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

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3   Diogo S. M. Samia[1], Eduardo Bessa[2], Daniel T. Blumstein[3], José A. C. C. Nunes[4],

4   Ernesto Azzurro[5,6], Lorenzo Morroni[5], Valerio Sbragaglia[5,7], Fraser A. Januchowski-

5   Hartley[8] and Benjamin Geffroy[8]

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7   *[1]Department of Ecology, Bioscience Institute, University of Sao Paulo, Sao Paulo,*

8   *Brazil, ORCID: 0000-0002-0487-8019*

9   *[2]Life and Earth Sciences Area, FUP, and Graduate Program in Ecology, Biology*

10   *Institute, University of Brasília, Distrito Federal, Brazil, ORCID: 0000-0003-0606-*

11   *5860*

12   *[3]Department of Ecology and Evolutionary Biology, University of California, 621 Young*

13   *Drive South, Los Angeles, CA 90095-1606, USA, ORCID: 0000-0001-5793-9244*

14   *[4]Laboratório de Ecologia e Conservação Marinha, Centro de Formação em Ciências*

15   *Ambientais, Universidade Federal do Sul da Bahia, Brazil, ORCID: 0000-0002-2743-*

16   *797X*

17   *[5] Institute for Environmental Protection and Research (ISPRA), Via del Cedro 38,*

18   *57122 Livorno, Italy*

19   *[6] Stazione Zoologica Anton Dohrn, Villa Comunale 80121, Napoles, Italy*

20   *[7] Department of Biology and Ecology of Fishes, Leibniz-Institute of Freshwater Ecology*

21   *and Inland Fisheries, Müggelseedamm 310, Berlin, Germany*

22   *[8]MARBEC, Ifremer, University Montpellier, CNRS, IRD, Palavas-Les-Flots, France,*

23   *ORCID: 0000-0001-6120-1103*

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

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26   Authors for correspondence:

27   D.S.M.S. (diogosamia@gmail.com) and B.G. (bgeffroy@ifremer.fr)

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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1. INTRODUCTION

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

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

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 disproportionally 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

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

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

2.3 Meta-analysis

We used multilevel mixed-effects meta-analysis to test for both overall effect sizes and the importance of our predictors (Nakagawa & Santos, 2012). The overall effect sizes (i.e., mean of the effect sizes weighted by the inverse of their variance) were considered significant if their 95% confidence intervals (CI) did not include zero (Koricheva et al., 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 ± 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 Heikkilï, & 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 spam it becomes quite important, contributing to
395 safety perception (Dehn, 1990). Solitary or paired species often relay 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   consumtive 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

471   modifying his R function to conduct multi-model inference using meta-regression

472   models.

473

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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 scaterred shoals weaking 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 thropic 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 relathionship 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	Rieucau 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 ofter 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 ofter 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 targetted 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 ± 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± 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 ± 95%
785   confidence intervals