

## A metaanalysis of fish behavioural reaction to underwater human presence

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### Abstract :

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

**Keywords** : antipredator behaviour, economic escape theory, fish size, flight initiation 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  $\lambda$  (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 =  $64.00 \pm 1.26$  cm/s (mean  $\pm$  s.e.), N = 120; Shoal size-FID meta-  
284 analysis:  $76.78 \pm 0.64$  cm/s, N = 59) and the starting distance used by experimenters  
285 (Individual body size-FID meta-analysis:  $8.22 \pm 0.22$  m, N = 67; Shoal size-FID meta-  
286 analysis:  $7.91 \pm 0.09$  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 ( $I^2_{\text{total}}$   
311 = 92.99%,  $I^2_{\text{studies}}$  = 12.09%,  $I^2_{\text{residual}}$  = 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

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- 750

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

<b>Predictor</b>	<b>Levels</b>	<b>Estimate</b>	<b>S.E.</b>	<b>z-value</b>	<b>Importance</b>
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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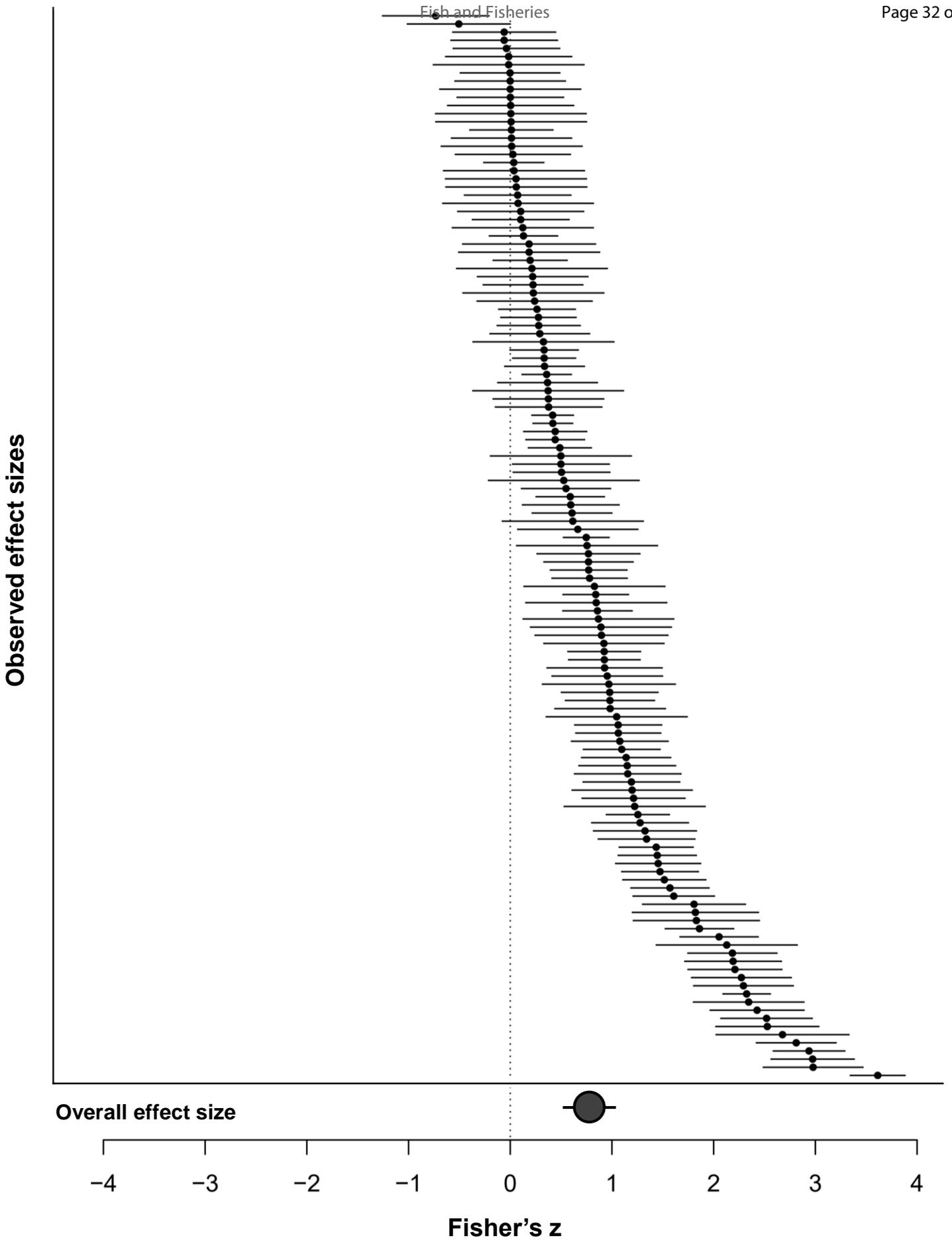
775 **Figure 2.** Funnel plots of (a) body size-FID and (b) group size-FID meta-analyses using  
776 both the effect sizes and the meta-analytic residuals

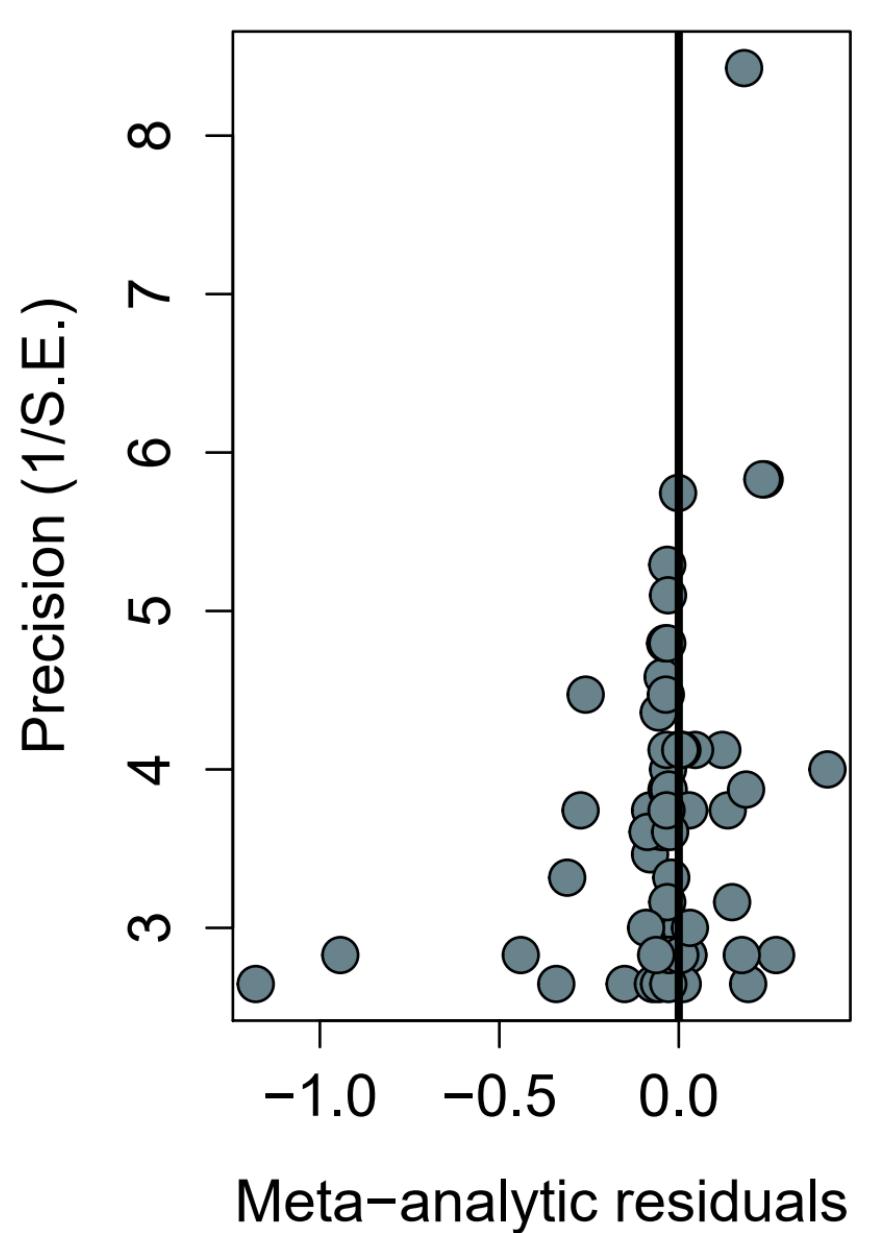
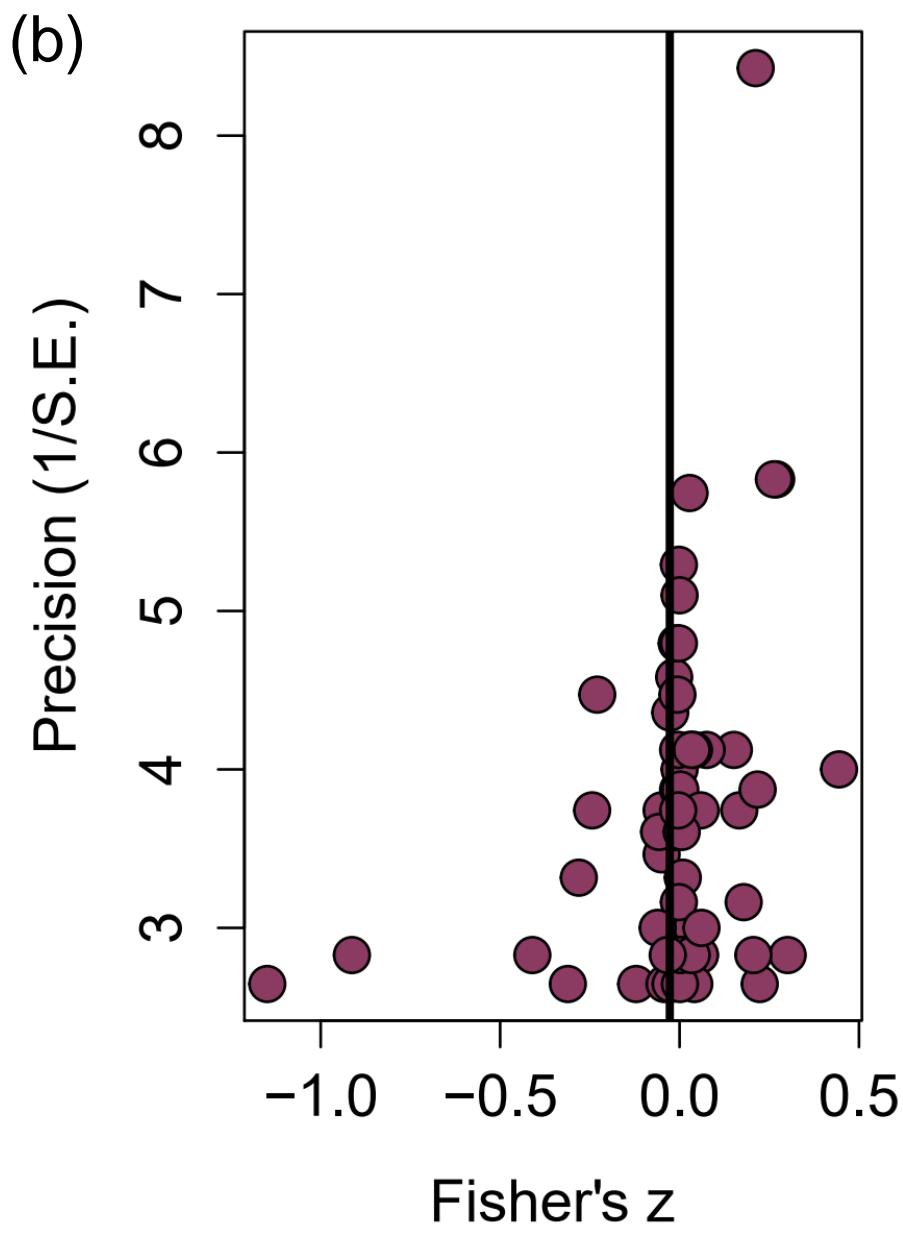
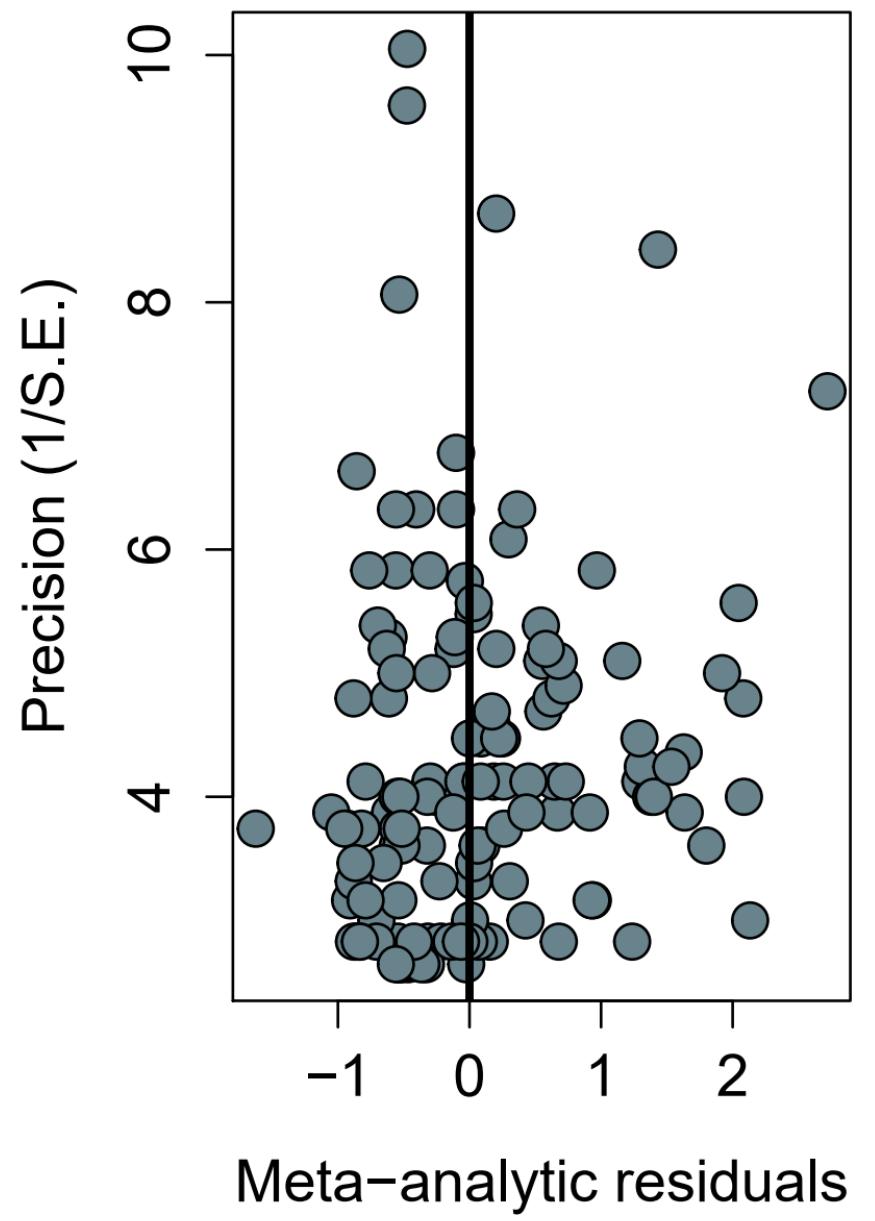
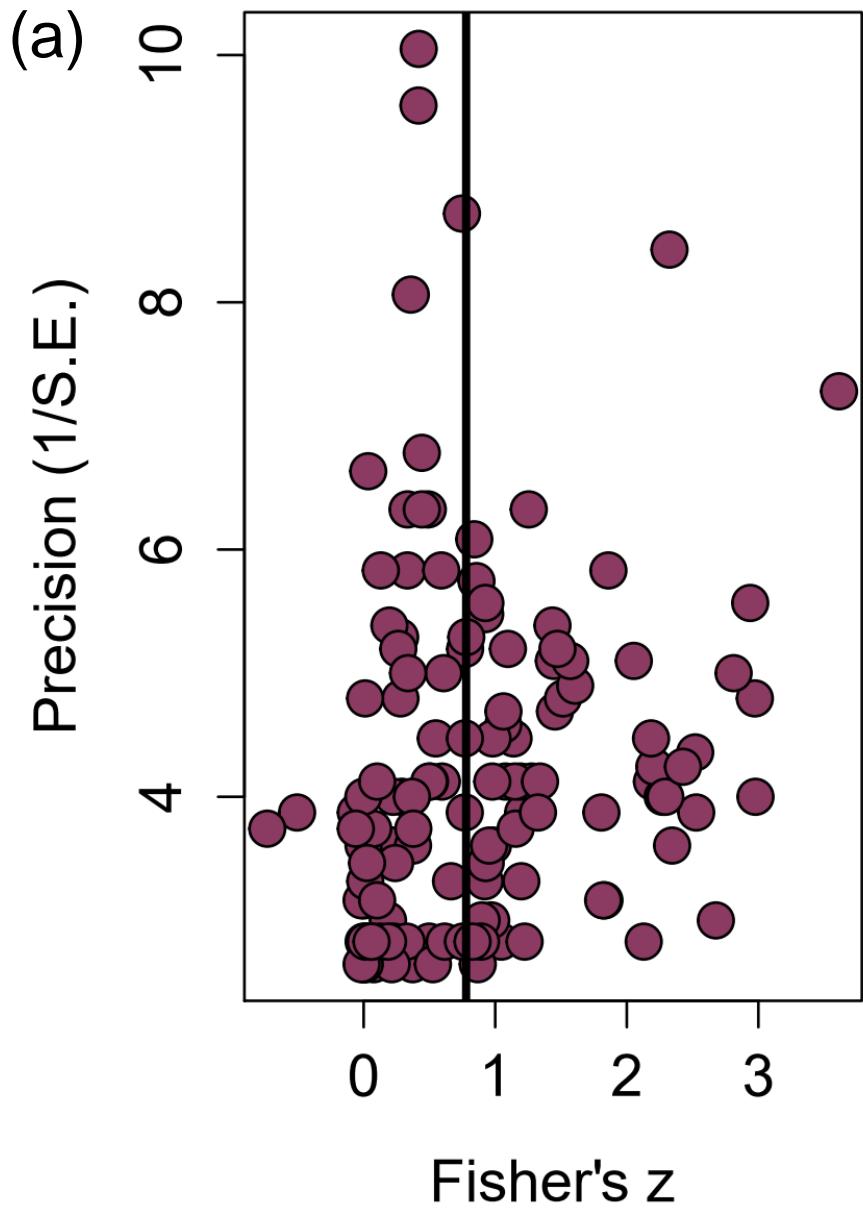
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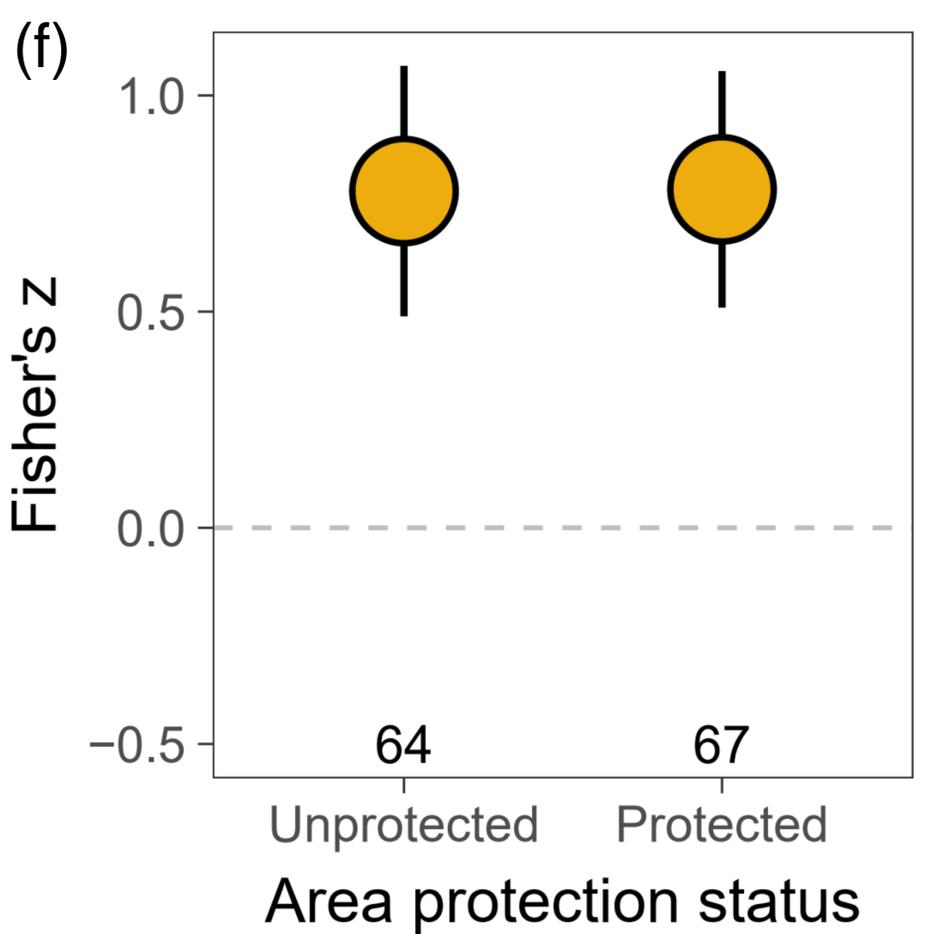
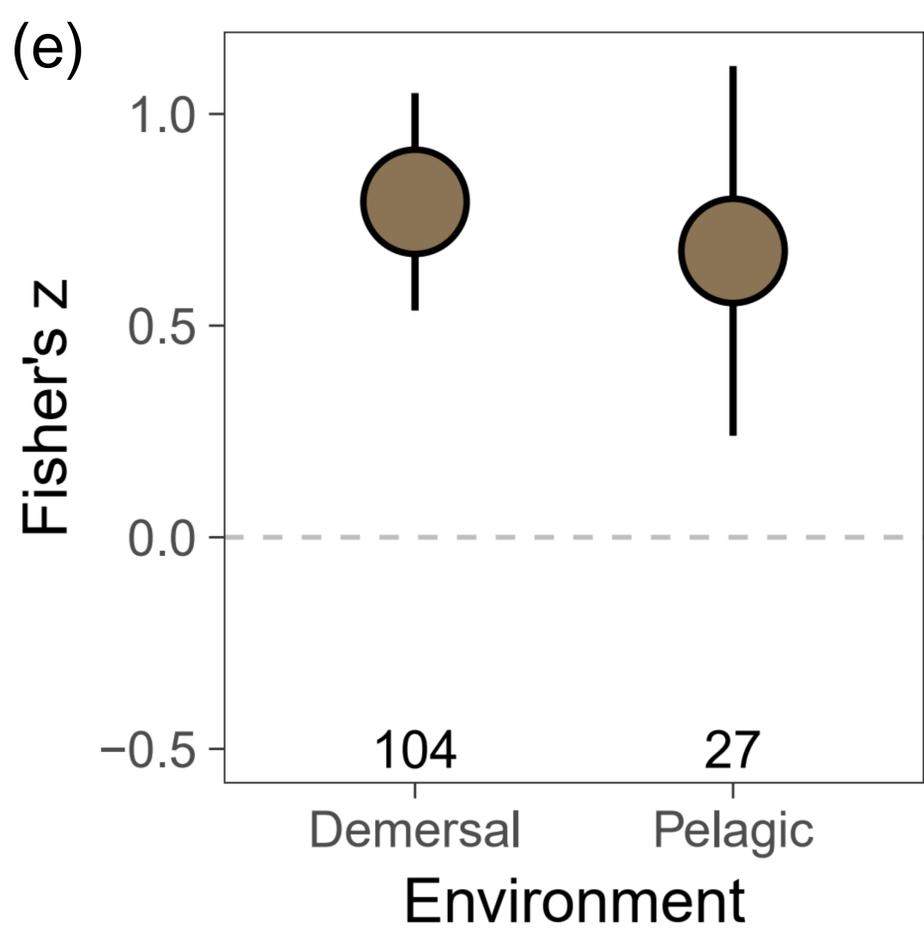
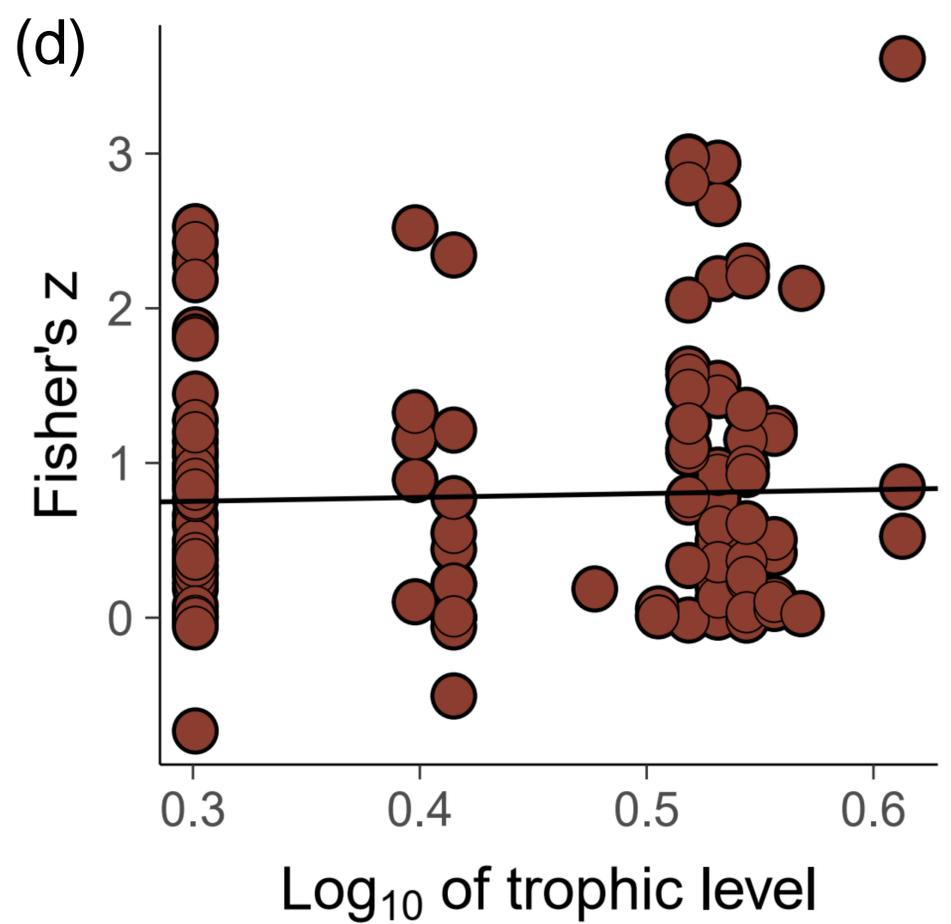
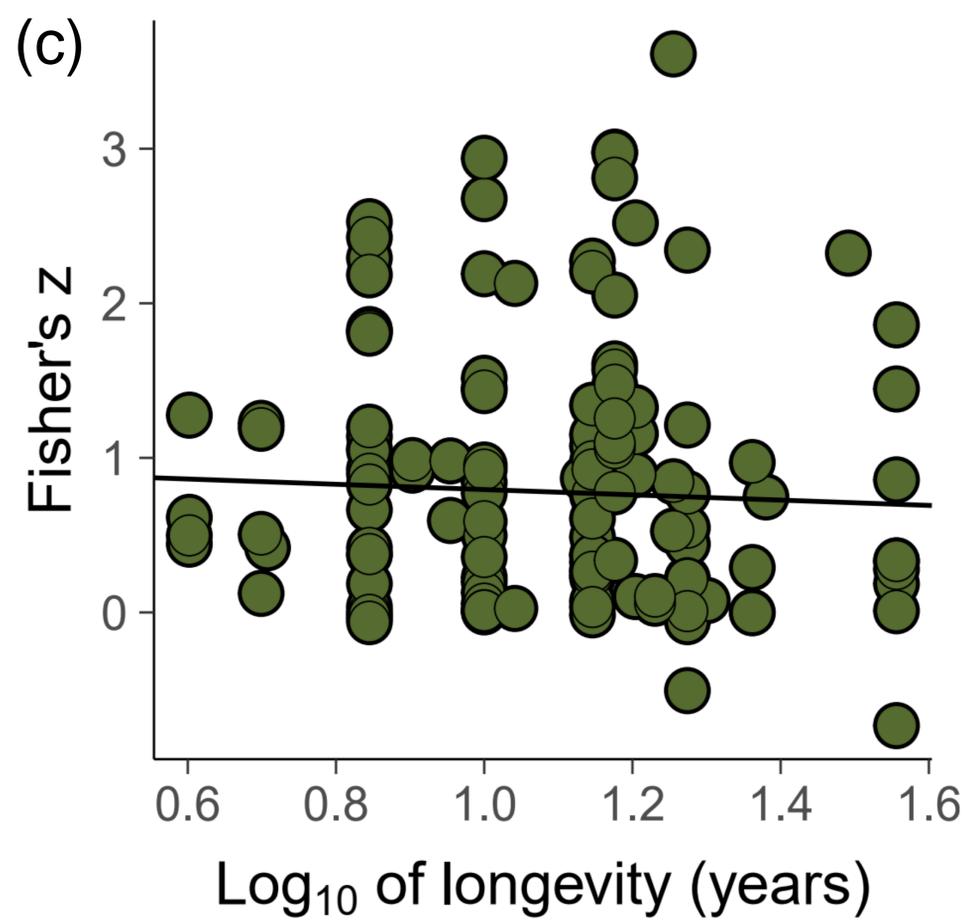
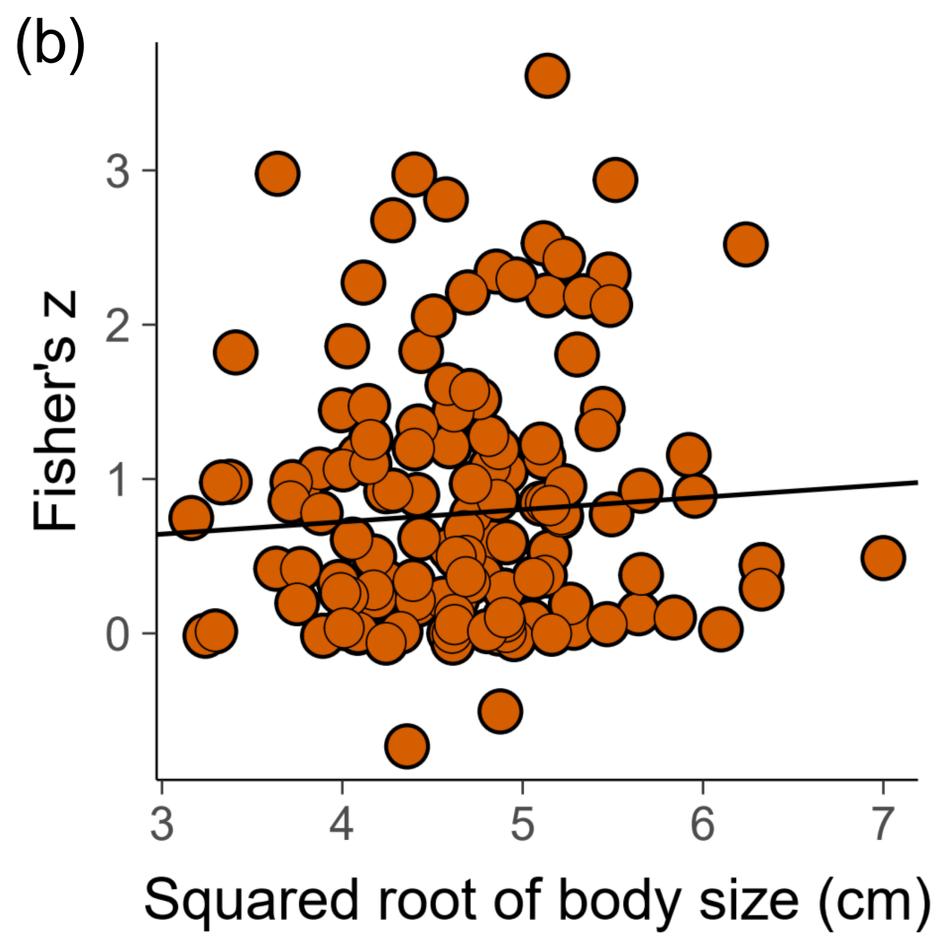
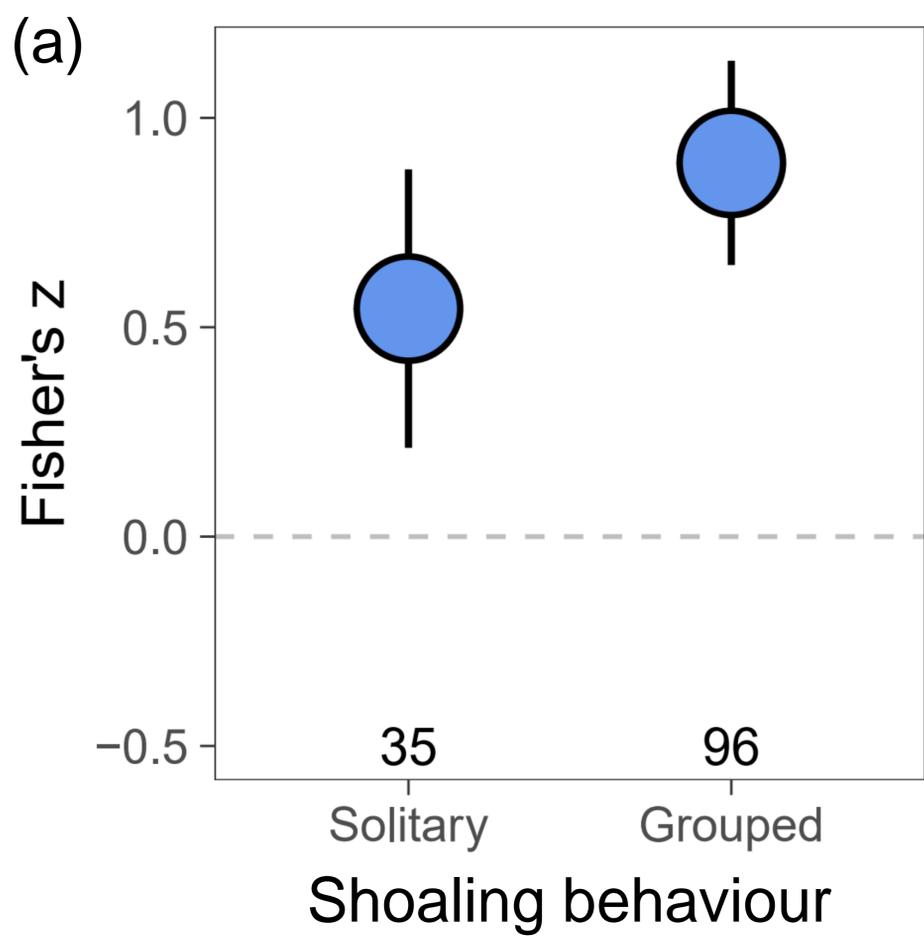
778 **Figure 3.** Effects of (a) shoaling behaviour, (b) species' body size, (c) longevity, (d)  
779 trophic level, (e) environment and (f) area protection status on the body size-FID  
780 relationship. Plots (a), (e) and (f) show mean  $\pm$  95% confidence intervals. The number of  
781 species tested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

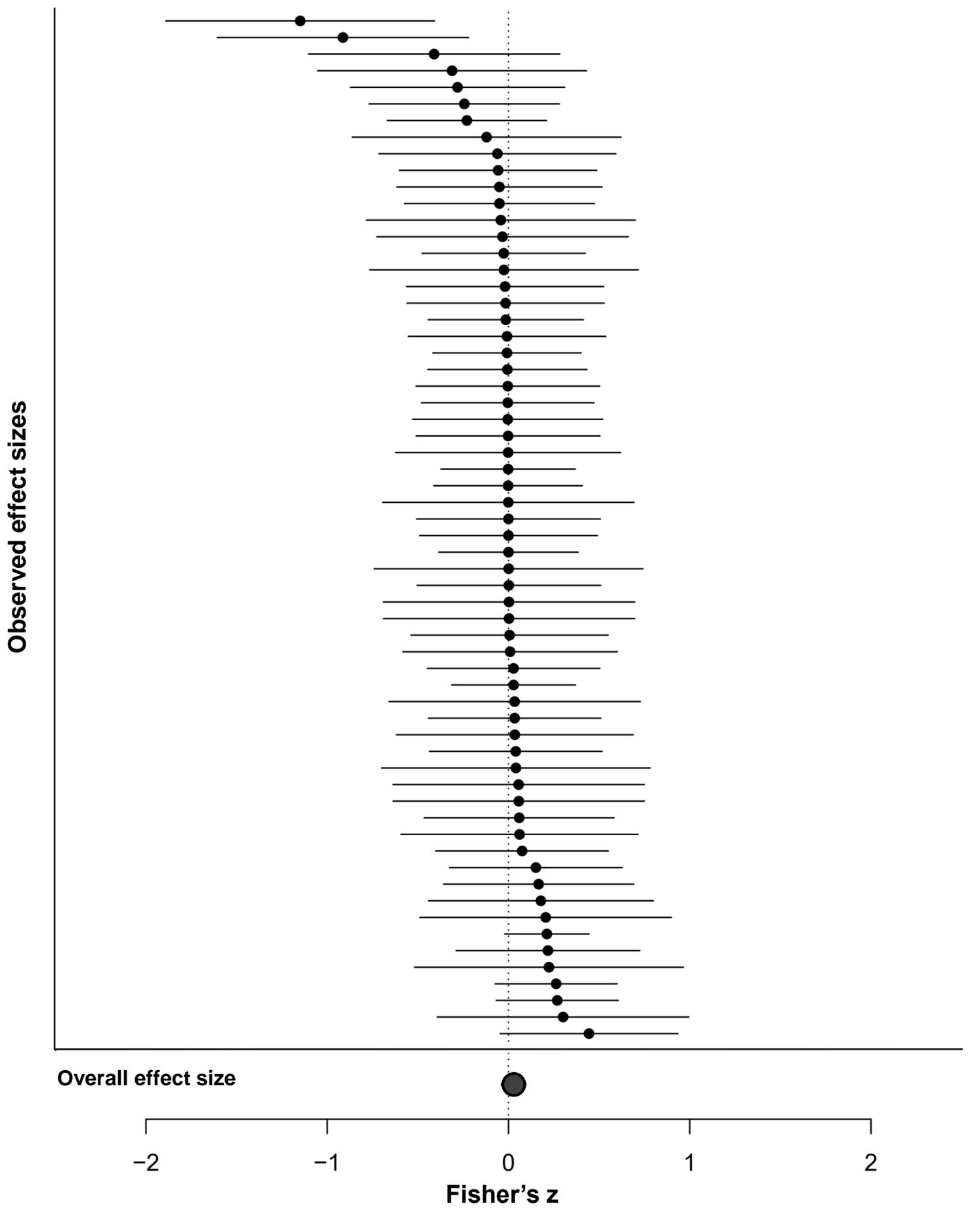
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783 **Figure 4.** Forest plot of the group size-FID effect sizes. Effect sizes are shown in  
784 ascending order. Filled circles with horizontal lines represent effect size  $\pm$  95%  
785 confidence intervals









<b>Moderator</b>	<b>Relationship</b>
Species' body size	Individual body size-FID  Shoal size-FID
Longevity	Individual body size-FID  Shoal size-FID
Shoaling behaviour	Individual body size-FID  Shoal size-FID
Trophic level	Individual body size-FID  Shoal size-FID
Habitat use	Individual body size-FID  Shoal size-FID
Conservation status of the studied area	Individual body size-FID  Shoal size-FID

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### Hypothesis

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Larger species should have a stronger individual body size-FID relationship.

Shoal size-FID relationships are weaker in larger species.

Species with longer life expectancies should have stronger individual body size-FID relationships.

Species with longer life expectancies should have weaker shoal size-FID relationships.

Species that shoal might have stronger individual body size-FID relationship than solitary species.

Species that often shoal may have greater shoal size-FID relationships.

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.

Shoal size-FID relationship is stronger in some trophic levels.

Demersal species should have weaker individual body size-FID relationships compared to pelagic species.

Demersal species should have lower shoal size-FID relationships compared to pelagic species.

Populations in unprotected areas should have stronger individual body size-FID relationships.

Population in unprotected areas should have a stronger shoal size-FID relationship.

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Rationale	References
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
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
Species with a longer life expectancy might be more cautious to guarantee that they reach maturity.	Blumstein 2006
Species with longer life expectancy often form small and scattered shoals weakening shoal size-FID relationship	Hoare et al. 2005
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
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
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
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	Rieucau et al. 2015
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
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
Big fish outside protected areas are preferentially targeted by fishers.	Johnston et al. 2012; Tsikliras and Polymeros 2014
The benefits from living in groups to better detect humans should be reduced within protected areas.	Goldenberg et al. 2014; Ioannou et al. 2017



## Supplementary Material

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

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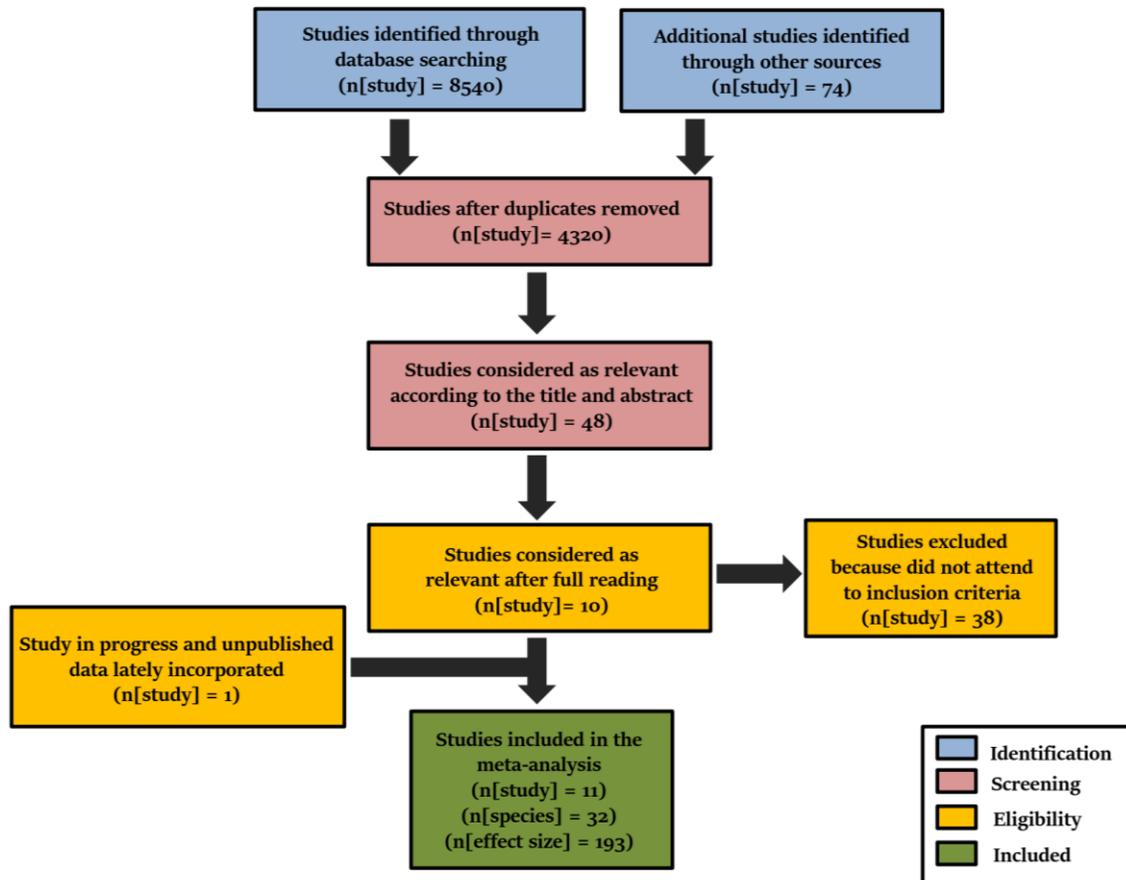
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**Appendix 2.** PRISMA diagram describing our literature search



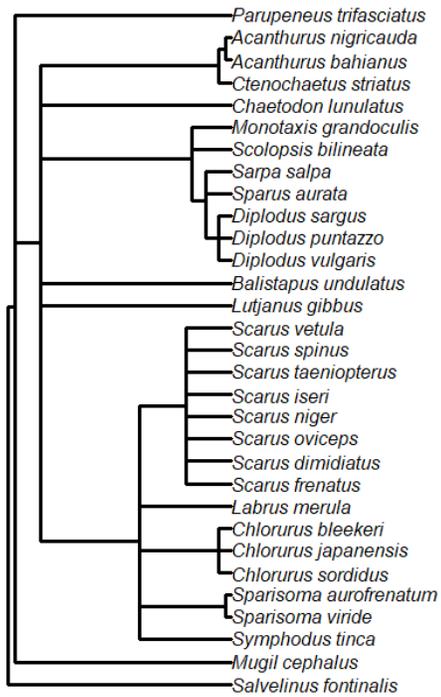
**Appendix 3.** Model selection for the most parsimonious combination among three random factors

<b>Meta-analysis</b>	<b>Study</b>	<b>Species</b>	<b>Phylogeny</b>	<b>AICc</b>	<b>ΔAICc</b>
<b><i>Body size-FID</i></b>					
Model 1*	●			324.55	0.00
Model 2	●	●		326.28	1.72
Model 3	●		●	326.68	2.13
Model 4		●		327.99	3.39
Model 5	●	●	●	328.44	3.89
Model 6		●	●	330.12	5.52
Model 7			●	331.29	6.97
Model 8				331.70	7.11
<b><i>Group Size-FID</i></b>					
Model 1*				-5.49	0.00
Model 2	●			-3.28	2.21
Model 3		●		-3.28	2.21
Model 4			●	-3.28	2.21
Model 5	●	●		-0.99	4.50
Model 6	●		●	-0.99	4.50
Model 7		●	●	-0.33	5.16
Model 8	●	●	●	1.38	6.87

The random factors are the study's identity to account for multiple effect sizes per study ("study"), species' identity to account for multiple effect sizes per species ("species") and the phylogenetic relationship to deal with the potential evolutionary dependency among species. AICc, Akaike information criteria corrected by sample size. ΔAICc, difference in relation to the best model, i.e., the model with the lowest AICc. The best models are indicated by asterisks.

**Appendix 4.** Phylogeny of species included in the meta-analysis

**Body size-FID meta-analysis**



**Group size-FID meta-analysis**

