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A meta-analysis 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

1 | INTRODUCTION

Avoiding predators is an important part of an animal's life that has profound influences on morphology, metabolism and behaviour (Arnett & Kinnison, 2017; Dalton, Tracy, Hairston, & Flecker, 2018; Ferrari et al., 2015). Avoiding predators may involve 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 (Blanchard, Blanchard, Rodgers, & Weiss, 1990; Ydenberg & Dill, 1986).

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 are low (Cooper & Frederick, 2007; Ydenberg & Dill, 1986). FID is one of the most commonly studied variables in the animal anti-predatory literature (Cooper & Blumstein, 2015; Geffroy, Sadoul, & Ellenberg, 2017; Samia, Blumstein, Blumstein, Stankowich, & Cooper, 2016) and sheds light on species' cognitive abilities and the evolutionary history of predator–prey interactions (Blumstein, 2006; Cooper, Pyron, & Garland, 2014; Møller & Erritzøe, 2014; Samia, Nakagawa, Nomura, Rangel, & Blumstein, 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 (Bergseth, Williamson, Williamson, Russ, Sutton, & Cinner, 2017; Geffroy et al., 2018; Januchowski-Hartley, Graham, Cinner, & Russ, 2015; Sbragaglia et al., 2018).

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

An important intrinsic driver of FID of fish is body size. Several studies have identified the positive link between individual fish size and FID in exploited populations (Benevides, Nunes, Costa, & Sampaio, 2016; Gotanda, Turgeon, & Kramer, 2009; Januchowski-Hartley, Graham, Feary, Morove, & Cinner, 2011; Sbragaglia et al., 2018). A seemingly reasonable assumption to explain this correlation involves fish fitness-related traits (i.e. age and size; Uusi-Heikkilä et al., 2015). First, larger fish are often the preferential target of fisherman; thus, they are more responsive to the threat (Johnston, Arlinghaus, & Dieckmann, 2013; Tsikliras & Polymeros, 2014). Second, larger fish are generally older, so assuming a learning mechanism, they have more experience with threats (Samia et al., 2016). Third, the relative fitness (in terms of reproductive output) is much higher in larger individuals than

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smaller ones. For example, a large female produces disproportionately more offspring than the same body mass' worth of smaller females (Barneche, Robertson, White, & Marshall, 2018) and also produces larvae with a greater chance of survival (Birkeland & Dayton, 2005). Thus, the correlation between FID and body size is of paramount importance in characterizing fish response towards humans. Protecting old and big fishes has become a priority for fisheries management and conservation policies (Collette et al., 2011; Gwinn et al., 2015; Jørgensen et al., 2007).

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

In addition to the negative impacts of harvesting activities, some fish populations are constantly exposed to a massive presence of tourists which may create a suite of physiological and behavioural consequences (Geffroy, Samia, Bessa & Blumstein, 2015; Geffroy et al., 2018). Indeed, the popularity of both snorkelling and diving activities has massively increased over the past several decades,

and there are an estimated 22 million divers worldwide (Musa & Dimmock, 2013). Recent studies demonstrate that SCUBA diving has impacted fish for the past 60 years (Rowe & de Santos, 2016) and spearfishing has also increased, often preferentially targeting the largest individuals (Giglio, Bender, Zapelini, & Ferreira, 2017). With increasing anthropogenic impacts, coastal ecosystems, particularly rocky and coral reef, are arguably the most impacted by both divers and fishers. Traditional methods employed to quantify the human "footprint" on fish populations focus on fish biomass assessment at both global (Cinner et al., 2018) and local (e.g. Goetze et al., 2017) scales. However, biomass estimates are often highly variable (McClanahan, Graham, Calnan, & MacNeil, 2007), which can mask both positive effects of management and lack of effect or compliance. Nevertheless, if FID varies consistently with both individual size and shoal size in different fish species, it has the potential to be a good proxy for the management status or intensity of human disturbance of a focal population (Benevides, Pinto, Nunes, & A. C. C., & Sampaio, C. L. S., 2018; Goetze et al., 2017).

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

2 | METHODS

2.1 | Literature survey

We used the Web of Science and Google Scholar databases to search for papers published before 1 April 2016. We used the following terms in our search in these databases: "fish*" AND ("flight initiation distance" OR "flight distance" OR "escape distance" OR "approach distance" OR "flushing distance" OR "response distance"). We checked all references of the retained papers to identify studies not located by our keywords survey. We also searched for relevant papers cited by the main reviews about escape theory (Cooper & Blumstein, 2015; Stankowich & Blumstein, 2005; Ydenberg & Dill, 1986). Non-published data were also included in the meta-analysis (see Appendix S1). The inclusion criterion was that studies must have tested the effect of body size and/or group/shoal size on FID of fishes approached by humans. A PRISMA diagram describing our literature search is available in Appendix S2. The data set of the fish individual body size-FID meta-analysis consisted of 131 effect sizes from 11 studies across 31 species distributed across 12 families

(Appendix S1). The group size-FID meta-analysis consisted of 62 effect sizes from 5 studies across 22 species distributed across 7 families (Appendix S1).

2.2 | Estimating effect sizes

We used Pearson's product-moment correlation coefficient, r , as our measure of effect size. Here, r represents the magnitude of the fish individual body size-FID relationship and the fish shoal size-FID relationship. Positive r -values represent a positive body size-FID relationship (i.e. that larger individuals flee sooner from humans than small individuals) and a positive shoal size-FID relationship (i.e. that individuals in larger shoals flee sooner from humans than solitary individuals or those in smaller shoals). Conversely, negative r -values represent a negative individual body size-FID relationship (i.e. that smaller individuals flee sooner from humans than larger individuals) and a negative shoal size-FID relationship (i.e. that solitary individuals or those in smaller shoals flee sooner from humans than individuals in larger shoals). When raw data were 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 (Cohen, 1992; Jennions & Møller, 2002). For analysis, r -values were transformed to Fisher's z to improve normality of data (Koricheva et al., 2013).

We used the raw data to calculate the effect sizes from Januchowski-Hartley's studies (Januchowski-Hartley, Graham, Cinner, & Russ, 2013; Januchowski-Hartley et al., 2011; Januchowski-Hartley, Nash, & Lawton, 2012). We therefore opted to include only those effect sizes with $N \geq 10$ 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) tends to homogenize the weight of individual effect sizes on the overall mean effect size independently of their sample size (Borenstein, Hedges, Higgins, & Rothstein, 2009; Koricheva et al., 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).

We used model selection to determine which random factors should be included in each meta-analysis (Nakagawa & Santos, 2012).

TABLE 1 List of hypotheses concerning moderators used to explain variation in body size-FID and group size-FID relationships in fish

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, Godin, and Brown (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, Krause, Peuhkuri, and Godin (2000)
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, Buhl, Hu, Ward, and Sumpter (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.	Capizzi 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	Rieucan, Fernö, Ioannou, and Handegard (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), José de Anchieta, Sampaio, and Barros (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.	McCormick, Chivers, Allan, and Ferrari (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. (2013); 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, Borcharding, and Heynen (2014); Ioannou, Ramnarine, and Torney (2017)

We controlled for non-independence of effect sizes within studies by including “study identity” as a random factor in the body size-FID model (Appendix 3). Data could exhibit non-independence caused either by phylogenetic inertia or by multiple estimates per species, and the model selection showed that inclusion of “phylogeny” and/or “species identity” as additional random effects did not improve the model (Appendix 3). Indeed, a model without random factors was the most parsimonious for the group size-FID meta-analysis (Appendix 3).

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

We used I^2 index as a measure of heterogeneity in the effect sizes in which the value represents the proportion of total variation in data that is not due to sampling error (0%—all sampling error; 100%—no sampling error) (Higgins, Thompson, Deeks, & Altman, 2003). We used an extended version of I^2 that partitions the total heterogeneity among different sources: variation explained by study identity and by the residual variation (i.e. that which remained to be explained by the predictor variables; (Nakagawa & Santos, 2012). We calculated the degree of phylogenetic signal in our effect size estimates using the phylogenetic heritability index, H^2 , which is the variance attributable to phylogeny in relation to the total variance expected in the data (Nakagawa & Santos, 2012). When the unit of analysis is species, H^2 is equivalent to Pagel's λ (Pagel, 1999), in which higher values are associated with stronger phylogenetic signals. Primary studies can suffer from publication bias, where studies with low sample size are more prone to be rejected due to their higher probability of not finding significant effects (Egger, Smith, Schneider, & Minder, 1997; Koricheva et al., 2013). We checked for publication bias using Egger's regression, in which intercepts significantly different from zero suggest potential publication bias (Egger et al., 1997). To overcome the non-independent nature of our data, we also applied the Egger's regression test on the meta-analytic residuals (Nakagawa & Santos, 2012). Analyses were conducted using the *metafor* R package v.2.0–0 (Viechtbauer, 2010).

2.4 | Moderators

A growing body of literature explains how species' morphology, life-history and natural history traits, as well as environmental and ecological traits, could impact the anti-predatory response of animals (Blumstein, 2006; Samia et al., 2016; Samia, Møller, & Blumstein, 2015b; Samia, Nakagawa, et al., 2015a). Here, we focused on six factors that we hypothesize that could impact the magnitude and direction of both individual body size-FID relationship and shoal size-FID relationship, namely species' shoaling behaviour (solitary vs. grouped), mean body size (cm),

longevity (years), species' trophic level (continuous variable varying from 2 to 4: the lower the number, the more basal is the species in a trophic chain), species' habitat use (demersal vs. pelagic) and protection status of the area (populations inside vs. outside protected areas). See Table 1 for rationale for each moderator. The variables shoaling behaviour, body size and protected area data were obtained from the primary papers. The remaining information was extracted from the FishBase website (<http://www.fishbase.org>). Importantly, multicollinearity was not an issue for our selected moderators (variance inflation factors < 1.15, below the suggested threshold of 3, (Zuur, Ieno, & Elphick, 2010).

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

2.5 | Multimodel inference

We used a multimodel inference approach based on Akaike's criteria corrected for small sample size (AICc) (Burnham & Anderson, 2002). To calculate the relative importance of each predictor, we first assessed the relative strengths of each candidate model by calculating its Akaike weight, to identify the most parsimonious model. A constant term (intercept) was included in all models. We estimated the importance of a predictor by summing the Akaike weights of all models in which that candidate variable appeared. This allowed to rank predictors in order of importance (Burnham & Anderson, 2002). We finally used a model averaging approach to estimate model parameters (Burnham & Anderson, 2002). Multimodel analyses were conducted using the *MuMIn* R package v. 1.40.0 (Barton, 2014).

3 | RESULTS

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

Overall, individual fish size was strongly and positively correlated with FID (Fisher's $z = 0.777$, $CI = 0.518 - 1.036$, Figure 1). We found

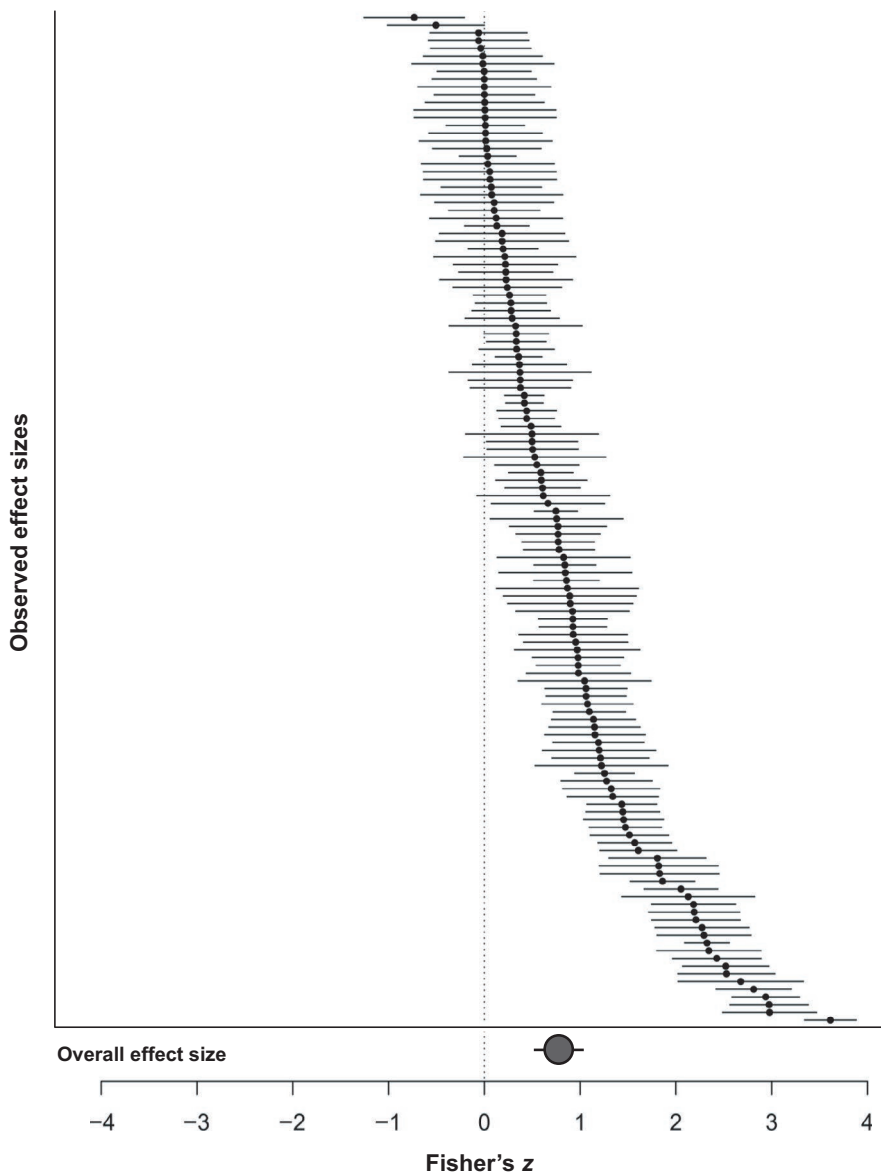


FIGURE 1 Forest plot of the body size-FID effect sizes. Effect sizes are shown in ascending order. Filled circles with horizontal lines represent effect size \pm 95% confidence intervals

considerable variation among effect sizes, with most of them having some variation that was explained by moderators ($I^2_{\text{total}} = 92.99\%$, $I^2_{\text{studies}} = 12.09\%$, $I^2_{\text{residual}} = 80.90\%$). The amount of heterogeneity found matches with that found in most ecological and evolutionary studies (Senior et al., 2016). There was a weak phylogenetic signal in the relationship between body size and FID ($H^2 = 2.92\%$). We found no evidence that potential publication bias affected the results (Egger's regression of effect sizes: Intercept = -1.256 , $p = 0.250$; Egger's regression of meta-analytic residuals: Intercept = -0.902 , $p = 0.397$; Figure 2).

The multimodel inference indicated that shoaling behaviour was the most important predictor of the magnitude of body size-FID relationship (Table 2). Species that shoal display a stronger and more positive individual body size-FID relationship compared to solitary species (Table 2 and Figure 3). The importance index of shoaling behaviour was two times larger than the second most important variable, the species' body size (Table 2, Figure 3). Species' body size

was followed by longevity, trophic level, environment and protected area with modest differences in their importance indexes (Table 2, Figure 3).

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

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

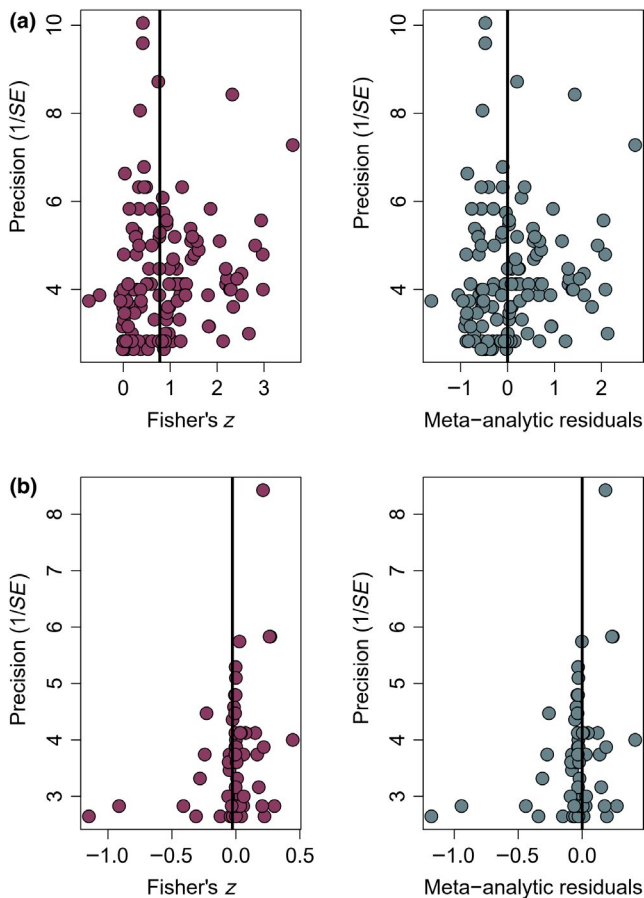


FIGURE 2 Funnel plots of (a) body size-FID and (b) group size-FID meta-analyses using both the effect sizes and the meta-analytic residuals

Intercept = -1.177 , $p < 0.001$; Egger's regression of meta-analytic residuals: Intercept = -1.177 , $p < 0.001$; Figure 2).

4 | DISCUSSION

Predator avoidance has a profound effect on individual fitness by allowing animals to escape from potential predators, including humans. Our first meta-analysis revealed that in almost all species investigated, FID was strongly and positively correlated with body

length. Shoaling behaviour was the most important predictor of the individual body size-FID relationship, with solitary species being less affected by individual size in their escape response compared to more gregarious species. Finally, our meta-analysis found no effect of shoal size on FID of fish. Interestingly, despite the large number of species studied, the results of shoal size showed absence of heterogeneity in data, which suggest highly conserved phenomena across species (Senior et al., 2016).

The positive relationship between body size and FID has been reported in birds (Møller, Samia, Weston, Guay, & Blumstein, 2014; Møller, Stokke, & Samia, 2015; Samia, Nakagawa, et al., 2015a) and lizards (Samia et al., 2016), particularly in unexploited or undisturbed populations (Samia, Nakagawa, et al., 2015a). Yet it is important to realize that predator avoidance strategy is highly species-specific (Domenici, 2010; Hodge et al., 2018), and while fish size is a reasonably good predictor of FID, various confounding factors can influence escape abilities. While experience accumulated with age (i.e. through learning) might partly explain why bigger fish flee at a greater distance (Kelley & Magurran, 2003), we could also expect that larger prey would have tolerated closer approach from predators than small prey, at both intra- and inter-specific levels. Life-history theory predicts that as reproductive value increases, risk-taking decreases (Cooper & Frederick, 2007). For example, fish reproductive potential rises markedly with size in females, when considering energy accumulated within eggs and their number (Barneche et al., 2018). Hence, the higher the reproductive output (and thus, the size), the higher the FID. Many alternative hypotheses have been highlighted to explain why larger fish flee at a greater distance than smaller fishes (Domenici, 2010). These hypotheses could be directly linked to the long-time evolutionary arms race between predators and prey, where morphological defences such as armour evolved in response to greater predation risk (Hodge et al., 2018), or they could be linked to energy requirements where smaller fish must act bolder to obtain food, or smaller fish pay a relatively higher opportunity cost for leaving—particularly if they are successfully foraging (Dill, 1990; Grand & Dill, 1997; Paglianti & Domenici, 2006; Polverino, Bierbach, Killen, Uusi-Heikkilä, & Arlinghaus, 2016). At a shorter time scale, larger (and older) fish might also have developed greater escape reactions because they have been longer exposed to fishing pressures (Biro & Post, 2008; Johnston et al., 2013; Tsikliras &

TABLE 2 Summary of the multimodel inference conducted to explain variation in the body size-FID relationship in fish

Predictor	Levels	Estimate	SE	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

Note: Estimates are average coefficients of the model, their associated standard error (SE) and the importance of each factor in explaining species responses to human disturbance (the closer than 1, the most important the factor).

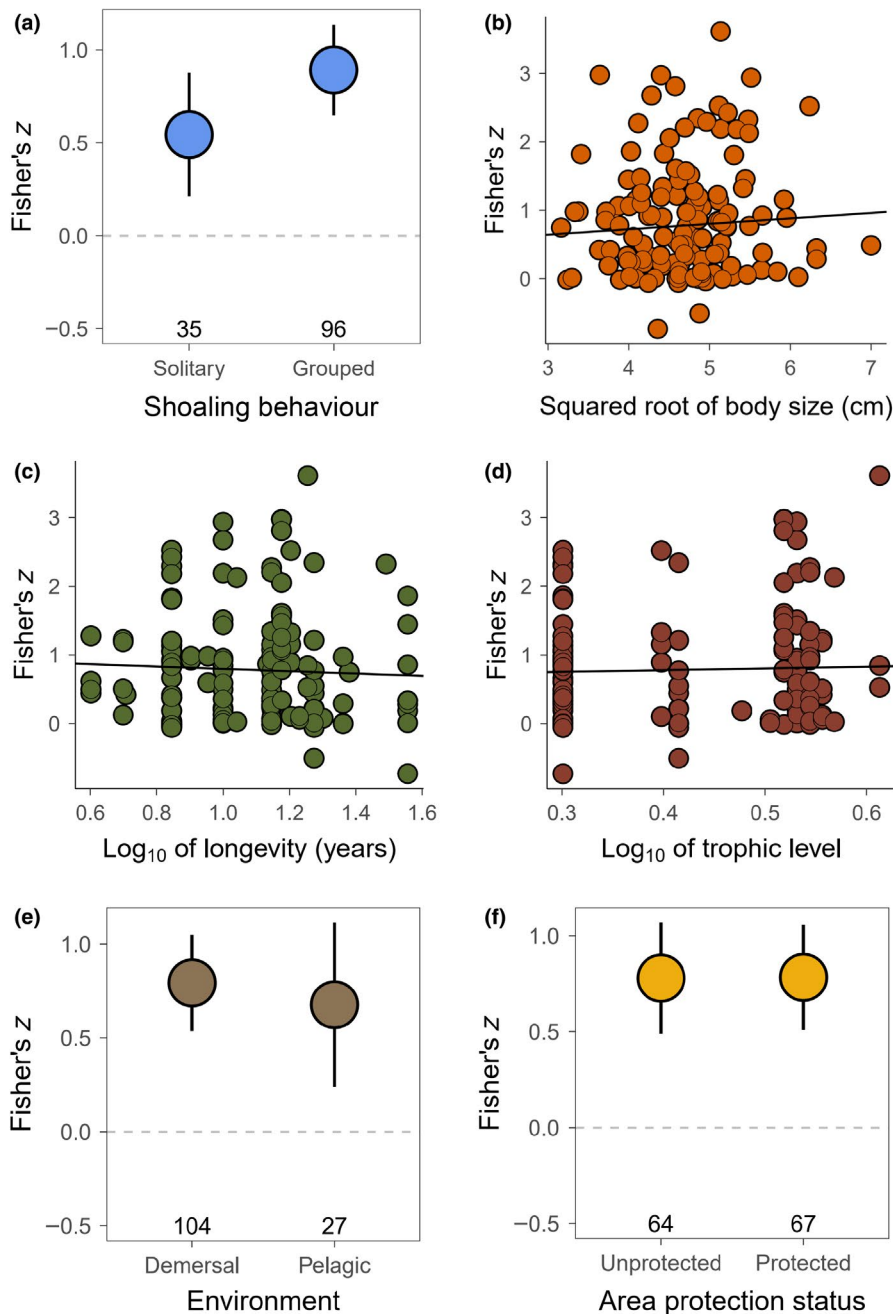


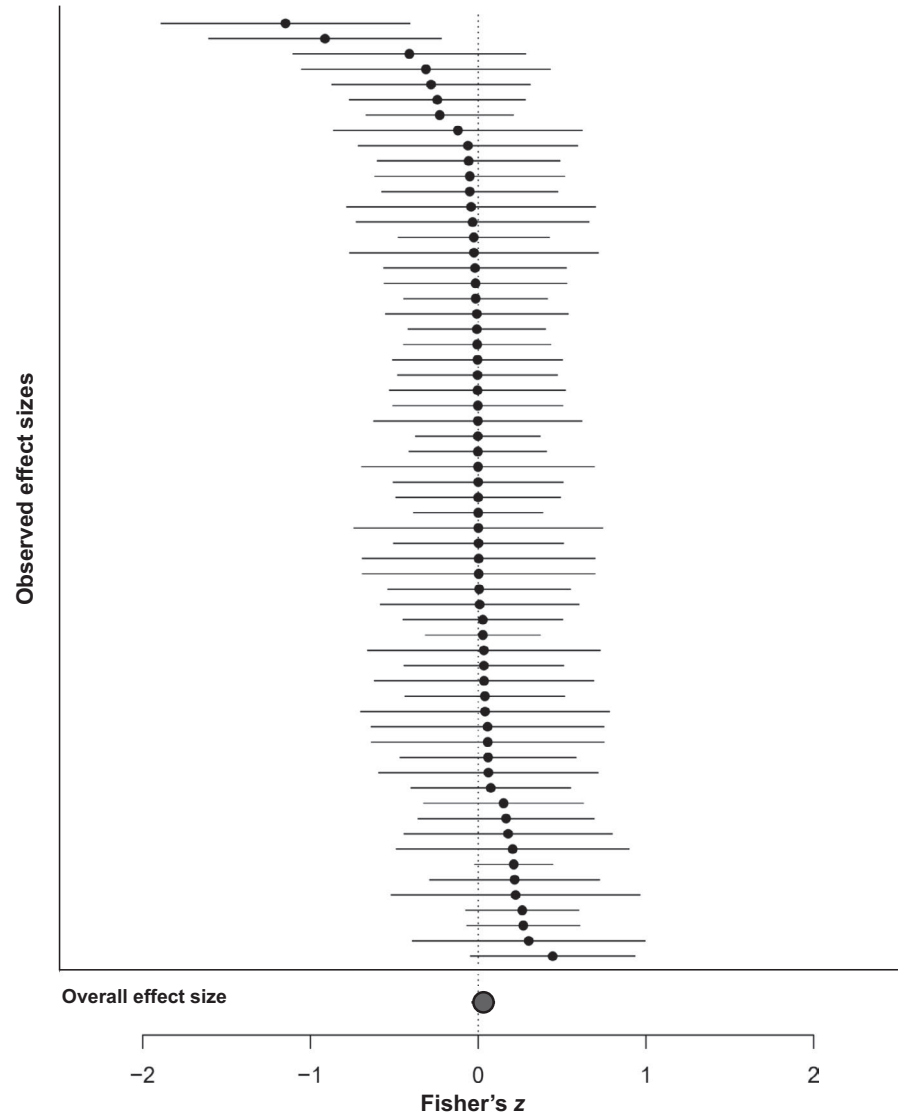
FIGURE 3 Effects of (a) shoaling behaviour, (b) species' body size, (c) longevity, (d) trophic level, (e) environment and (f) area protection status on the body size-FID relationship. Plots (a), (e) and (f) show mean \pm 95% confidence intervals. The number of species tested at each factor level is shown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

Polymeros, 2014). To date, no single factor explains the intra-specific correlation between FID and fish size, and it may have emerged from the interaction of several variables.

Shoaling and habitat preferences were recently recognized as two major ecological traits that balance the evolutionary trade-offs in antipredator morphological adaptations in fishes (Hodge et al., 2018). Here, we also show that shoaling behaviour is of primary importance to explain the strength of the relationship between individual body size and FID, while habitat preference is a relatively minor factor in explaining this relationship. The size of individuals of solitary species has less effect on escape response than individual size in group-living species. It is known that social group size positively influences vigilance in animals (Lima, 1995; Pitcher, 1986; Ward et

al., 2011). Yet, the absence of a group size effect on FID, but the major effect of grouping on the body size-FID relationship suggests that being gregarious (or not) is more important in explaining fish escape response than the size of the group per se. Another interpretation is that there is an optimal balance between two forces acting on group size. Both dilution effect and detectability by the predators increase with group size, making a larger group more conspicuous to predators, but although individuals therein are less likely to be targeted individually, throughout their lifetime, they are attacked more often. Therefore, even if vigilance adds just a small contribution to survival, during an individual's life span, it becomes quite important, contributing to safety perception (Dehn, 1990). Solitary or paired species often rely on morphological defences, such as

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



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

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

We also did not find that longevity, trophic level or an area's protected status explained much variation in the body size-FID relationship. Species with longer life expectancies were expected to be more cautious (longer FID) to guarantee that they reach maturity (Blumstein, 2006). Larger species ranking low in the food chain were expected to be preferred by predators because they provide more energy intake than smaller species from the same trophic level; moreover, species ranking higher in the food chain have fewer predators, and thus, the selective pressure on them should be weaker along the evolutionary time (Capizzi, Luiselli, & Vignoli, 2007). While this could be expected for the two former variables, this was less expected for marine protected areas. Indeed, larger fish outside protected areas are preferentially targeted by spearfishers, while all fish are protected within conservation zones, regardless of their body size. Indeed, recent studies have shown that large fish become more wary when FID is measured during the fishing seasons in periodically harvested areas (Goetze et al., 2017) or outside permanent marine protected (Sbragaglia et al., 2018). Our meta-analysis that used a substantially larger data set could not detect such a pattern.

Two explanations are possible. First, Goetze et al. (2017) used only remote video sensing that provided a minimum approach distance (MAD) data instead of FID. Importantly, MAD can be recorded even when flight does not occur, so that MAD is generally larger than FID. Second, Sbragaglia et al. (2018) focused only on highly exploited species, while we incorporated data on fish also exposed to non-consumptive tourism.

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

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

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

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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