



Weak evidence for a relationship between group size and flight initiation distance in response to underwater human presence in an exploited fish species

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Abstract

Group size can influence flight initiation distance (FID), a key antipredator behavior, in many animal species. In fishes, however, the effect of group size on FID remains unclear. Two different mechanisms might explain a putative relationship between group size and FID. If fish benefited from having more vigilant individuals around, we would expect group size to be positively associated with FID (considering collective vigilance in the context of the many eyes hypothesis). By contrast, if fish benefited from a predator dilution effect, we would expect group size to be negatively associated with FID. Importantly, such relationships should be critically sensitive to background risk levels. We capitalized on FID observations inside and outside marine protected areas and simulated risk by having a risky spearfisher or a non-risky snorkeler swim towards white seabream (*Diplodus sargus*) to estimate the relationship between FID and group size. Model selection provides weak evidence that group size positively influences FID of white seabream when group size was modelled two ways: categorically (alone vs. shoal), and continuously (range 2–15). While the results suggest that overall group size has a measurable impact on FID, the presence of spearfishers or snorkelers had a weak effect on the relationship of group size and FID, which seems to be more sensitive exclusively to the protection level (inside/outside marine protected areas). Our findings align with previous studies showing mixed results on the relationship between group size and FID. This study underscores the complexity of antipredator behaviors in natural settings and suggests that multiple interlinked factors, rather than group size alone, drive FID in fishes. Future research should integrate field observations, laboratory experiments, and modeling to study the ecological influence of group size on FID more comprehensively.

Significance statement

The relationship between group size and flight initiation distance is a key component to understand predator-prey interactions in fishes, but empirical support for such relationship is mixed. We used an experimental system where the relationship between group size and flight initiation distance of an exploited fish is measured across a gradient of risk associated to underwater human presence (i.e., spearfishing/snorkeling and inside/outside marine protected areas). We found weak evidence for group size to influence flight-initiation distance in response to risk associated to underwater human presence; rather protection level seems to be the most important factor influencing it. These results highlight the complexity of studying antipredator behavior in fishes and underscores the need for integrative approaches (laboratory-field-modelling) to fully understand the ecological influence of group size in predator-prey dynamics.

Keywords Fear · Predator-prey · Human predator · Marine protected areas · Fishing · Mediterranean sea

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Introduction

When exposed to the risk of predation, animals engage in a variety of anti-predatory behaviours, including escape. The distance at which animals escape from an approaching predator (i.e., flight initiation distance, FID; Ydenberg and Dill 1986) has been extensively used to study predator-prey behavioural interactions, and to gain insights into how humans are perceived as potential predators (Stankowich and Blumstein 2005; Cooper and Blumstein 2015; Samia et al. 2016, 2019; Nunes et al. 2018). In this context, when humans are apex predators, there may be profound effects of animals responding fearfully to them and this may drive ecological and evolutionary dynamics (Arlinghaus et al. 2017; Suraci et al. 2019). However, fear of humans also provides an opportunity to test specific hypotheses because, for example, underwater human activity (e.g., snorkelers and spearfishers; Sbragaglia et al. 2018) and level of exploitation by humans (e.g., fished vs. unfished areas; Januchowski-Hartley et al. 2011) can be used as an experimental treatment in empirical research (Sbragaglia et al. 2023).

Flight initiation distance may be influenced by a number of external factors that together determine an optimal anti-predator response. Group size is one important external factor that influences FID in many group-living species (Stankowich and Blumstein 2005). In aquatic ecosystems, fish shoaling behaviour— i.e., the action of forming social groups, from the simplest form of aggregation and interactions in time and space to coordinated movements such as schooling— has a strong ecological value (Pitcher 1986). Several interlinked and non-mutually exclusive hypotheses support the ecological value of fish shoaling behaviour (Lehtonen and Jaatinen 2016). Some hypotheses focus on prey such as the “many eyes hypothesis” (Lima 1995), the “dilution effect hypothesis” (Foster and Treherne 1981), or simply highlight that grouping increases coordinated movement to escape predators (Handegard et al. 2012). By contrast, other predictions focus on predators such as the “confusion effect” (Milinski 1977; Ioannou et al. 2009).

In the context of understanding how FID is influenced by group size, there are two main hypotheses that deserve specific attention because they predict a decrease of the individual probability of predation as a function of increased group size. The “many eyes hypothesis” (Lima 1995) suggests that as the size of a group increases, the overall vigilance effort required from each individual decreases. This happens because there are more individuals available to scan the environment for potential threats, increasing the likelihood of detecting predators or other dangers. The result is that each individual can afford to spend less time being vigilant because they can rely on the vigilance of other group members. This allows individuals to allocate more time

and energy towards other activities such as feeding or resting while still maintaining the individual safety by being in groups (Lima 1995). The “dilution effect hypothesis” is another mechanism (Foster and Treherne 1981) assuming that the risk of predation for an individual prey decreases as the number of prey in a group increases. This is based on the principle that predators have a limited capacity to consume prey (i.e., one single prey of the group at a time), and that grouping does not increase attractiveness to predators - an assumption that may be violated in large schools of fishes (Pitcher 1986; Lehtonen and Jaatinen 2016). These two hypotheses could make contrasting predictions; The many eyes hypothesis predicts that FID will increase with group size (i.e., more eyes detect predators faster), but this prediction holds only when FID is measured as a collective response of the group (i.e., collective vigilance). In the case in which the focus is a target fish in the group, FID could decrease with group size (i.e., individual vigilance decreases with increasing group size which is associated with decreasing individual efficiency to detect predators and leads to a shorter FID). While the predator dilution hypothesis predicts that FID will decrease with group size (i.e., there is a decreasing likelihood of predation with increasing group size which leads to a shorter FID).

Evidence on the general relationship between FID and group size is mixed, which means that some species tolerate a closer approach when in larger groups, while other species are seemingly better able to detect approaching threats in groups and thus initiate flight at a greater distance (Stankowich and Blumstein 2005). A previous meta-analysis showed that group size had no overall significant effect on FID, but when taxonomic level was considered, fish were found to tolerate closer approach by simulated natural predators when grouped, while other taxa were more sensitive when grouped and fled at greater distances (Stankowich and Blumstein 2005). Recent empirical studies showed mixed evidence for a relationship between group size and FID in fishes, especially in response to underwater human presence (Samia et al. 2019). Two studies found a significant positive relationship between FID and group size in response to underwater human presence. Januchowski-Hartley et al. (2011) simulated the action of spearfishers on six families of fishes across four areas with varying levels of fishing pressure and found a positive relationship between FID and group size in only one family (i.e., one of the highly exploited: Acanthuridae). They also found that the relationship between FID and group size was seen in all four areas, a finding that suggested that this antipredator behaviour was not sensitive to fishing pressure. Similarly, Benevides et al. (2018) simulated the action of a spearfisher on three species differentially exposed to fishing pressure inside and outside management areas created for fishing and tourism activities.

They found a positive relationship between FID and group size in two species - the highly exploited *Epinephelus adscensionis* when studied outside a management area for fishing, and *Acanthurus bahianus* which had a longer FID in larger groups outside a management area for tourism activities (Benevides et al. 2018). Other studies reported different results. Gotanda et al. (2009) simulated the presence of a SCUBA diver as a possible threat to parrotfish inside and outside marine protected areas and found no strong differences in FID for solitary fish compared to fish in a group. Benevides et al. (2016) simulated spearfishing of the barber surgeonfish (*Acanthurus bahianus*) in a fished area and did not find any effect of group size on FID. Also, Nunes et al. (2016) simulated spearfishing with SCUBA in fished and unfished areas on two exploited (*Sparisoma axillare* and *Scarus trispinosus*) and one non-exploited (*Halichoeres poeyi*) labrid species. They found no significant effects of group size on FID in any of the species. Therefore, the relationship between group size and FID in fishes and its ecological influence is still not properly understood. In particular, the risk of predation imposed by humans offers an ideal context to study the relationship between group size and FID. Indeed, none of the above mentioned studies measured the relationship between FID and group size inside and outside marine protected areas in the presence of two different types of underwater human activities— spearfisher and snorkeler, which could contribute to better understand the mixed results obtained so far. In a previous study, Sbragaglia et al. (2018) showed how the presence of spearfishers or snorkelers inside/outside marine protected areas created an experimental gradient of perceived risk by fish with the highest risk in the presence of a spearfisher outside a marine protected area, and lowest risk in the presence of a snorkeler inside a marine protected area. Importantly, this gradient or perceived risk can have important implications on fishing mortality (Sbragaglia et al. 2024).

Here, we take advantage of these previous results by investigating the relationship between group size and FID in white seabream (*Diplodus sargus*), a gregarious species that is abundant in shallow water where it is exploited by spearfishers in the Mediterranean Sea (see methods for more details). We test the hypothesis that fish outside marine protected areas, where spearfishing is allowed (i.e., a high-risk situation), will show a stronger relationship between FID and group size when encountering a spearfisher, compared to fish inside marine protected areas where spearfishing is not allowed, when they encounter a snorkeler. Under the many eyes hypothesis (Lima 1995), and in terms of individual vigilance, FID is expected to decrease with group size and show shallower slopes in high-risk context than low-risk one. Similarly, according to the predator dilution hypothesis, FID is expected to decrease with group

size— and similarly to the individual vigilance case— have shallower slopes in the high-risk context than the low-risk one (Foster and Treherne 1981). By examining this scenario, we aim to better understand the relationship between group size and FID in response to underwater human presence in an exploited fish species.

Materials and methods

Study areas and species

Flight initiation distance was measured between May and October 2016 in three different marine protected areas of the Northwest Mediterranean Sea, specifically: Bonifacio Straits (established in 1999; size: 130 km²; Fig. 1), Corsica, France (protected zone survey: 4135.280 N, 921.760 E; non-protected zone survey: 4136.990 N, 921.190 E); Cerbère-Banyuls (established in 1974; size: 6.2 km²; Fig. 1), France (protected zone survey: 4228.580 N, 39.400 E; non-protected zone survey: 4229.310 N, 37.790 E); and Medes islands (established in 1983; size: 1 km²; Fig. 1), Spain (protected zone survey: 422.670 N, 313.400 E; non-protected zone survey: 426.200 N, 310.500 E).

Adult white seabream are residential and territorial species (Macpherson 1998; Giacalone et al. 2022), with home ranges of between 0.5 and 393 ha (Giacalone et al. 2022). Adult white seabream can reach a maximum length of more than 55 cm and maximum body mass around 2 kg, and it is common to find them in shallow water rocky reef areas up to 50 m depth (Giacalone et al. 2022). White seabream are subjected to semi-industrial, artisanal and recreational fishing with various types of gear, and they are highly desired by recreational spearfishers (Sbragaglia et al. 2018). In particular, white seabream are gregarious, forming shoals that vary in size but generally consist of about 20–30 individuals (Macpherson 1998).

Experimental design and data collection

We measured FID and group size in response to two treatments under two conditions: two diver configurations (potentially threatening spearfishing with a speargun and non-threatening snorkeling without a speargun) in two different areas with different levels of harvesting protection status (protected/unprotected from spearfishing). All observations were conducted at a minimum distance of 750 m from the MPA borders, to avoid potential spill over of naive fish from the MPAs (Januchowski-Hartley et al. 2013). All sites were surveyed by the same observer collecting observations at similar depth (between one and three meter) and habitat type (a mix of rocky reefs and posidonia meadows)

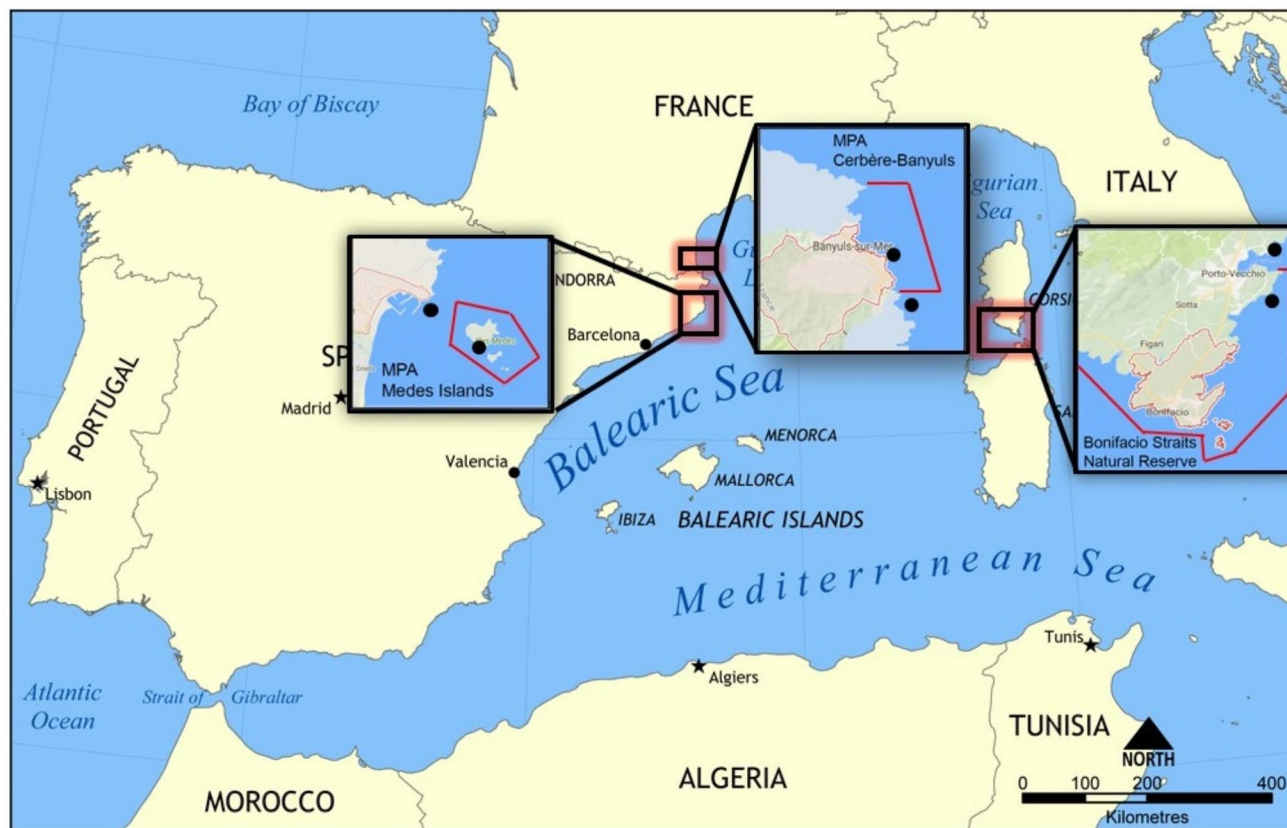


Fig. 1 The three areas where we collected the data presented in this study Bonifacio Straits, Cerbère-Banyuls, Medes islands. Inlets represent a zoom of each area where borders of the marine protected areas

are represented by the red lines and the sampling points (inside and outside marine protected areas) by the black dots. More information is reported in the main text

across areas to avoid possible confounding effects of uncontrolled variables such as habitat complexity or habitat type (Nunes et al. 2015). Observations were collected along one random transect per day by applying two treatments under two conditions in each day (four days in total for each area: snorkeler/spearfisher and inside/outside protected area). The two treatments (snorkeler/spearfisher) were applied randomly across the two conditions (inside/outside protected area) during the four days across a maximum of seven days (i.e., observations sometimes were not collected during four consecutive days). The spearfisher was equipped with a speargun (100 cm long, slings were removed and substituted with PVC tubes to not violate regulations of the MPAs) and with the typical spearfishing equipment (black wetsuit, long black fins and black mask). The snorkeler's equipment consisted of a short blue wetsuit, short blue fins and a coloured mask.

The observer swam on the surface along a linear transect, identifying the target fish from the surface, and then swimming on the surface towards it at a steady speed of ± 0.5 m/s. When fish were in groups, the observer randomly selected one fish of the shoal as target fish. When the fish fled, the observer recorded the FID (by marking his position with a

small weight connected to a metric rope that was used to calculate the distance to the point at which the fish fled), and number of fish in the shoal. Consecutive measurements were conducted a minimum of 10 m apart, and in the opposite direction to which a disturbed fish fled, to ensure independence of samples within sites. Considering the protocol used to measure FID, it was not possible to record data blind because our study involved target fish in the field.

Data analysis and statistical approach

Considering that fishing may have consequences on shoaling behaviour and that there may be density dependent effects on shoal size (Sbragaglia et al. 2021), it is conceivable to expect that outside of marine protected areas—where most fishing activities are allowed—white seabream population density may be reduced and consequently the lower encounter rate between individuals may result in smaller group sizes compared to those inside marine protected areas (Sbragaglia et al. 2021). Therefore, we tested possible differences in group size inside and outside protected areas as a potential confounding effect. First, we implemented a generalized linear model with a binomial distribution to model

group size as a binary variable: 0 (solitary individuals) and 1 (group size > 1). Then we used protection level as a fixed effect (two levels; inside and outside marine protected areas) and the three areas (Bonifacio, Banyuls, and Medes) were fitted as random effects. Second, we implemented a linear model with a Gamma family distribution with group size as a response variable (a numerical value from 2 to 15) and protection level as fixed effect.

Considering the high number of observations during which white seabream individuals were measured alone, we modelled the data with two different global models (i.e., including all hypothesized predictors and their interactions). The first global model was fitted with generalized linear mixed effects models with a Gamma family distribution because the response variable (FID) was positive-valued and skewed to the right. There were three interacting fixed effects: group size (a categorical variable with two levels; alone: group size = 1; shoal: group size > 1), diver configuration (2 levels: spearfisher and snorkeler), and level of protection (2 levels: protected and non-protected). The three areas (Bonifacio, Banyuls, and Medes) were fitted as random intercepts. The second global model was fitted with generalized linear models with a Gamma family distribution (we removed the random structure because the reduced and unequal number of observations across areas prevented model convergence during model selection where fitting multiple models with different combinations of predictors). In this second model the response variable was FID with three interacting fixed effects: group size (a numerical value from 2 to 15), diver configuration (2 levels: spearfisher and snorkeler), and level of protection (2 levels: protected and non-protected).

Model fit was examined by checking (see text S1 for results) several diagnostics. (i) Pearson residuals are a standardized residual used in generalized linear models and generalized linear mixed models (Cordeiro and Simas 2009). They are particularly useful for checking model fit, as they adjust the raw residuals by the estimated standard deviation of the response variable. We implemented a formal statistical approach to determine whether the model adequately fitted the data by assessing the goodness-of-fit of a model by conducting a Chi-square test comparing the sum of the squared Pearson residuals to the degrees of freedom of the model with a 95% confidence interval. (ii) The plot of residuals vs. fitted values which is an essential diagnostic tool to assess the assumptions of a regression model, including generalized linear mixed models (GLMMs). Specifically, we visually inspected the plot for homoscedasticity (i.e., residuals should have constant variance across all levels of the fitted values), linearity (i.e., residuals should be randomly scattered around zero, without any discernible pattern), and model fit (i.e., clear trends in the residuals might

indicate that the model is missing key predictors, see also *i*). (iii) We checked for overdispersion where the assumption is that the mean and variance of the response variable are equal (Hinde and Demétrio 1998; Fletcher 2012).

We selected models by comparing all possible combinations of fixed effects to identify the best-fitting models (Johnson and Omland 2004; Symonds and Moussalli 2011). To identify the most parsimonious model explaining the variation in FID (both for the first and second global models), we generated all possible subsets of each global model. We used two different metrics to identify the best model. First, we used the Delta Akaike Information Criterion corrected for small sample sizes (ΔAICc) to compare how close each model is to the best model based on the AICc values (only models with $\Delta\text{AICc} < 2$ were kept). Second, we used the Akaike weights to provide a relative measure of the likelihood of a model among the set previously selected (weights > 1). Both metrics are useful for model comparison and selection, with ΔAICc helping to identify a subset of competitive models and weights aiding in model averaging and understanding the relative evidence for each model. In cases where multiple models were competitive (models with $\Delta\text{AICc} < 2$), we performed model averaging where predictions or estimates are averaged across the set of competitive models with weights based on their Akaike weights (Symonds and Moussalli 2011). Specifically, we used conditional model averaging because it provided an estimate of the effect size under the assumption that the predictor was relevant (i.e., if the conditional average is large, it suggests that the predictor is considered important). Additionally, we calculated the importance values for each predictor across the competitive models. Importance values are determined by summing the Akaike weights of the models in which a particular predictor appears (Symonds and Moussalli 2011). These values range from 0 to 1, where a value closer to 1 indicates that the predictor is consistently included in the top-ranked models and is therefore likely to be an important factor influencing FID. Conversely, a lower importance value suggests that the predictor may have a less consistent or weaker influence. This combined approach of model averaging calculating importance values allows us to not only estimate the effect sizes of the predictors, but also assess the relative importance of each predictor across the competitive models, providing a robust understanding whether and at what extent group size influences FID.

We display results graphically by using boxplot (group size as a categorical variable) and scatter plot (group size as a numerical value) to highlight overall differences and patterns with respect to fixed effects. All analyses were conducted in R 3.3.1 with the additional packages “*lme4*” (Bates et al. 2012) for generalized linear mixed effects models and

Table 1 Number of observations of FID and group size for each of the three areas. Observations are reported according to the diver configuration (spearfisher and snorkeler), and level of protection (protected and non-protected). Observations during which white seabream was found in pairs or shoals (group size ≥ 2) is reported between parenthesis

Area	Snorkeling protected	Spearfishing protected	Snorkeling Non-protected	Spearfishing Non-protected
Banyuls	68 (9)	37 (6)	32 (5)	36 (6)
Bonifacio	34 (5)	30 (6)	20 (8)	16 (7)
Medes	25 (5)	33 (10)	26 (2)	32 (9)

“MuMIn” (Bartoń 2014) automatic model selection, model averaging and the calculation of importance values.

Results

We collected a total of 389 measurements of FID and group size of white seabream simulating the presence of spearfishers and snorkelers inside and outside marine protected areas in three different geographic regions (see Table 1 for more details). Flight initiation distance ranged between 0.2 and 20 m (mean ± SD = 4.65 ± 3.26 m), while group size ranged between 1 and 15 individuals. White seabream was found in pairs or shoals (group size ≥ 2) in 78 out of 389 observations (median = 3 individuals; mean ± SD = 4.27 ± 3.21; see Table 1 for more details). In terms of difference in group size inside and outside marine protected areas, the first model

(group as a binary variable: solitary or grouped) showed that there was no significant difference in the chances to find white seabream alone or in shoals (from 2 to 15 individuals) between inside and outside marine protected areas ($Z = -1.148; p = 0.251$). Similarly, the second model (where group size was a numerical value from 2 to 15) showed that there was no significant difference in the shoal size of white seabream between inside and outside marine protected areas ($t = -0.073; p = 0.942$).

Model selection indicated competitive models in both cases (4 competitive models in the first and 3 in the second global model; Tables 2 and 3). The first global model (i.e., group size as categorical variable) identified four models with AIC values < 2. The first model included group size as a categorical variable (2 levels: alone and shoal), diver configuration (2 levels: spearfisher and snorkeler), and level of protection (2 levels: protected and non-protected) and their interaction (Diver x Protection; model 1 in Table 2). The second best model included diver configuration, level of protection, and their interaction ($\Delta AICc = 1.15$; Table 2). The third best model included diver configuration, level of protection, and group size as categorical variable ($\Delta AICc = 1.16$; Table 2). The fourth best model included group size as categorical variable, diver configuration and level of protection with their interaction, and the interaction between group size and protection ($\Delta AICc = 1.52$; model 4 in Table 2). Additionally, the combined approach

Table 2 Results of the model selection to estimate the relationship between flight initiation distance and group size as categorical variable (alone vs. shoal), diver configuration (2 levels: spearfisher and snorkeler), level of protection (2 levels: protected and non-protected), as well as all possible interactions. Models that passed the AIC values < 2 (weight > 0.1) threshold assumed in this study are bolded

model	(Intercept)	Diver	Protection	Group	Diver X Protection	Diver X Group	Protection X Group	Diver X Protection X Group	df	logLik	AICc	delta	weight
1	1.695	X	X	X	X				7	-834.2	1682.7	0.00	0.24
2	1.718	X	X		X				6	-835.8	1683.9	1.15	0.14
3	1.639	X	X	X					6	-835.9	1683.9	1.16	0.13
4	1.706	X	X	X	X		X		8	-833.9	1684.2	1.52	0.11
5	1.697	X	X	X	X	X			8	-834.2	1684.8	2.05	0.09
6	1.663	X	X						5	-837.4	1684.9	2.12	0.08
7	1.655	X	X	X			X		7	-835.4	1685.1	2.40	0.07
8	1.641	X	X	X		X			7	-835.8	1685.9	3.22	0.05
9	1.710	X	X	X	X	X	X		9	-833.9	1686.3	3.54	0.04
10	1.658	X	X	X		X	X		8	-835.4	1687.2	4.45	0.03
11	1.723	X	X	X	X	X	X	X	> 10	-833.5	1687.6	4.90	0.02
12	1.800		X	X					5	-852.2	1714.5	31.82	0.00
13	1.814		X	X			X		6	-851.9	1716.0	33.25	0.00
14	1.836		X						4	-854.6	1717.2	34.52	0.00
15	1.346	X		X					5	-880.9	1771.9	89.15	0.00
16	1.373	X							4	-882.7	1773.5	90.81	0.00
17	1.349	X		X		X			6	-880.9	1773.9	91.17	0.00
18	1.507			X					4	-895.5	1799.1	116.41	0.00
19	1.549								3	-898.4	1802.8	120.05	0.00

Table 3 Results of the model selection to estimate the relationship between flight initiation distance and group size as numerical variable (range=2–15), diver configuration (2 levels: spearfisher and snorkeler), level of protection (2 levels: protected and non-protected), as well as all possible interactions. Models that passed the AIC values <2 (weight>0.1) threshold assumed in this study are bolded

model	(Intercept)	Diver	Protection	Group	Diver X Protection	Diver X Group	Protection X Group	Diver X Protection X Group	df	logLik	AICc	delta	weight
1	1.861	X	X						4	-194.3	397.2	0.00	0.24
2	1.583	X	X	0.056			X		6	-192.4	398.0	0.76	0.17
3	2.035		X						3	-196.2	398.9	1.66	0.11
4	1.819	X	X	0.009					5	-194.2	399.3	2.08	0.09
5	1.872	X	X		X				5	-194.3	399.5	2.27	0.08
6	1.497	X	X	0.076		X	X		7	-192.2	400.0	2.77	0.06
7	1.604	X	X	0.055	X		X		7	-192.3	400.3	3.13	0.05
8	1.798		X	0.052			X		5	-194.8	400.6	3.36	0.05
9	1.968		X	0.014					4	-196.9	400.7	3.46	0.04
10	1.701	X	X	0.037		X			6	-193.9	401.1	3.86	0.04
11	1.191	X	X	0.152	X	X	X	X	9	-190.4	401.4	4.22	0.03
12	1.825	X	X	0.009	X				6	-194.2	401.6	4.43	0.03
13	1.513	X	X	0.076	X	X	X		8	-192.2	402.4	5.24	0.02
14	1.680	X	X	0.039	X	X			7	-193.9	403.5	6.25	0.01
15	1.572	X							3	-202.9	412.2	15.00	0.00
16	1.247	X		0.082		X			5	-201.3	413.5	16.35	0.00
17	1.480	X		0.022					4	-202.5	413.6	16.36	0.00
18	1.758								2	-204.9	414.0	16.77	0.00
19	1.647			0.025					3	-204.3	415.0	17.84	0.00

of model averaging and calculating the importance value indicated that diver configuration and protection level were the most critical predictors of FID, consistently included in all top models (importance=1). The interaction between diver configuration and protection level (diver x protection) and the main effect of group size as categorical variable (alone or shoal) also have considerable importance, though to a slightly lesser extent (included in 3 out of four models; importance=0.78). The interaction between protection level and group size appears to be less influential, as it was included in only one of the top models (importance=0.18).

The second global model (i.e., group size as numerical variable that ranged between 2 and 15) identified three models with AIC values <2 (Table 3). The first model included diver configuration (2 levels: spearfisher and snorkeler), and level of protection (2 levels: protected and non-protected; Model 1 in Table 3). The second best model included group size as a numeric value, diver configuration, level of protection, and their interaction (Δ AICc=0.76; Table 3). The third best model only included protection (Δ AICc=1.66; Table 3). Additionally, the combined approach of model averaging and importance value indicated that protection level was the most influential predictor included in all top models (importance=1). Diver configuration had a moderate importance value (included in 2 out of 3 models; importance=0.79). By contrast, group size as a numerical variable and its interaction with protection level had a

weaker influence on FID (included in 1 out of 3 models; importance=0.32).

Discussion

We did not find support for the hypothesis that fish outside marine protected areas, where spearfishing is allowed, had a stronger relationship between FID and group size when encountering a spearfisher (i.e., a high-risk situation), compared to fish inside marine protected area where spearfishing was not allowed when they encountered a snorkeler (i.e., a low-risk situation). Therefore, both the many eyes hypothesis (Lima 1995), and the dilution hypothesis (Foster and Treherne 1981) seems to not play an important role in shaping the relationship between group size and FID, especially when risk is determined by the interaction between underwater human presence (snorkeler/spearfisher) across different environmental conditions (inside/outside marine protected areas). However, we found other results that are worthy of discussion.

The interaction between group size and protection level had a measurable impact of FID both when group size was considered as a categorical and as a continuous variable. In particular, the relationship between group size and FID was positive and steeper outside of marine protected areas than inside (Fig. 3B), which supports the many eyes hypothesis

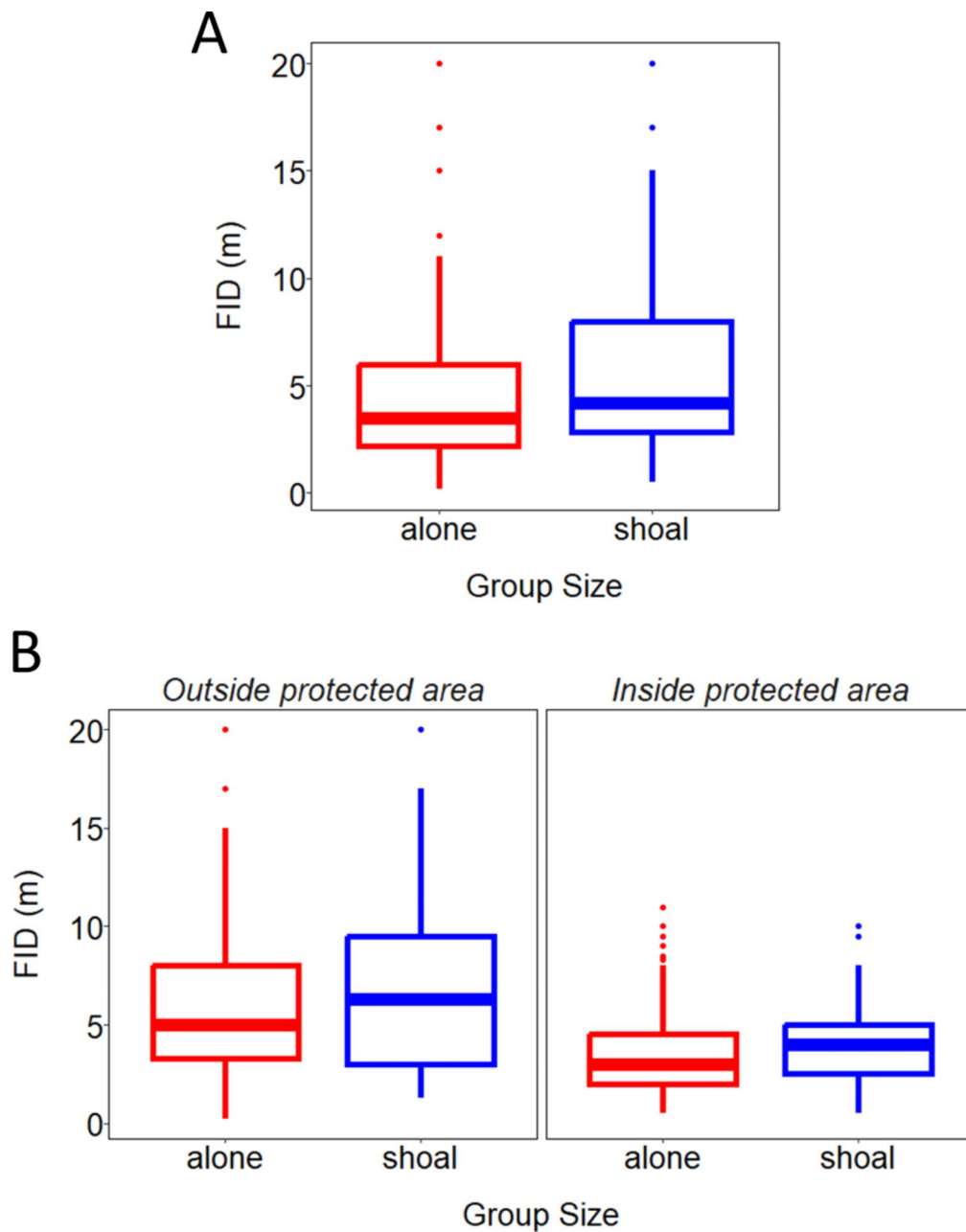


Fig. 2 Boxplots of the relationship between FID and group size as categorical variable (alone vs. shoal; **A**) and according to level of protection (outside and inside protected areas; **B**). The horizontal bold

line represents the median, the box corresponds to the first and third quartiles, and the whiskers extend to the largest value no further than $1.5 \times$ inter-quartile range, and outliers

in terms of collective vigilance (i.e., a positive and steeper slope in high-risk situations where fishing is allowed). These results agree with previous studies where the relationship between group size and FID was found to be stronger outside management areas for fishing and tourism (Benevides et al. 2018). However, it should be considered that here and in previous studies, FID was measured on individual target fish, which means that it likely represents a measure of individual rather than collective vigilance. This means that in high-risk situations, such as outside marine protected

areas where fishing is allowed, the many eyes hypothesis would predict that FID should decrease with group size (i.e., a reduction of individual vigilance with increasing group size should be associated with decreasing individual efficiency to detect predators and this should lead to a shorter FID). This controversial result should be considered in future studies aiming to unravel the mechanisms governing the relationship between group size and FID in fishes. Another aspect to consider in relation to the results reported inside/outside marine protected areas, is that fishing may

have consequences on shoaling behaviour including density dependent effects on shoal size (Sbragaglia et al. 2021). For example, outside of marine protected areas where most fishing activities are allowed, white seabream population density may be reduced and consequently there may be reduced encounter rates between individuals resulting smaller group sizes (Sbragaglia et al. 2021). However, we did not find significant differences between group sizes outside and inside marine protected areas.

Despite previous results showed that white seabream is able to adjust FID to the presence of spearfishers or snorkelers inside/outside marine protected areas (Sbragaglia et al. 2018), here we showed that the same did not happen with the relationship between group size and FID, which seems to be sensitive exclusively to the protection level (inside/outside marine protected areas). A possible interpretation is that purely FID responses—without considering the relationship with group size—are exclusively related to anti-predator strategies (Stankowich and Blumstein 2005). However, shoaling behaviour in fishes is an anti-predator strategy as much as it is a foraging strategy (Pitcher et al. 1982; Pitcher 1986), and this could explain the weak effects found in this study. For example, social dynamics of the white seabream could be more about agonistic dynamics associated with feeding than anti-predator behaviour. Indeed, experiments showed that groups of juvenile white seabream engaged in more aggression when food was spatially variable compared to when it was spatially fixed, indicating that food distribution significantly influences their social interactions and competition levels (Castro and Santiago 1998). Therefore, feeding dynamics and food spatial variability could play a role in the dynamics of the antipredator benefits of grouping because anti-predator responses could be masked by agonistic interactions. This is a speculative interpretation, but it could be an interesting aspect to develop in future studies across a range of species—accounting for their level of human exploitation.

We also found that group size had a measurable impact on overall FID both as a categorical variable (i.e., slightly shorter FID when fish are alone than in two or more individuals; Fig. 2A) and continuous variable (i.e., slightly positive relationship; Fig. 3A). This agrees with previous studies that found a positive relationship between FID and group size (Januchowski-Hartley et al. 2011; Benevides et al. 2018). However, other studies showed no effects of group size on FID (Gotanda et al. 2009; Benevides et al. 2016; Nunes et al. 2016). Indeed, Samia et al. (2019) conducted a meta-analysis and showed that group size had no overall effect on FID of fishes in response to underwater human presence, which highlights the mixed empirical evidences on this specific topic. Furthermore, Samia et al. (2019) showed that shoaling tendency of species is of primary importance to

explain the strength of the relationship between individual body size and FID (i.e., the size of individuals of solitary species had less effect on FID than individual size in group-living species). The fact that shoaling tendencies is important to explain variation in the relationship between body size and FID, suggests that group size may indeed have a role in shaping FID in fishes, which is also reinforced by the results we report here (see discussion above).

The experimental approach used here and in other studies that have aimed to characterize the relationship between group size and FID in response to underwater human presence may have limitations. Here we discussed such limitations and highlighted unanswered questions for future studies. First, the target species used here (white seabream) it is not an obligate schooling species, and hence it may not be the most appropriate species to test the hypothesis. For example, obligate schooling species may rely more on group size to mediate predator avoidance than species that are often found alone. Nevertheless, as highlighted above, meta-analyses, such as Samia et al. (2019), require data from a variety of different types of species to draw generalizations, which make it essential to collect empirical data from both obligate and facultative schooling species. Second, escape from an approaching threat is linked to the cost of fleeing (Ydenberg and Dill 1986), which is an aspect not accounted for in this and other studies that measured the relationship between group size and FID. Because shoaling behaviour in fishes is an anti-predator strategy as much as it is a foraging strategy (Pitcher et al. 1982; Pitcher 1986), quantifying the cost of fleeing is imperative in future studies aiming to study the relationship of group size and FID in fishes exposed to underwater human presence. Third, although the range of group size investigated is comparable across studies (i.e., from 2 to about 45 individuals; Gotanda et al. 2009; Januchowski-Hartley et al. 2011; Nunes et al. 2015; Benevides et al. 2016; Benevides et al. 2018), the way in which target individuals within the group are measured is not always clearly reported. For example, it is not always clear whether FID of a fish in a group has been measured (as we did in the present study) by randomly selecting one fish of the shoal as target fish. This may represent a bias because fish in the front of the shoal may have more chances to be selected as target fish, but they may be also those individuals within the shoals that can have both higher feeding success and greater predation risk (Krause and Ruxton 2002). Therefore, measuring FID in a randomly targeted fish may not represent the response of the group (i.e., the first fish that reacts within the group), which may have implications to understand escape responses such as the relationship between group size and FID. Rather, the FID of the first fish that responds within the group and its relative position may be more informative to advance the understanding of the

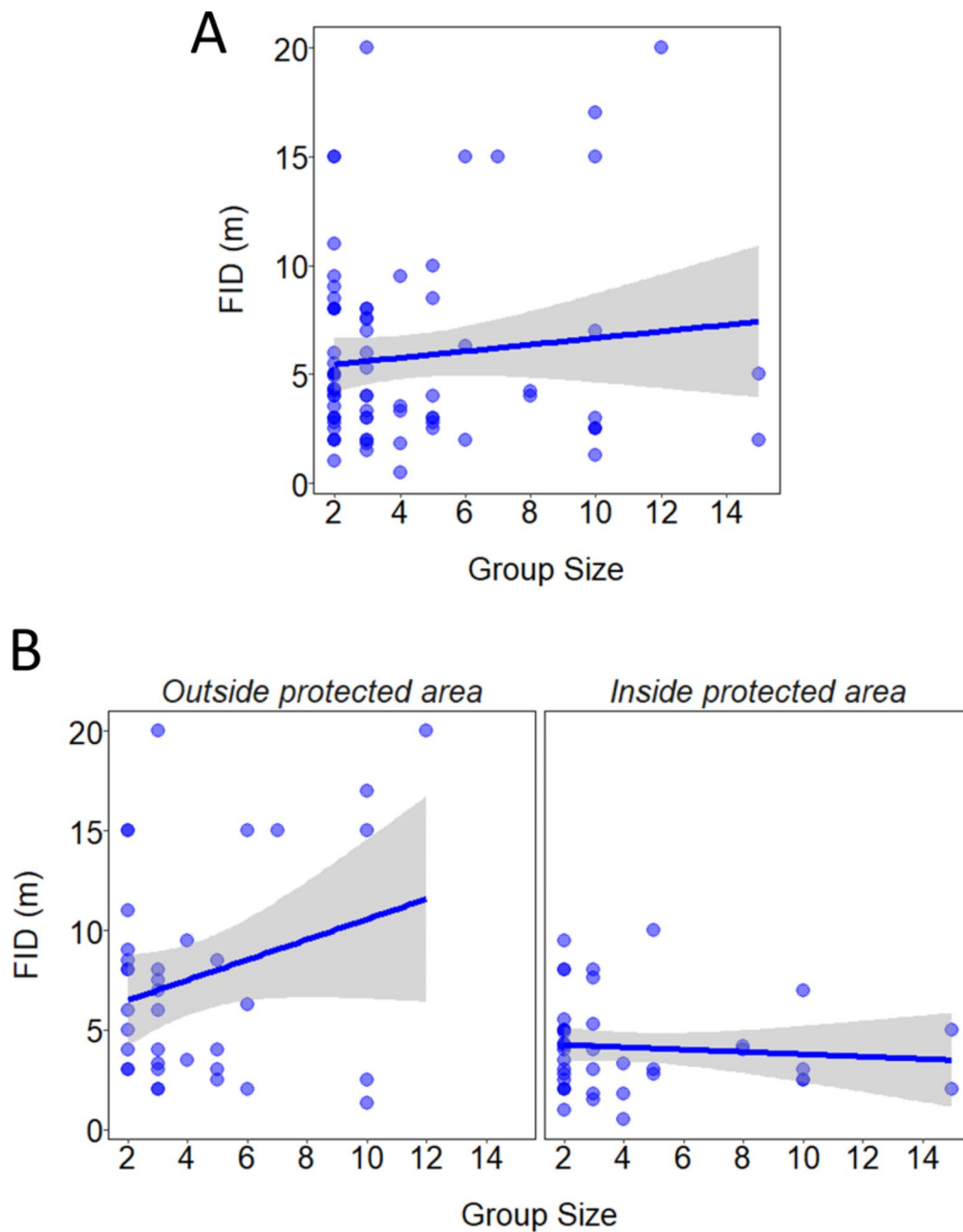


Fig. 3 Scatterplot of the relationship between FID and group size as numerical variable (range 2–15; **A**) overall and according to level of protection (inside and outside protected areas; **B**). Bold blue lines represent a linear regression line with 95% confidence interval (grey area)

relationship between group size and FID. Fourth, previous studies suggested that context-dependent factors may affect FID. For example, fish in more complex habitats or deeper waters can have shorter FID (Nunes et al. 2015; Stamoulis et al. 2019). In the present study we collected observations at similar habitat types and depth across areas to avoid possible confounding effects. However, future studies could benefit by explicitly accounting for these factors and determining whether they explain variability in the relationship between group size and FID. Finally, future studies should

consider integrating field studies with laboratory studies to better understand how fish process the information of an approaching threat and consequently adjust FID according to group size. For example, according to laboratory experiments, the presence of conspecifics can significantly influenced fish escape responses (Domenici 2010). Importantly, the escape latency of fish was observed to increase when they were in the presence of shoaling neighbors compared to when they were alone, indicating a lower perceived risk and a higher cost of immediate escape (Domenici 2010).

Additionally, escape trajectories were more variable and less predictable in solitary fish, whereas shoaling fish had more uniform escape directions, likely due to the need to maintain group cohesion during an escape (Domenici 2010). This variability in escape responses is critical to better understanding the relationship between group size and FID in different social and environmental contexts. Such quantitative experimental results may be integrated with the development of models (e.g., agent-based models; Peterson et al. 2021; or conceptual models), and test hypotheses as well as predict patterns that could be seen when conducting underwater empirical research (Sbragaglia et al. 2024).

In conclusion, this study provides weak– but still measurable– evidence that group size explains variation in white seabream FID. Almost 40 years after the influential paper by Ydenberg and Dill (1986)– that already highlighted diversity in the form of relationship between group size and FID as well as raising questions about experimental control when studying these relationships– we still are not clear on the ecological influence of the relationship of group size and FID, especially in fish exposed to underwater human presence. We hope this article stimulates more integrative research combining field observations with laboratory experiments and simulations to provide a more robust ecological understanding of this important phenomenon.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00265-025-03563-x>.

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Author contributions VS and DTB conceived the idea. LM collected the data with the help of VS. VS analyzed the empirical data. VS and DTB wrote the manuscript with feedback from LM.

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Data availability All data generated or analyzed during this study are included in this published article as supplementary material.

Declarations

Ethical approval All applicable international, national, and/or institutional guidelines for the use of animals were followed. The measurements reported in the study are based on underwater observations of fish behavior. For this type of measurements ethical approval is not required in the country where the study was conducted.

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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