions the total heterogeneity amongst
244 different sources: variation explained by study identity and by the residual variation (i.e.,
245 that which remained to be explained by the predictor variables; (Nakagawa & Santos,

246 2012). We calculated the degree of phylogenetic signal in our effect size estimates using
247 the phylogenetic heritability index, H^2 , which is the variance attributable to phylogeny in
248 relation to the total variance expected in the data (Nakagawa & Santos, 2012). When the
249 unit of analysis is species, H^2 is equivalent to Pagel's λ (Pagel, 1999), in which higher
250 values are associated with stronger phylogenetic signals. Primary studies can suffer from
251 publication bias, where studies with low sample size are more prone to be rejected due to
252 their higher probability of not finding significant effects (Egger, Smith, Schneider, &
253 Minder, 1997; Koricheva, Gurevitch, & Mengersen, 2013). We checked for publication
254 bias using Egger's regression, in which intercepts significantly different from zero
255 suggest potential publication bias (Egger et al., 1997). To overcome the non-independent
256 nature of our data, we also applied the Egger's regression test on the meta-analytic
257 residuals (Nakagawa & Santos, 2012). Analyses were conducted using the *metafor* R
258 package v.2.0-0 (Viechtbauer, 2010).

259

260 2.4 Moderators

261 A growing body of literature explains how species' morphology, life history and natural
262 history traits, as well as environmental and ecological traits could impact the anti-
263 predatory response of animals (Blumstein, 2006; Samia et al., 2015b; Samia, Nakagawa,
264 Nomura, Rangel, & Blumstein, 2015; Samia et al., 2016). Here, we focused on six factors
265 that we hypothesise that could impact the magnitude and direction of both individual body
266 size-FID relationship and shoal size-FID relationship. Namely, species' shoaling
267 behaviour (solitary *vs.* grouped), mean body size (cm), longevity (years), species' trophic
268 level (continuous variable varying from 2 to 4: the lower the number, the more basal is
269 the species in a trophic chain), species' habitat use (demersal *vs.* pelagic) and protection
270 status of the area (populations inside *vs.* outside protected areas). See Table 1 for rationale

271 for each moderator. The variables shoaling behaviour, body size and protected area data
272 were obtained from the primary papers. The remaining information were extracted from
273 the FishBase website (<http://www.fishbase.org>). Importantly, multi-collinearity was not
274 an issue for our selected moderators (variance inflation factors < 1.15, below the
275 suggested threshold of 3, (Zuur, Ieno, & Elphick, 2010).

276

277 Previous evidence shows that a predator's approach speed and starting distance (i.e.,
278 predator-prey distance when the approach begins) could affect FID (Blumstein, 2003;
279 Samia, Nomura, & Blumstein, 2013; Cooper Jr, Samia, & Blumstein, 2015). Numerous
280 primary studies did not report these parameters, while those that did standardised
281 approach speed and starting distance at a fixed value. For those studies providing the
282 information, we detected low variation for both the approach speed (Individual body size-
283 FID meta-analysis = 64.00 ± 1.26 cm/s (mean \pm s.e.), N = 120; Shoal size-FID meta-
284 analysis: 76.78 ± 0.64 cm/s, N = 59) and the starting distance used by experimenters
285 (Individual body size-FID meta-analysis: 8.22 ± 0.22 m, N = 67; Shoal size-FID meta-
286 analysis: 7.91 ± 0.09 m, N = 55). Furthermore, separate meta-regressions between the
287 effect size and both approach speed and starting distance showed absence of an effect
288 (Individual body size-FID meta-analysis – approach speed: $b = -0.006$, $P = 0.633$, starting
289 distance: $b = 0.008$, $P = 0.876$; Shoal size-FID meta-analysis – approach speed: $b = -$
290 0.004 , $P = 0.597$, starting distance: $b = -0.039$, $P = 0.165$). These results imply that
291 methodical differences among studies were not important to explain variation in the data
292 and were thus not included in our statistical models.

293

294 2.5 Multi-model inference

295 We used a multi-model inference approach based on Akaike's criteria corrected for small

296 sample size (AICc) (Burnham & Anderson, 2002). To calculate the relative importance
297 of each predictor, we first assessed the relative strengths of each candidate model by
298 calculating its Akaike weight, to identify the most parsimonious model. A constant term
299 (intercept) was included in all models. We estimated the importance of a predictor by
300 summing the Akaike weights of all models in which that candidate variable appeared.
301 This allowed to rank predictors in order of importance (Burnham & Anderson, 2002). We
302 finally used a model averaging approach to estimate model parameters (Burnham &
303 Anderson, 2002). Multi-model analyses were conducted using the *MuMIn* R package v.
304 1.40.0 (Barton, 2014).

305

306 **3. RESULTS**

307 3.1 Meta-analysis of the effect of individual body size on flight initiation distance of fish

308 Overall, individual fish size was strongly and positively correlated with FID (Fisher's z
309 = 0.777, CI = 0.518 – 1.036, Figure 1). We found considerable variation among effect
310 sizes, with most of them having some variation that was explained by moderators (I^2_{total}
311 = 92.99%, I^2_{studies} = 12.09%, I^2_{residual} = 80.90%). The amount of heterogeneity found
312 matches with that found in most ecological and evolutionary studies (Senior et al. 2016).
313 There was a weak phylogenetic signal in the relationship between body size and FID (H^2
314 = 2.92%). We found no evidence that potential publication bias affected the results
315 (Egger's regression of effect sizes: Intercept = -1.256, P = 0.250; Egger's regression of
316 meta-analytic residuals: Intercept = -0.902, P = 0.397; Figure 2).

317

318 The multi-model inference indicated that shoaling behaviour was the most important
319 predictor of the magnitude of body size-FID relationship (Table 2). Species that shoal
320 display a stronger and more positive individual body size-FID relationship compared to

321 solitary species (Table 2 and Figure 3). The importance index of shoaling behaviour was
322 two-times larger than the second most important variable, the species' body size (Table
323 2, Figure 3). Species' body size was followed by longevity, trophic level, environment
324 and protected area with modest differences in their importance indexes (Table 2, Figure
325 3).

326

327 3.2 Meta-analysis of the effect of group size on flight initiation distance of fish

328 We found that shoal size had no effect on fish FID (Fisher's $z = 0.027$, $CI = -0.037 -$
329 0.092 , Figure 4). The I^2 index indicated no variation among effect sizes, leaving no
330 variation to be explaining by moderators ($I^2_{total} = 0\%$, $I^2_{residual} = 0\%$). In fact, only two of
331 62 effect sizes differed significantly from zero (Figure 4). The absence of residual
332 variation in the shoal size meta-analysis makes it unnecessary to further explore the
333 potential effect of moderators. There was no phylogenetic signal in the relationship
334 between shoal size and FID ($H^2 = 0\%$). We found evidence of publication bias in the
335 group size-FID meta-analysis (Egger's regression of effect sizes: Intercept = -1.177 , $P <$
336 0.001 ; Egger's regression of meta-analytic residuals: Intercept = -1.177 , $P < 0.001$;
337 Figure 2).

338

339 4. DISCUSSION

340 Predator avoidance has a profound effect on individual fitness by allowing animals to
341 escape from potential predators, including humans. Our first meta-analysis revealed that
342 in almost all species investigated, FID was strongly and positively correlated with body
343 length. Shoaling behaviour was the most important predictor of the individual body size-
344 FID relationship, with solitary species being less affected by individual size in their
345 escape response compared to more gregarious species. Finally, our meta-analysis found

346 no effect of shoal size on FID of fish. Interestingly, despite the large number of species
347 studied, the results of shoal size showed absence of heterogeneity in data, which suggest
348 a highly conserved phenomena across species (Senior et al. 2016).

349

350 The positive relationship between body size and FID has been reported in birds (Møller,
351 Samia, Weston, Guay, & Blumstein, 2014; Møller, Stokke, & Samia, 2015; Samia et al.,
352 2015) and lizards (Samia et al., 2016), particularly in unexploited or undisturbed
353 populations (Samia et al., 2015a). Yet it is important to realize that predator avoidance
354 strategy is highly species-specific (Domenici, 2010; Hodge et al., 2018) and while fish
355 size is a reasonably good predictor of FID, various confounding factors can influence
356 escape abilities. While experience accumulated with age (i.e., through learning) might
357 partly explain why bigger fish flee at a greater distance (Kelley & Magurran, 2003), we
358 could also expect that larger prey would have tolerated closer approach from predators
359 than small prey, at both intra- and inter-specific levels. Life-history theory predicts that
360 as reproductive value increases, risk-taking decreases (Cooper Jr & Frederick, 2007). For
361 example, fish reproductive potential rises markedly with size in females, when
362 considering energy accumulated within eggs and their number (Barneche, Robertson,
363 White, & Marshall, 2018). Hence, the higher the reproductive output (and thus, the size),
364 the higher the FID. Many alternative hypotheses have been highlighted to explain why
365 larger fish flee at a greater distance than smaller fishes (Domenici, 2010). These
366 hypotheses could be directly linked to the long-time evolutionary arms race between
367 predators and prey, where morphological defences such as armour evolved in response to
368 greater predation risk (Hodge et al., 2018), or they could be linked to energy requirements
369 where smaller fish must act bolder to obtain food, or smaller fish pay a relatively higher
370 opportunity cost for leaving—particularly if they are successfully foraging (Dill, 1990;

371 Grand & Dill, 1997; Paglianti & Domenici, 2006; Polverino, Bierbach, Killen, Uusi-
372 Heikkilä, & Arlinghaus, 2016). At a shorter time scale, larger (and older) fish might also
373 have developed greater escape reactions because they have been longer exposed to fishing
374 pressures (Biro & Post, 2008; Johnston et al., 2013; Tsikliras & Polymeros, 2014). To
375 date, no single factor explains the intra-specific correlation between FID and fish size,
376 and it may have emerged from the interaction of several variables.

377

378 Shoaling and habitat preferences were recently recognized as two major ecological traits
379 that balance the evolutionary trade-offs in antipredator morphological adaptations in
380 fishes (Hodge et al., 2018). Here we also show that shoaling behaviour is of primary
381 importance to explain the strength of the relationship between individual body size and
382 FID, while habitat preference is a relatively minor factor in explaining this relationship.
383 The size of individuals of solitary species has less effect on escape response than
384 individual size in group-living species. It is known that social group size positively
385 influences vigilance in animals (Pitcher, 1986; Lima, 1995; Ward, Herbert-Read,
386 Sumpter, & Krause, 2011). Yet, the absence of a group size effect on FID, but the major
387 effect of grouping on the body size-FID relationship suggests that being gregarious (or
388 not) is more important in explaining fish escape response than the size of the group *per*
389 *se*. Another interpretation is that there is an optimal balance between two forces acting on
390 group size. Both dilution effect and detectability by the predators increase with group
391 size, making a larger group more conspicuous to predators, but, although individuals
392 therein are less likely to be targeted individually, throughout their lifetime they are
393 attacked more often. Therefore, even if vigilance adds just a small contribution to
394 survival, during an individual's life span it becomes quite important, contributing to
395 safety perception (Dehn, 1990). Solitary or paired species often rely on morphological

396 defences, such as seen in butterflyfishes (Hodge et al., 2018). Hence, it is likely that
397 regardless of their size, solitary species evolved a number of morphological adaptations
398 that shoaling species lack, to compensate for predatory threats and the lack of “many
399 eyes” to detect them. These compensatory traits may reduce susceptibility to predation,
400 and thus be associated with a reduction in FID when compared to similar sized individuals
401 of more social species.

402

403 It might be assumed that fish found in the benthic zone would have more refuges (Tupper
404 & Boutilier, 1995; Angel & Ojeda, 2001) and would thus be less influenced by their own
405 size in their decision to flee (Killen, Atkinson, & Glazier, 2010). In addition, one might
406 expect that benthic species will generally have more morphological defences compared
407 to pelagic ones (Hodge et al., 2018), and thus would be more prone to take risks
408 independent of their size. However, we detected no significant effect of habitat type on
409 the individual size-FID relationship. This may reflect a sampling bias: humans interact
410 much more with benthic fishes compared to pelagic fishes, and thus our estimates of
411 pelagic fishes were characterised by few effect sizes with high confidence intervals (see
412 Figure 3-e).

413

414 We also did not find that longevity, trophic level or an area’s protected status explained
415 much variation in the body size-FID relationship. Species with longer life expectancies
416 were expected to be more cautious (longer FID) to guarantee that they reach maturity
417 (Blumstein, 2006). Larger species ranking low in the food chain were expected to be
418 preferred by predators because they provide more energy intake than smaller species from
419 the same trophic level, moreover, species ranking higher in the food chain have fewer
420 predators and thus the selective pressure on them should be weaker along the evolutionary

421 time (Cappizzi et al. 2007). While this could be expected for the two former variables,
422 this was less expected for marine protected areas. Indeed, larger fish outside protected
423 areas are preferentially targeted by spear-fishers, while all fish are protected within
424 conservation zones, regardless of their body size. Indeed, recent studies have shown that
425 large fish become more wary when FID is measured during the fishing seasons in
426 periodically harvested areas (Goetze et al., 2017) or outside permanent marine protected
427 (Sbragaglia et al., 2018). Our meta-analysis that used a substantially larger dataset could
428 not detect such a pattern. Two explanations are possible. First, Goetze *et al.* (2017) used
429 only remote video sensing that provided a minimum approach distance (MAD) data
430 instead of FID. Importantly, MAD can be recorded even when flight does not occur, so
431 that MAD is generally larger than FID. Second, Sbragaglia *et al.* (2018) focused only on
432 highly exploited species, while we incorporated data on fish also exposed to non-
433 consumptive tourism.

434

435 Fishing is known to impact population growth rate, behaviour (Biro & Post, 2008, Diaz
436 Pauli and Sih, 2017) and social structure (Conrad, Weinersmith, Brodin, Saltz, & Sih,
437 2011). To improve catchability by reducing wariness, temporal closures have been
438 actively implemented in different fishing zone (Cohen & Foale, 2013). This management
439 strategy recognizes the importance of managing risk-taking in fishes. More generally, our
440 results suggest that human harvesting pressure does not alter the relationship between fish
441 body size and FID – only the magnitude of FID. Our findings suggest that it is the species'
442 traits relative to their reproductive potential and life history trajectory that shape the
443 strength of individual body size-FID relationship. Hence, our analysis stresses the value
444 of focusing on this behavioural trait to manage fish populations (Goetze et al., 2017;
445 Benevides et al., 2018).

446

447 We nevertheless identified some gaps in our literature review. Although we collected data
448 on various continents (America, Asia, Oceania and Europe), we found no data from
449 African fish populations. Similarly, most studies were performed in tropical regions
450 (Nunes et al., 2018). We encourage scientists from data-pauperate zones to collect these
451 needed data. While our study increased our knowledge on two of the most studied
452 variables explaining variation in fish FID, limited data on other potential moderating
453 factors is understudied. For instance, much remains to be learned about the effects of
454 predator size, levels of human disturbance and depth of the water column on FID. Yet,
455 the influence of speargun presence seems to have an effect on FID (Tran, Langel, Thomas,
456 & Blumstein, 2016; Sbragaglia et al., 2018) but see (Januchowski-Hartley et al., 2012),
457 but further studies are needed to clarify if and at to what extent fish are able to recognise
458 spear fishers. With such data in hand, we then would have an additional valuable tool to
459 identify spearfishing pressure on populations or have a metric that tells us whether there
460 is illegal harvesting.

461

462 Future studies focusing on the effect of human presence on fishes should consider the use
463 of flight initiation distance along with a suite of functional traits. By doing so we will
464 develop a better understanding of how behavior and morphology interact to modulate
465 predation avoidance behavior in an increasingly human dominated world.

466

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473

474 **REFERENCES**

475 Angel, A., & Ojeda, F. P. (2001). Structure and trophic organization of subtidal fish
476 assemblages on the northern Chilean coast: The effect of habitat complexity.
477 *Marine Ecology Progress Series*, *217*, 81–91. doi:10.3354/meps217081

478 Arnett, H. A., & Kinnison, M. T. (2017). Predator-induced phenotypic plasticity of shape
479 and behavior: Parallel and unique patterns across sexes and species. *Current*
480 *Zoology*, *63*, 369–378. doi:10.1093/cz/zow072

481 Barneche, D. R., Robertson, D. R., White, C. R., & Marshall, D. J. (2018). Fish
482 reproductive-energy output increases disproportionately with body size. *Science*,
483 *360*, 642–645. doi:10.1126/science.aao6868

484 Barton, K. (2014). MuMIn: Multi-model inference. R package version 1.40.0.

485 Benevides, L. J., Nunes, J. de A. C. C., Costa, T. L. A., & Sampaio, C. L. S. (2016). Flight
486 response of the barber surgeonfish, *Acanthurus bahianus* Castelnau, 1855
487 (Teleostei: Acanthuridae), to spearfisher presence. *Neotropical Ichthyology*, *14*.
488 doi:10.1590/1982-0224-20150010

489 Benevides, L. J., Pinto, T. K., Nunes, J. de A. C. C., & Sampaio, C. L. S. (2018). Fish
490 escape behavior as a monitoring tool in the largest Brazilian multiple-use Marine
491 Protected Area. *Ocean & Coastal Management*, *152*, 154–162.
492 doi:10.1016/j.ocecoaman.2017.11.029

493 Bergseth, B. J., Williamson, D. H., Russ, G. R., Sutton, S. G., & Cinner, J. E. (2017). A
494 social–ecological approach to assessing and managing poaching by recreational
495 fishers. *Frontiers in Ecology and the Environment*, *15*, 67–73.
496 doi:10.1002/fee.1457

497 Birkeland, C., & Dayton, P. K. (2005). The importance in fishery management of leaving
498 the big ones. *Trends in Ecology & Evolution*, *20*, 356–358.
499 doi:10.1016/j.tree.2005.03.015

500 Biro, P. A., & Post, J. R. (2008). Rapid depletion of genotypes with fast growth and bold
501 personality traits from harvested fish populations. *Proceedings of the National*
502 *Academy of Sciences*, *105*, 2919–2922. doi:10.1073/pnas.0708159105

- 503 Blanchard, R. J., Blanchard, D. C., Rodgers, J., & Weiss, S. M. (1990). The
504 characterization and modelling of antipredator defensive behavior. *Neuroscience*
505 *and Biobehavioral Reviews*, *14*, 463–472. doi:10.1016/S0149-7634(05)80069-7
- 506 Blumstein, D. T. (2003). Flight initiation distance in birds is dependent on intruder
507 starting distance. *Journal of Wildlife Management*, *67*, 852–857.
- 508 Blumstein, D. T. (2006). Developing an evolutionary ecology of fear: how life history
509 and natural history traits affect disturbance tolerance in birds. *Animal Behaviour*,
510 *71*, 389–399. doi:10.1016/j.anbehav.2005.05.010
- 511 Borenstein, M., Hedges, L. V., Higgins, J. P. T., & Rothstein, H. R. (2009). *Introduction*
512 *to Meta-Analysis*. Chichester, UK: John Wiley & Sons, Ltd.
513 doi:10.1002/9780470743386
- 514 Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: a*
515 *practical information-theoretic approach* (2nd edn). New York, NY: Springer.
516 doi:10.1016/j.ecolmodel.2003.11.004
- 517 Capizzi, D., Luiselli, L., & Vignoli, L. (2007). Flight initiation distance in relation to
518 substratum type, sex, reproductive status and tail condition in two lacertids
519 with contrasting habits. *Amphibia-Reptilia*, *28*, 403–407.
520 doi:10.1163/156853807781374827
- 521 Cinner, J. E., Maire, E., Huchery, C., MacNeil, M. A., Graham, N. A. J., Mora, C., ...
522 Mouillot, D. (2018). Gravity of human impacts mediates coral reef conservation
523 gains. *Proceedings of the National Academy of Sciences*, 201708001.
524 doi:10.1073/pnas.1708001115
- 525 Cohen, J. (1992). A power primer. *Psychological Bulletin*, *112*, 155–159.
- 526 Cohen, P. J., & Foale, S. J. (2013). Sustaining small-scale fisheries with periodically
527 harvested marine reserves. *Marine Policy*, *37*, 278–287.
528 doi:10.1016/j.marpol.2012.05.010
- 529 Collette, B. B., Carpenter, K. E., Polidoro, B. A., Juan-Jordá, M. J., Boustany, A., Die,
530 D. J., ... Yáñez, E. (2011). High Value and Long Life—Double Jeopardy for
531 Tunas and Billfishes. *Science*, 1208730. doi:10.1126/science.1208730
- 532 Conrad, J. L., Weinersmith, K. L., Brodin, T., Saltz, J. B., & Sih, A. (2011). Behavioural
533 syndromes in fishes: a review with implications for ecology and fisheries
534 management. *Journal of Fish Biology*, *78*, 395–435. doi:10.1111/j.1095-
535 8649.2010.02874.x

- 536 Cooper Jr, W. E., & Blumstein, D. T. (2015). *Escaping from predators: an integrative*
537 *view of escape decisions*. (W. E. J. Cooper & D. T. Blumstein, Eds.). New York:
538 Cambridge University Press.
- 539 Cooper Jr, W. E., & Frederick, W. G. (2007). Optimal flight initiation distance. *Journal*
540 *of Theoretical Biology*, 244, 59–67. doi:10.1016/j.jtbi.2006.07.011
- 541 Cooper Jr, W. E., Pyron, R. A., & Garland, T. (2014). Island tameness: living on islands
542 reduces flight initiation distance. *Proceedings of the Royal Society B*, 281(1777),
543 20133019.
- 544 Cooper Jr, W. E., Samia, D. S. M., & Blumstein, D. T. (2015). *FEAR, spontaneity, and*
545 *artifact in economic escape theory: a review and prospectus*. *Advances in the*
546 *Study of Behavior* (Vol. 47). Elsevier Ltd. doi:10.1016/bs.asb.2015.02.002
- 547 Couzin, I. D. (2009). Collective cognition in animal groups. *Trends in Cognitive Sciences*,
548 13, 36–43. doi:10.1016/j.tics.2008.10.002
- 549 Dalton, C. M., Tracy, K. E., Hairston Jr, N. G., & Flecker, A. S. (2018). Fasting or fear:
550 disentangling the roles of predation risk and food deprivation in the nitrogen
551 metabolism of consumers. *Ecology*, 99, 681–689. doi:10.1111/ijlh.12426
- 552 Dehn, M. M. (1990). Vigilance for predators: detection and dilution effects. *Behavioral*
553 *Ecology and Sociobiology*, 26, 337–342. doi: 10.1007/BF00171099
- 554 Dill, L. M. (1974). The escape response of the zebra danio (*Brachydanio rerio*) I. The
555 stimulus for escape. *Animal Behaviour*, 22, 711–722.
- 556 Dill, L. M. (1990). Distance-to-cover and the escape decisions of an African cichlid fish,
557 *Melunochromis chipokae*. *Environmental Biology of Fishes*, 27, 147–152.
- 558 Dimmock, K., & Cummins, T. (2013). History of scuba diving tourism. In G. Musa & K.
559 Dimmock (Eds.), *Scuba diving tourism* (pp. 14–28). Routledge.
- 560 Domenici, P., & Batty, R. S. (1997). Escape behaviour of solitary herring (*Clupea*
561 *harengus*) and comparisons with schooling individuals. *Marine Biology*, 128, 29–
562 38. doi:10.1007/s002270050065
- 563 Domenici, P., (2010). Context-dependent variability in the components of fish escape
564 response: Integrating locomotor performance and behavior. *Journal of*
565 *Experimental Zoology Part A: Ecological Genetics and Physiology*, 313, 59–79.
566 doi:10.1002/jez.580
- 567 Egger, M., Smith, G. D., Schneider, M., & Minder, C. (1997). Bias in meta-analysis
568 detected by a simple, graphical test. *BMJ*, 315, 629–634.

569 Ferrari, M. C. O., McCormick, M. I., Allan, B. J. M., Choi, R., Ramasamy, R. A.,
570 Johansen, J. L., ... Chivers, D. P. (2015). Living in a risky world: The onset and
571 ontogeny of an integrated antipredator phenotype in a coral reef fish. *Scientific*
572 *Reports*, 5, 1–13. doi:10.1038/srep15537

573 Garamszegi, L. Z. (2014). *Modern phylogenetic comparative methods and their*
574 *application in evolutionary biology: concepts and practice*. (L. Z. Garamszegi,
575 Ed.). New York, NY: Springer.

576 Geffroy, B., Sadoul, B., Bouchareb, A., Prigent, S., Bourdineaud, J. P., Gonzalez-Rey,
577 M., ... Bessa, E. (2018). Nature-based tourism elicits a phenotypic shift in the
578 coping abilities of fish. *Frontiers in Physiology*, 9, 1–17.
579 doi:10.3389/fphys.2018.00013

580 Geffroy, B., Sadoul, B., & Ellenberg, U. (2017). Physiological and Behavioral
581 Consequences of Human Visitation. In *Ecotourism's Promise and Peril* (pp. 9–
582 27). Springer, Cham. doi:10.1007/978-3-319-58331-0_2

583 Giglio, V. J., Bender, M. G., Zapelini, C., & Ferreira, C. E. L. (2017). The end of the line?
584 Rapid depletion of a large-sized grouper through spearfishing in a subtropical
585 marginal reef. *Perspectives in Ecology and Conservation*, 15, 115–118.
586 doi:10.1016/j.pecon.2017.03.006

587 Goetze, J. S., Januchowski-Hartley, F. A., Claudet, J., Langlois, T. J., Wilson, S. K., &
588 Jupiter, S. D. (2017). Fish wariness is a more sensitive indicator to changes in
589 fishing pressure than abundance, length or biomass. *Ecological Applications*, 27,
590 1178–1189. doi:10.1002/eap.1511

591 Goldenberg, S. U., Borchering, J., & Heynen, M. (2014). Balancing the response to
592 predation—the effects of shoal size, predation risk and habituation on behaviour
593 of juvenile perch. *Behavioral Ecology and Sociobiology*, 68, 989–998.
594 doi:10.1007/s00265-014-1711-1

595 Gotanda, K. M., Turgeon, K., & Kramer, D. L. (2009). Body size and reserve protection
596 affect flight initiation distance in parrotfishes. *Behavioral Ecology and*
597 *Sociobiology*, 63(11), 1563–1572. doi:10.1007/s00265-009-0750-5

598 Grand, T. C., & Dill, L. M. (1997). The energetic equivalence of cover to juvenile coho
599 salmon (*Oncorhynchus kisutch*): ideal free distribution theory applied. *Behavioral*
600 *Ecology*, 8(4), 437–447.

601 Gwinn, D. C., Allen, M. S., Johnston, F. D., Brown, P., Todd, C. R., & Arlinghaus, R.
602 (2015). Rethinking length-based fisheries regulations: The value of protecting old

603 and large fish with harvest slots. *Fish and Fisheries*, 16, 259–281.
604 doi:10.1111/faf.12053

605 Herbert-Read, J. E., Buhl, J., Hu, F., Ward, A. J. W., & Sumpter, D. J. T. (2015). Initiation
606 and spread of escape waves within animal groups. *Open Science*, 2, 140355.
607 doi:10.1098/rsos.140355

608 Higgins, J. P. T., Thompson, S. G., Deeks, J. J., &
609 Altman, D. G. (2003). Measuring inconsistency in meta-analyses. *BMJ*, 327, 557–
560. doi:10.1136/bmj.327.7414.557

610 Hodge, J. R., Alim, C., Bertrand, N. G., Lee, W., Price, S. A., Tran, B., & Wainwright,
611 P. C. (2018). Ecology shapes the evolutionary trade-off between predator
612 avoidance and defence in coral reef butterflyfishes. *Ecology Letters*, 21, 1033–
613 1042. doi:10.1111/ele.12969

614 Ioannou, C. C., Ramnarine, I. W., & Torney, C. J. (2017). High-predation habitats affect
615 the social dynamics of collective exploration in a shoaling fish. *Science Advances*,
616 3, e1602682. doi:10.1126/sciadv.1602682

617 Januchowski-Hartley, F. A., Graham, N. A. J., Cinner, J. E., & Russ, G. R. (2013).
618 Spillover of fish naïveté from marine reserves. *Ecology Letters*, 16, 191–197.
619 doi:10.1111/ele.12028

620 Januchowski-Hartley, F. A., Graham, N. A. J., Cinner, J. E., & Russ, G. R. (2015). Local
621 fishing influences coral reef fish behavior inside protected areas of the Indo-
622 Pacific. *Biological Conservation*, 182, 8–12. doi:10.1016/j.biocon.2014.11.024

623 Januchowski-Hartley, F. A., Graham, N. A. J., Feary, D. A., Morove, T., & Cinner, J. E.
624 (2011). Fear of fishers: human predation explains behavioral changes in coral reef
625 fishes. *PloS One*, 6, e22761. doi:10.1371/journal.pone.0022761

626 Januchowski-Hartley, F. A., Nash, K. L., & Lawton, R. J. (2012). Influence of spear guns,
627 dive gear and observers on estimating fish flight initiation distance on coral reefs.
628 *Marine Ecology Progress Series*, 469, 113–119. doi:10.3354/meps09971

629 Jennions, M., & Møller, A. P. (2002). How much variance can be explained by ecologists
630 and evolutionary biologists? *Oecologia*, 132, 492–500. doi:10.1007/s00442-002-
631 0952-2

632 Johnston, F. D., Arlinghaus, R., & Dieckmann, U. (2013). Fish life history, angler
633 behaviour and optimal management of recreational fisheries. *Fish and Fisheries*,
634 14, 554–579. doi:10.1111/j.1467-2979.2012.00487.x

635 Jørgensen, C., Enberg, K., Dunlop, E. S., Arlinghaus, R., Boukal, D. S., Brander, K., ...
636 Rijnsdorp, A. D. (2007). Managing the world's evolving fish stocks. *Science*, *318*,
637 1247–1248. doi:10.1126/science.1148089

638 Keenleyside, M. H. A. (1962). Skin-diving Observations of Atlantic Salmon and Brook
639 Trout in the Miramichi River, New Brunswick. *Journal of the Fisheries Research*
640 *Board of Canada*, *19*, 625–634. doi:10.1139/f62-042

641 Kelley, J. L., & Magurran, A. E. (2003). Learned predator recognition and antipredator
642 responses in fishes. *Fish and Fisheries*, *4*, 216–226. doi:10.1046/j.1467-
643 2979.2003.00126.x

644 Kembel, S. W., Cowan, P. D., Helmus, M. R., Cornwell, W. K., Morlon, H., Ackerly, D.
645 D., ... Webb, C. O. (2010). Picante: R tools for integrating phylogenies and
646 ecology. *Bioinformatics*, *26*, 1463–1464.

647 Killen, S. S., Atkinson, D., & Glazier, D. S. (2010). The intraspecific scaling of metabolic
648 rate with body mass in fishes depends on lifestyle and temperature. *Ecology*
649 *Letters*, *13*, 184–193. doi:10.1111/j.1461-0248.2009.01415.x

650 Koricheva, J., Gurevitch, J., & Mengersen, K. (2013). *Handbook of meta-analysis in*
651 *ecology and evolution*. (J. Koricheva, J. Gurevitch, & K. Mengersen, Eds.).
652 Princeton, New Jersey: Princeton University Press.

653 Langridge, K. V., Broom, M., & Osorio, D. (2007). Selective signalling by cuttlefish to
654 predators. *Current Biology*, *17*, 1044–1045. doi:10.1016/j.cub.2007.10.028

655 Lima, S. L. (1995). Back to the basics of anti-predatory vigilance: the group-size effect.
656 *Animal Behaviour*, *49*, 11–20. doi:10.1016/0003-3472(95)80149-9

657 McClanahan, T. R. T. R., Graham, N. A. J. N. A., Calnan, J. M. J. M., & MacNeil, M. A.
658 M. A. (2007). Toward pristine biomass: reef fish recovery in coral reef marine
659 protected areas in Kenya. *Ecological Applications*, *17*, 1055–1067.
660 doi:10.1890/06-1450

661 McCormick, M. I., Chivers, D. P., Allan, B. J. M., & Ferrari, M. C. O. (2017). Habitat
662 degradation disrupts neophobia in juvenile coral reef fish. *Global Change*
663 *Biology*, *23*, 719–727. doi:10.1111/gcb.13393

664 Møller, A. P., & Erritzøe, J. (2014). Predator-prey interactions, flight initiation distance and brain size. *Journal of*
665 *Evolutionary Biology*, *27*, 34–42. doi:10.1111/jeb.12272

666 Møller, A. P., Samia, D. S. M., Weston, M. A., Guay, P.-J., & Blumstein, D. T. (2014).
667 American exceptionalism: population trends and flight initiation distances in birds
668 from three continents. *PloS One*, *9*, e107883. doi:10.1371/journal.pone.0107883

669 Møller, A. P., Stokke, B. G., & Samia, D. S. M. (2015). Hawk models, hawk mimics, and
670 antipredator behavior of prey. *Behavioral Ecology*, 26, 1039–1044.
671 doi:10.1093/beheco/arv043

672 Nakagawa, S., & Santos, E. S. A. (2012). Methodological issues and advances in
673 biological meta-analysis. *Evolutionary Ecology*, 26, 1253–1274.
674 doi:10.1007/s10682-012-9555-5

675 Nunes, J. A. C. C., Costa, Y., Blumstein, D. T., Leduc, A. O. H. C., Dorea, A. C.,
676 Benevides, L. J., ... Barros, F. (2018). Global trends on reef fishes' ecology of
677 fear: Flight initiation distance for conservation. *Marine Environmental Research*,
678 136, 153–157. doi:10.1016/j.marenvres.2018.02.011

679 Pagel, M. (1999). Inferring the historical patterns of biological evolution. *Nature*, 401,
680 877–884. doi:10.1038/44766

681 Paglianti, A., & Domenici, P. (2006). The effect of size on the timing of visually mediated
682 escape behaviour in staghorn sculpin *Leptocottus armatus*. *Journal of Fish*
683 *Biology*, 68, 1177–1191. doi:10.1111/j.1095-8649.2006.00991.x

684 Pitcher, T. J. (1986). Functions of Shoaling Behaviour in Teleosts. In *The Behaviour of*
685 *Teleost Fishes* (pp. 294–337). Springer, Boston, MA. doi:10.1007/978-1-4684-
686 8261-4_12

687 Polverino, G., Bierbach, D., Killen, S. S., Uusi-Heikkili, S., & Arlinghaus, R. (2016).
688 Body length rather than routine metabolic rate and body condition correlates with
689 activity and risk-taking in juvenile zebrafish *Danio rerio*. *Journal of Fish Biology*,
690 89, 2251–2267. doi:10.1111/jfb.13100

691 Preisser, E. L., & Orrock, J. L. (2012). The allometry of fear: interspecific relationships
692 between body size and response to predation risk. *Ecosphere*, 3, art77.
693 doi:10.1890/ES12-00084.1

694 Rieucou, G., Fernö, A., Ioannou, C. C., & Handegard, N. O. (2015). Towards of a firmer
695 explanation of large shoal formation, maintenance and collective reactions in
696 marine fish. *Reviews in Fish Biology and Fisheries*, 25, 21–37.
697 doi:10.1007/s11160-014-9367-5

698 Rowe, R. Y. G., & Santos, G. E. de O. (2016). Turismo de mergulho: análise do
699 comportamento de viagem dos mergulhadores brasileiros. *Caderno Virtual de*
700 *Turismo*, 16, 61–75.

- 701 Samia, D. S. M., Nakagawa, S., Nomura, F., Rangel, T. F., & Blumstein, D. T. (2015a).
702 Increased tolerance to humans among disturbed wildlife. *Nature*
703 *Communications*, 6, 1–8.
- 704 Samia, D. S. M., Møller, A. P., & Blumstein, D. T. (2015b). Brain size as a driver of avian
705 escape strategy. *Scientific Reports*, 5, 11913. doi:10.1038/srep11913
- 706 Samia, D. S. M., Nomura, F., & Blumstein, D. T. (2013). Do animals generally flush early
707 and avoid the rush? A meta-analysis. *Biology Letters*, 9, 20130016.
708 doi:10.1098/rsbl.2013.0016
- 709 Samia, D. S.M., Blumstein, D. T., Stankowich, T., & Cooper Jr, W. E. (2016). Fifty years
710 of chasing lizards: new insights advance optimal escape theory. *Biological*
711 *Reviews*, 91, 349–366.
- 712 Sbragaglia, V., Morroni, L., Bramanti, L., Weitzmann, B., Arlinghaus, R., & Azzurro, E.
713 (2018). Spearfishing modulates flight initiation distance of fishes: the effects of
714 protection, individual size, and bearing a speargun. *ICES Journal of Marine*
715 *Science*, 75, 1779-1789. doi:10.1093/icesjms/fsy059
- 716 Seghers, B. H. (1981). Facultative schooling behavior in the spottail shiner (*Notropis*
717 *hudsonius*): possible costs and benefits. *Environmental Biology of Fishes*, 6, 21–
718 24. doi:10.1007/BF00001795
- 719 Semeniuk, C. A. D., & Dill, L. M. (2005). Cost/benefit analysis of group and solitary
720 resting in the cowtail stingray, *Pastinachus sephen*. *Behavioral Ecology*, 16, 417–
721 426. doi:10.1093/beheco/ari005
- 722 Senior, A. M., Grueber, C. E., Kamiya, T., Lagisz, M., O'Dwyer, K., Santos, E. S. A. &
723 Nakagawa S. (2016). Heterogeneity in ecological and evolutionary meta-analyses:
724 its magnitudes and implications. *Ecology*, 97, 3293-3299.
- 725 Stankowich, T., & Blumstein, D. T. (2005). Fear in animals: a meta-analysis and review
726 of risk assessment. *Proceedings of the Royal Society B*, 272, 2627–2634.
727 doi:10.1098/rspb.2005.3251
- 728 Tran, D. S. C., Langel, K. A., Thomas, M. J., & Blumstein, D. T. (2016). Spearfishing-
729 induced behavioral changes of an unharvested species inside and outside a marine
730 protected area. *Current Zoology*, 62, 39–44. doi:10.1093/cz/zov006
- 731 Tsikliras, A. C., & Polymeros, K. (2014). Fish market prices drive overfishing of the ‘big
732 ones’. *PeerJ*, 2, e638. doi:10.7717/peerj.638

- 733 Tupper, M., & Boutilier, R. G. (1995). Effects of habitat on settlement, growth, and
734 postsettlement survival of Atlantic cod (*Gadus morhua*). *Canadian Journal of*
735 *Fisheries and Aquatic Sciences*, 52, 1834–1841. doi:10.1139/f95-176
- 736 Uusi-Heikkilä, S., Whiteley, A. R., Kuparinen, A., Matsumura, S., Venturelli, P. A.,
737 Wolter, C., ... Arlinghaus, R. (2015). The evolutionary legacy of size-selective
738 harvesting extends from genes to populations. *Evolutionary Applications*, 8, 597–
739 620. doi:10.1111/eva.12268
- 740 Viechtbauer, W. (2010). Conducting meta-analyses in R with the metafor package.
741 *Journal of Statistical Software*, 36, 1–48.
- 742 Ward, A. J. W., Herbert-Read, J. E., Sumpter, D. J. T., & Krause, J. (2011). Fast and
743 accurate decisions through collective vigilance in fish shoals. *Proceedings of the*
744 *National Academy of Sciences*, 201007102. doi:10.1073/pnas.1007102108
- 745 Ydenberg, R. C., & Dill, L. M. (1986). The economics of fleeing from predators.
746 *Advances in the Study of Behavior*, 16, 229–249.
- 747 Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid
748 common statistical problems. *Methods in Ecology & Evolution*, 1, 3–14.
749 doi:10.1111/j.2041-210X.2009.00001.x
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751 **Table 1.** List of hypotheses concerning moderators used to explain variation in body
 752 size-FID and group size-FID relationships in fish.

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Moderator	Relationship	Hypothesis	Rationale	References
Species' body size	Individual body size-FID	Larger species should have a stronger individual body size-FID relationship.	FID increases with body mass for a variety of possible reasons that may include: larger animals are less agile; larger animals are a preferred prey, smaller animals may take greater risks because of their relatively higher metabolic rates, and because larger species may have greater reproductive value.	Gotanda et al. 2009
	Shoal size-FID	Shoal size-FID relationships are weaker in larger species.	If larger species are under less predation risk, they may not need to group to escape predators. Because of their body size, larger species are likely to be relatively rare and thus may be less likely to form large shoals.	Preisser and Orrock 2012; Krause et al. 1997
Longevity	Individual body size-FID	Species with longer life expectancies should have stronger individual body size-FID relationships.	Species with a longer life expectancy might be more cautious to guarantee that they reach maturity.	Blumstein 2006
	Shoal size-FID	Species with longer life expectancies should have weaker shoal size-FID relationships.	Species with longer life expectancy often form small and scattered shoals weakening shoal size-FID relationship	Hoare et al. 2005
Shoaling behaviour	Individual body size-FID	Species that shoal might have stronger individual body size-FID relationship than solitary species.	Detection cues should increase in groups and, that groups of small fishes (e.g., larvae) may be less able to escape than groups of larger fish.	Ward et al. 2011
	Shoal size-FID	Species that often shoal may have greater shoal size-FID relationships.	In denser shoals the relationship between shoal size and FID will be more evident because of increases in shoal communication provide by reduced distances between fish.	Herbert-Read et al. 2015
Trophic level	Individual body size-FID	Species low in the food chain might have a stronger positive relationship between individual body size and FID than species higher in the food chain.	Larger species ranking low in the food chain are preferred by predators because they provide more energy intake than smaller species from the same trophic level. Yet, species ranking higher in the food chain have fewer predators and thus the selective pressure on them should have been weaker along the evolutionary time.	Cappizzi et al. 2007
	Shoal size-FID	Shoal size-FID relationship is stronger in some trophic levels.	There is a relationship between shoal size and trophic level. Fish that use more available resources often form bigger shoals, which can influence vigilance time reflecting on FID	Rieucou et al. 2015
Habitat use	Individual body size-FID	Demersal species should have weaker individual body size-FID relationships compared to pelagic species.	Because demersal fish are often closer to shelters, fear responses might be less linked to size.	Dill 1990, Nunes et al. 2015, Benevides et al. 2016
	Shoal size-FID	Demersal species should have lower shoal size-FID relationships compared to pelagic species.	Because demersal fish are often closer to shelters, fear responses might be less linked to shoal size.	McCornick et al. 2017; Hodge et al. 2018
Conservation status of the studied area	Individual body size-FID	Populations in unprotected areas should have stronger individual body size-FID relationships.	Big fish outside protected areas are preferentially targeted by fishers.	Johnston et al. 2012; Tsikliras and Polymeros 2014
	Shoal size-FID	Population in unprotected areas should have a stronger shoal size-FID relationship.	The benefits from living in groups to better detect humans should be reduced within protected areas.	Goldenberg et al. 2014; Ioannou et al. 2017

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765 **Table 2.** Summary of the multi-model inference conducted to explain variation in the

766 body size-FID relationship in fish

Predictor	Levels	Estimate	S.E.	z-value	Importance
Intercept		0.507	0.494	1.03	
Shoaling behaviour	Grouped	0.362	0.185	1.97	0.67
Species body size		0.086	0.105	0.81	0.32
Longevity		-0.213	0.314	0.68	0.30
Trophic level		0.450	0.709	0.63	0.29
Environment	Pelagic	-0.094	0.204	0.46	0.27
Area protection status	Protected	-0.022	0.150	0.14	0.25

767 Estimates are average coefficients of the model, their associated standard error (S.E.), and
768 the importance of each factor in explaining species responses to human disturbance (the
769 closer than 1, the most important the factor).

770 **Figure Captions:**

771 **Figure 1.** Forest plot of the body size-FID effect sizes. Effect sizes are shown in
772 ascending order. Filled circles with horizontal lines represent effect size \pm 95%
773 confidence intervals.

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775 **Figure 2.** Funnel plots of (a) body size-FID and (b) group size-FID meta-analyses using
776 both the effect sizes and the meta-analytic residuals

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778 **Figure 3.** Effects of (a) shoaling behaviour, (b) species' body size, (c) longevity, (d)
779 trophic level, (e) environment and (f) area protection status on the body size-FID
780 relationship. Plots (a), (e) and (f) show mean \pm 95% confidence intervals. The number of
781 species tested at each factor level is shown in the bottom of plots.

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783 **Figure 4.** Forest plot of the group size-FID effect sizes. Effect sizes are shown in
784 ascending order. Filled circles with horizontal lines represent effect size \pm 95%
785 confidence intervals