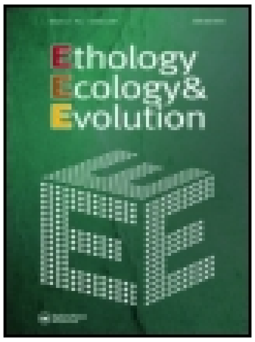

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Reef fish antipredator behavior in remote islands does not reflect patterns seen in coastal areas

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The reduction or loss of antipredator behavior is expected for animals isolated on islands, but most of studies have focused on terrestrial rather than aquatic species. Two different processes may modulate fish antipredator behavior in the waters off remote archipelagos. First, places with low human density may have reduced fishing pressure. Second, due to their remoteness and lack of other human impacts, these isolated places may have more intact fish assemblages. We investigated antipredator behavior off the smallest archipelago in the Equatorial Atlantic not subjected to regular spearfishing by quantifying flight initiation distance (FID) — the distance a diver can approach a fish before it flees. Our goal was to identify natural patterns of risk assessment in reef fish. We focused on five common species and investigated how body size, group size and depth influence on the FID. In contrast to previous studies, we found that *Caranx lugubris* had significantly negative relationships between body size and FID, whereas *Kyphosus sectatrix* showed an opposite relationship. Finally, only a single species (*Melichthys niger*) had a significant relationship between depth and FID. Given we found small FID for all species studied, we suggest that much of our understanding of fish antipredator behavior studied using FID may reflect the somewhat ubiquitous impact of humans on species' risk assessments and not reflect patterns seen in areas with very low human density/disturbance. Our results suggest that fish antipredator behavior may be a metric of human impacts.

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KEY WORDS: ecology of fear, flight initiation distance, remote fish assemblages, Saint Peter and Saint Paul Archipelago.

INTRODUCTION

Studying antipredator behavior is important because predation can affect prey population dynamics, mediate cascading effects in food webs and influence the likelihood of rapid extinctions, and this is exacerbated if antipredator behavior is insufficient to deal with novel predators (Orrock & Fletcher 2014). Flight initiation distance (FID) – the distance from an approaching predator at which prey first initiates an escape (Cooper & Blumstein 2015) – should be modified in populations actively subjected to spearfishing (Nunes et al. 2016). Most studies of FID in fish were conducted in locations with fishing or other human activities and it is known that human presence influences risk assessment (Januchowski-Hartley et al. 2013; Benevides et al. 2018). There are few studies on the FID of fish in remote oceanic archipelagos and such studies can be very revealing. For instance, knowledge about FID in the waters off remote islands may help us identify species are most vulnerable to spearfishing if they are particularly tolerant of humans in areas where they are not hunted.

Oceanic islands provide unparalleled opportunities to understand natural community dynamics because of their isolation, overall low diversity, and high endemism eliminates confounding effects found in more human-impacted areas (Sandin et al. 2008; Hachich et al. 2015; Quimbayo et al. 2019). Even on remote oceanic islands, where diversity, including predator diversity, is expected to be lower than mainland (Rosa et al. 2016; Pinheiro et al. 2017; Quimbayo et al. 2019), predator-prey interactions may still affect the structure of biological assemblages and ecosystem functioning, shaping prey distribution in different habitats (Hixon & Beets 1993).

Much of what we know about isolation comes from studies of terrestrial animals on islands. In the ocean, two different processes may occur in the waters off remote archipelagos. First, due to their remoteness and lack of human impacts, there may be a more intact community of predatory fish. Because of its remoteness, this community may be relatively small in terms of species richness, but nonetheless, it may be intact. Second, in remote areas there may be few humans, which means that fish are not frequently speared or otherwise caught by people. While fisheries-induced changes in life-histories have been well studied (Uusi-Heikkilä et al. 2015; Sullivan et al. 2017), the possibility of fisheries altering the composition of fish behavior has been less explored (Heino et al. 2015), especially around remote oceanic islands (but see Januchowski-Hartley et al. 2015). Recently, it been proposed that behavior is a sensitive indicator of exploitation in the marine environment (Goetze et al. 2017; Sbragaglia et al. 2018). The exploitation-induced behavioral effect has been defined as a “timidity syndrome”, which may have ecological, social and economic consequences, most notably by altering the catchability of exploited populations (Arlinghaus et al. 2017).

Spearfishers, like terrestrial hunters, visually target and select their prey (Dalzell 1996). Similar to trophy hunting (e.g., Coltman et al. 2003; Sbragaglia et al. 2018), spearfishers often select the largest individuals, and – because the capture depends on physical proximity between the fish and the spearfisher –

there is also the potential for selection on behavioral phenotypes, such as boldness (e.g., Januchowski-Hartley et al. 2011). Most fishing methods directly select for bold individuals and increased fishing mortality favors bold behaviors by devaluing survival. Although evidence of evolutionary changes in behavioral traits in wild fish has so far been limited, experimental studies have clearly shown the effect of selection on behaviors (Uusi-Heikkilä et al. 2008; Heino et al. 2015; Sbragaglia et al. 2019).

We studied FID in five species of reef fishes in the remote Saint Peter and Saint Paul oceanic Archipelago. We investigated whether body size, group size and depth explain variation on FID for each species. In general, the current available literature on fish FID suggests that larger species have greater FIDs (Januchowski-Hartley et al. 2011, 2013; Sbragaglia et al. 2018), and that fish tolerate closer approach as group size increases (Benevides et al. 2016). We know little about the effect of depth on FID (Andradi-Brown et al. 2017). Most human-fish interactions occur near the surface, so it is reasonable to hypothesize that fish in deeper water may perceive a reduced risk of predation and thus tolerate a closer approach by a human (Feary et al. 2011).

MATERIALS AND METHODS

Study area

The remote Saint Peter and Saint Paul Archipelago (SPSPA) is a small group of five islets and rocks (total emerged area ca 15,000 m^2) located in the central equatorial Atlantic Ocean, just above the Mid-Atlantic Ridge and about 1000 km off the northeastern Brazilian coast (Edwards & Lubbock 1983a, 1983b; Feitoza et al. 2003). The SPSPA is influenced by the surface South Equatorial Current, which flows westwards. Shallow rocky reefs of the SPSPA are covered mainly by the zoanthid *Palythoa caribaeorum* and algae of the genera *Bryopsis, Caulerpa* and *Dictyota* (Rosa et al. 2016). Due to its isolation and small area this archipelago has around 60 species of reef fish (Feitoza et al. 2003). We studied five of them and collected data in November 2017 within the Cove, a small inlet protected from the main westward surge, forming a gentle slope from 3 to ~ 20 m deep. The five species studied herein (black triggerfish, *Melichthys niger*; black jack, *Caranx lugubris*; whitespotted filefish, *Canterhines macrocerus*; puddingwife wrasse, *Halichoeres radiatus*; and Bermuda chub, *Kyphosus sectatrix*) are not fished off these islands.

Flight initiation distance

Because prior studies found no differences between FID collected by snorkel or by scuba (Januchowski-Hartley et al. 2011, 2012; Samia et al. 2019) and others noted that the differences are only detectable in areas with high fishing intensity (Lindfield et al. 2014a; Gray et al. 2016), we used both and combined data for analysis. An observer holding a fake speargun swam at a constant speed (~ 0.7 m/sec^{-1}) directly toward a focal fish that was either feeding or swimming normally (methods follow DeLoach & Humann 1999). When the fish fled, the distance between the end of the fake speargun and the place where the fish was, prior to fleeing, was measured with a tape measure and this was recorded as the FID. Flight was defined when the fish increased its swim speed to greater than the approach speed of the diver (Januchowski-Hartley et al. 2011, 2012). To avoid resampling the same individuals, each flight experiment was conducted at least 5 m away from the previous FID experiment.

Before flushing a fish, we visually estimated the body sizes (total length in cm) and, when applicable, the number of fishes forming its mono- or hetero-specific group. For this study, we defined a group as consisting of all individuals within 1 m of the focal fish (Nunes et al. 2016).

Table 1.

Results of linear models fitted to explain variation in FID in reef fish. Variance Inflation Factor (VIF) is shown for individual factor. Bold values indicate statistical significance ($P < 0.05$).

Species/Factors	Estimate	t-value	*P*-value	VIF
Melichthys niger				
Body size	0.03	1.17	0.24	1.07
Depth	– 0.02	– 2.02	**0.05**	1.12
Group size	– 0.0006	– 0.05	0.96	1.19
Caranx lugubris				
Body size	– 0.05	– 2.35	**0.02**	1.00
Depth	– 0.0008	– 0.03	0.97	1.01
Group size	0.017	0.57	0.57	1.00
Cantherhines macrocerus				
Body size	0.01	0.61	0.61	0.54
Depth	– 0.02	– 0.59	– 0.59	0.55
Group size	– 0.001	– 0.12	– 0.12	0.90
Halichoeres radiatus				
Body size	– 0.03	– 1.32	0.19	1.01
Depth	– 0.02	– 0.91	0.37	1.04
Group size	– 0.006	0.41	0.68	1.03
Kyphosus sectatrix				
Body size	0.02	2.56	**0.01**	1.27
Depth	– 0.0007	– 0.02	0.98	1.27
Group size	– 0.01	– 1.07	0.28	1.04

After flushing, we measured the depth with a digital diving computer. All observations were conducted between 09:00 and 16:00.

Data analyses

To test if there were differences in FID among all species studied, we fitted linear models. The FID $\ln(x + 1)$ transformed prior to statistical analysis to conform to the assumptions of parametric statistics. Normality was tested using a Shapiro-Wilk W test while a Bartlett's test was used to examine homogeneity of variance. For all analyses, we set our alpha to 0.05. Additionally, we fitted five separate models (one for each species) to ask how body size, depth and group size (as fixed factors) explained variation in FID. We tested the significance of each individual factor by dropping each of them from the full model and performing a Likelihood Ratio Test. We estimated the Variance Inflation Factor (VIF) to measure multicollinearity between all continuous factors in each linear model (final models presented low multicollinearity with VIF values < 2; Table 1). Residual analysis was performed to evaluate the quality of final models (Crawley

2007). We illustrate these relationships with FID by plotting body size, depth and group size against FID and calculating 95% confidence intervals around the mean. All analyses were performed in the R environment (R Core Team 2018).

RESULTS

We estimated FID of 328 fishes and found significant differences in the FID among species (LM; df = 4; $P = < 0.001$; Fig. 1). Our sample contained 66 individuals of *Melichthys niger* (mean FID = 19.86 cm ± 15.3 SD), 66 *Caranx lugubris* (12.9 ± 11.06), 63 *Canterhines macrocerus* (1.9 ± 4.52), 66 *Halichoeres radiatus* (17.13 ± 11.55) and 67 *Kyphosus sectatrix* (81.4 ± 46.5).

Depth was negatively associated with FID only for *M. niger*, (Fig. 2a; Table 1). Body size estimates varied between 15–30 cm in *M. niger* (22.6 ± 4.1), 16–45 cm in *C. lugubris* (27.3 ± 6.15), 18–40 cm in *C. macrocerus* (27.7 ± 6.14), 8–30 cm in *H. radiatus* (16 ± 4.64) and 15–50 cm in *K. sectatrix* (28.7 ± 7.65). Body size explained significant variation in FID for *C. lugubris*, and *K. sectatrix* (Fig. 2b-c; Table 1). We observed no effects of group size on the FID despite the substantial variation in group size among species.

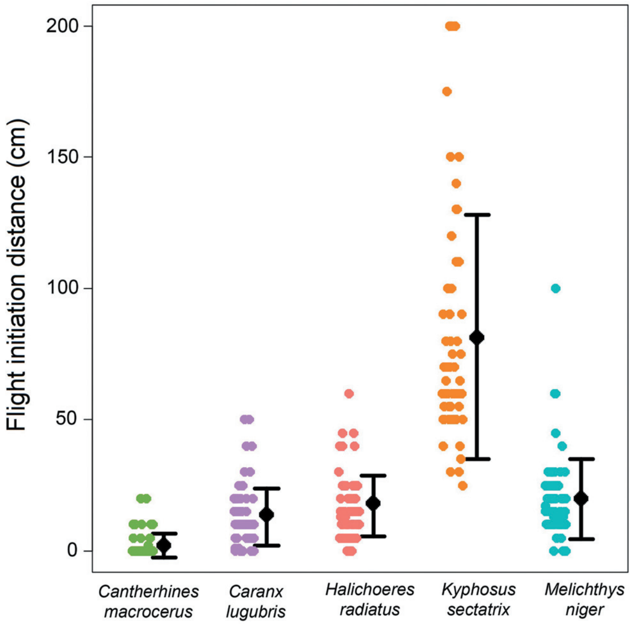

Fig. 1. — Flight initiation distance (FID) among species studied. FID average, standard deviation and raw data (dots) are shown.

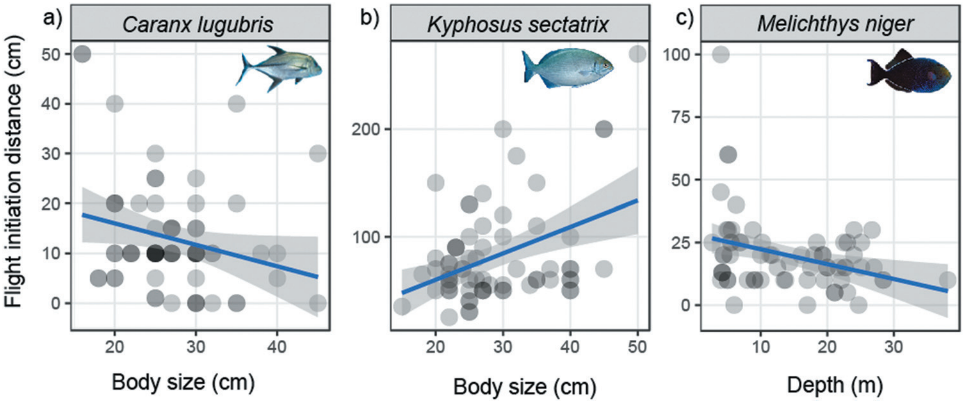

Fig. 2. — Significant relationships between body size and flight initiation distance (FID) for *Caranx lugubris* and *Kyphosus sectatrix* (a and b). Significant relationship between depth and FID for *Melichthys niger* (c). Best fit regressions (± 95% CI) are plotted.

DISCUSSION

We found remarkable differences between the behavior of the five species of fish studied in a remote archipelago compared to what we know from studies in more human-dominated, coastal systems. Unlike coastal systems where larger body size is associated with increased FID, likely because fish are exploited by humans or because they are less agile (Witter et al. 1994; Sbragaglia et al. 2018), *C. lugubris* reduced FID as a function of body size while the *K. sectatrix* increased FID. Differences between these species may be related to different antipredatory strategies and natural histories. For example, while *C. lugubris* is a species with great swimming ability, *K. sectatrix* despite swimming in the water column, frequently visits the reef bottom to feed on algae, where it is sheltered from possible predators. For *C. lugubris*, where larger individuals were more tolerant of human approach, we can predict that this species would be especially vulnerable to spearfishing. More generally, it is likely that some fish living near remote islands, where spearfishing is not a common fishing practice, may have increased vulnerability to human harvesting. The influence of body size in explaining variation in fish FID is unresolved. Body size in Caribbean parrotfish was the largest single determinant of increases in FID (Gotanda et al. 2009), while in Indo-Pacifc reef fish, body size explained no significant variation in FID (Feary et al. 2011).

We found no relationship between group size and FID. The relationship between group size and FID is complex. For instance, Semeniuk and Dill (2005) found longer reaction distances in groups than in solitary individuals of the cowtail stingray, *Pastinachus sephen*. Similarly, Januchowski-Hartley et al. (2011) observed an increase of FID related to group size for surgeonfishes (Acanthuridae). While some fish can tolerate a closer approach to a threat when grouped, and tolerate closer approaches due to the risk dilution effect (Lima & Bednekoff 1999), grouping in other species permits individuals to detect approaching threats sooner and flee at greater distances (Benevides et al. 2018).

M. niger tolerated closer approach in deeper water. This species is found commonly in shallow waters, suggesting that this perceived greater safety in deeper water.

Many factors co-vary with depth, and depth influences fish assemblage structure, light, water temperature, current regimes and food availability (e.g., McGehee 1994; Brokovich et al. 2008; Pereira-Filho et al. 2011; Fitzpatrick et al. 2012). Depth can also alter predation risk, but prior work has suggested that shallow water was relatively safer. Reduced predation in shallow water may be due to several factors including limited visual perspective, limited maneuverability that differentially impacts larger predators, and physiological stress associated with unsuitable habitat (Angermeier 1992). Under experimental conditions, potential prey typically respond to the presence of predatory fish by restricting their activity to the shallows (Power et al. 1985; Schlosser 1987, 1988) or search out structural cover (Fraser & Cerri 1982; Schlosser 1987). By contrast, light refraction may affect risk perception as a function of depth because the difference between the perceived position and the real position is greater if prey is located deeper in the water column (Reyer et al. 1988).

In contrast with shallow reefs, deeper reefs are often considered to be less susceptible to local and global disturbances, such as overfishing, pollution and climate change. Thus, deeper reefs may work as refuges and sources of propagules for shallow threatened reefs (the deep reef refugee hypothesis; Lesser et al. 2009; Bongaerts et al. 2010). An important assumption of this hypothesis is that these deep-water refuges are connected to the shallows. In remote oceanic islands with relatively few shallow areas, this assumption may be met, however recent evidences suggest that deep reefs are distinct and impacted (Rocha et al. 2018).

Despite the increase in the literature on fish assemblage structure in deep and/or mesophotic reefs, little is known about behavioral change in relation to the depth gradient (but see Andradi-Brown et al. 2017). Our study showed that the relationship between depth and antipredator behavior varies by species. Certain fishing methods performed on coral reefs, particularly breath-hold spearfishing, have obvious depth limitations, thus it is assumed that a proportion of the fish population can obtain refuge in deeper water (Lindfield et al. 2014b). Without spearfishing, we expected that fish will be more tolerant of humans in deeper water, but we found this only *M. niger*. We suggest that this unexpected finding warrants further study in other species.

Remote archipelagos have a reduced diversity of both terrestrial and reef-dwelling animals and this includes a reduced predator community. The loss of some predators does not always result in a complete loss of antipredator behavior and the multi-predator hypotheses predicts, and a variety of species from diverse taxa reveal, that antipredator behavior persists when isolated from some, but not all predators (Blumstein 2006; Rasheed et al. 2017).

In general, we found shorter FIDs than previous work on four labrid species in coastal reefs subjected to spearfishing. One of these species (*H. brasiliensis*) is a sister species of *H. radiatus* studied here. Interestingly, similar FID estimates were found in three labrids (*Sparisoma axillare, Scarus trispinosus* and *H. poeyi*) on reefs close to islands inside a no-take marine protected area (Abrolhos National Marine Park, Brazil) (Nunes et al. 2016). That study site, while not oceanic, was located 74 km from land. Thus, isolation and protection can have similar effects on fish FID when spearfishing is absent. Taken together, our results are also consistent with the multi-predator hypothesis. Future studies that compare identical species in coastal areas and around remote oceanic islands are required to formally test the multi-predator hypothesis.

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DISCLOSURE STATEMENT

No potential conflict of interest was reported by the authors.

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