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Global trends on reef fishes' ecology of fear: Flight initiation distance for conservation

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ABSTRACT

Escape behaviors have a great potential as an indicator of the efficacy of management. For instance, the degree of fear perceived by fishes targeted by fisheries is frequently higher in unprotected marine areas than in areas where some protection is provided. We systematically reviewed the literature on how fear, which we define as variation in escape behavior, was quantified in reef fishes. In the past 25 years, a total of 33 studies were identified, many of which were published within the last five years and nearly 40% of those (n = 13) focused on Indo-Pacific reefs, showing that there are still many geographical gaps. While eleven escape metrics were identified to evaluate fish escape, flight initiation distance (FID) was the most commonly employed (n = 23). FID was used to study different questions of applied and theoretical ecology, which involved 14 reef fish families. We also used a formal meta-analysis to investigate the effects of fishing by comparing FID inside and outside marine protected areas. Fishes outside MPAs had increased FID compared to those inside MPAs. The Labridae family had a significantly higher effect sizes than Acanthuridae and Epinephelidae, suggesting that fishes in this family may be indicators of effective MPAs using FID. We conclude that protocols aimed to quantify fear in fishes, which provide accurate assessments of fishing effects on fish escape behavior, will help gauge the compliance of marine protected areas.

1. Introduction

Behaviorally-mediated indirect interactions between predators and prey are widely documented for both terrestrial (Brown et al., 1999; Ripple and Beschta, 2004) and aquatic systems (Dill, 1987; Madin et al., 2010a,b). Such studies change the emphasis from the direct effects of predators on prey to the indirect effects of prey avoiding predators, which are mediated by fear and threat sensitivity (see Brown et al., 1999). These indirect effects are typically quantified by the frequency and/or intensity of antipredator behavior displayed by prey. Importantly, the population consequences of behaviorally-mediated responses led by predation risks and the antipredator response may be proportionally greater than those of predation itself (Cooper and Blumstein, 2015).

To compensate for the risks imposed by predation risk, animals have a suite of behavioral responses; escaping is a key one. Optimal escape theory (Ydenberg and Dill, 1986 with modifications by Blumstein, 2003; Cooper and Frederick, 2007, reviewed in Cooper, 2015) was developed to predict flight initiation distance (FID), the distance of an approaching predator at which prey first initiate an escape. Importantly, by measuring FID, we measure an animal's perception of a risk associated with a particular context and its willingness to accept that risk (Ydenberg and Dill, 1986). When humans are used to experimentally flush prey, FID data may be used to study the relative level of tolerance to humans, especially current human exploitation patterns. Wildlife managers have used FID data to identify set-back zones – areas beyond which individuals of a species are not impacted by humans – to provide protection to specific species (Rodgers and Smith, 1995; Fernandez-Juricic et al., 2005).

In marine protected areas (MPAs), which are areas designated and effectively managed to protect marine ecosystems, processes, habitats, and species, which can contribute to the restoration and replenishment of resources for social, economic, and cultural enrichment (WWF, 2018). The MPAs of the type 'no-take zones' (NTZs) is one action of upmost importance to promote fish stock recovery (Hoegh-Guldberg, 2006; Edgar et al., 2014; MacNeil et al., 2015). The compliance of NTZs

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for the recovery of fish stocks to adjacent areas through spillover and the migration of individuals is being debated and tested worldwide (Francini-Filho and Moura, 2008; Di Lorenzo et al., 2016). Because fishes that are actively hunted by people (e.g., spear fishing) should respond to people differently than those that are not, studies have used escape responses to humans as a metric of fishing pressure. The assumption behind such context-specific response to human-induced pressure is that fishes subjected to spear fishing will be warier of approaching divers or snorkelers and consequently flee at a greater distance than those not hunted (Tran et al., 2016). For instance, studies conducted inside and outside of MPAs revealed differences in individual escape behavior (Januchowski-Hartley et al., 2013; Tran et al., 2016; Nunes et al., 2016) which is consistent with the idea that hunted fish flee humans at a greater distance. However, other studies of fish escape behavior have addressed questions with important implications for the reef fishes' ecology of fear, such as the influence of the observer, prey body size, the benefits of the presence of shelter, mutualism between preys and group size (Januchowski-Hartley et al., 2012; Lyons, 2013; Nunes et al., 2015, 2016).

We summarize global trends in the study of reef fish escape behavior, specifically focusing on the relevance of these studies for conservation and management of these often overexploited species (Nash and Graham, 2016). We conduct a systematic review to answer the following questions: i) how many studies compared inside vs. outside of MPAs/NTZs, ii) which reef fish families were studied, iii) which escape metrics were used, iv) which diving techniques were undertaken to study FID in reef fish, and finally v) where and when were these studies conducted. Furthermore, we estimated the magnitude the effect the presence of MPAs/NTZs, which we quantified as the effect size of FID, using a formal meta-analysis of three reef fish families. These fishes are commonly found on reef ecosystems worldwide and are often targeted for fishing, including spear fishing (Bonaldo et al., 2014; Januchowski-Hartley et al., 2011).

2. Materials and methods

2.1. Literature search and selection criteria

We performed a comprehensive literature search for studies published that reported the use of escape metrics in reef fishes. We searched Google Scholar, Scopus and Web of Science (ISI) using these combination of keywords, using Boolean operators “in” and “or”: *reef fish ecology of fear*; *escape metric*; *reef fish escape metric*; *reef fish escape decision*; *flight initiation distance*; *reef fish flight study; reef fish predator avoidance*, *reef fish flight ecology*; *reef fish in marine protected areas*. We additionally searched for studies using the citations within each of these collected papers. We did not applied time restriction and our research occurred between January 2016 and January 2017. In total, this initial search yielded 153 studies that potentially included information about reef fish escape behavior. We searched for: number of papers that used escape metrics inside and outside MPAs (especially FID), escape metrics used, which reef fish families were studied, diving techniques employed, where and when the studies were conducted, the total number of FID samples, FID standard deviation and FID average. All abstracts were read and only those aligned with our objectives were selected. A paper was retained if it unambiguously reported the use of any escape metric. Overall, 33 studies met the aforementioned criterion. Following perusal, we extracted all relevant information from these articles (SM1). Thereafter, temporal and spatial trends were graphically evaluated. We summarized this search with a PRISMA diagram (Preferred Reporting Items for Systematic Reviews and Meta-Analyses), which is an evidence-based minimum set of items for reporting in systematic reviews and meta-analyses (see SM2).

2.2. Effect sizes of MPAs on escape behavior

Meta-analysis is a set of methods designed to quantitatively summarize research findings across studies (Hedges and Olkin, 1985). The method was developed primarily in medicine and the social sciences, however this method has been used in ecological studies (Côté and Sutherland, 1997; Gurevitch et al., 2001), and conservation research (Fernandez-Duque and Vallegia, 1994).

To investigate the magnitude of the effect of MPAs on escape behavior, we conducted a formal meta-analysis based on 11 studies on three reef fish families (Labridae, Epinephelidae and Acanthuridae) that are often hunted by humans.

FID data (the total number of FID samples, FID standard deviation and FID average) were extracted from figures, tables, texts and/or supplementary material. When necessary, we used Web Plot Digitizer (version 3.12; Rohatgi, 2017) to extract data from published figures. Prior work has shown the dive method (scuba or snorkel) does not significantly influence FID estimation (see Januchowski-Hartley et al., 2012). Thus, we included studies conducted with both methods. Using Standardized Mean Difference (SMD), we quantified the effect size of fishing pressure on FID, in which the difference between treatment (fished areas) and control (no-take areas) group means were standardized using the standard deviations of control and treatment groups. The SMD estimates were pooled and we calculated Hedges *g* for the fixed effects (Hedges and Olkin, 1985).

The effect size metric Hedges’ g is a bias-corrected measure of standardized mean differences that does not overestimate the magnitude of an effect when sample size is small (Hedges and Olkin, 1985). Calculations were performed using the metafor package in R (R Development Core Team, 2015). The complete list of effect sizes is provided in SM3 and analyses of publication bias (Funnel and Quantile-Quantile plots) are provided in SM4.

3. Results

3.1. Number of studies

Of the 33 studies, 13 used FID to investigate the effects fishing pressure and protection by making comparisons inside and outside MPAs. The remaining 20 studies did not focus on the effects of MPAs on FID but rather asked how FID may be modulated by different variables, namely the presence of invasive species, the influence of body size, ocean acidification effects on antipredator behavior, predator recognition abilities, the magnitude of behaviorally mediated trophic cascades, mutualisms between preys, the benefits of the presence of shelter, the costs of group size, the influence of tourism on antipredator behavior and the effect of habitat complexity.

3.2. Escape metrics used

In addition to FID (which was also called minimum approach distance, flight distance, closest approach distance, n = 23 studies) researchers quantified, alert distance, response distance, reaction distance, line crosses, fish reaction, maximum response speed, maximum approach distance and mean distance hovered.

3.3. Reef fish families studied

Investigations comparing FID inside vs. outside of MPAs were conducted in Acanthuridae, Epinephelidae, Chaetodontidae, Balistidae, Pomacentridae, Pinguipididae, Cheylodactilidae, Holocentridae, Labridae, Mullidae, Scorpaenidae and Sparidae. In addition, FID of the families Nemipteridae, Gobiidae, Pomacentridae, Caesionidae and Dasyatidae were studied with objectives unrelated to MPA effects.

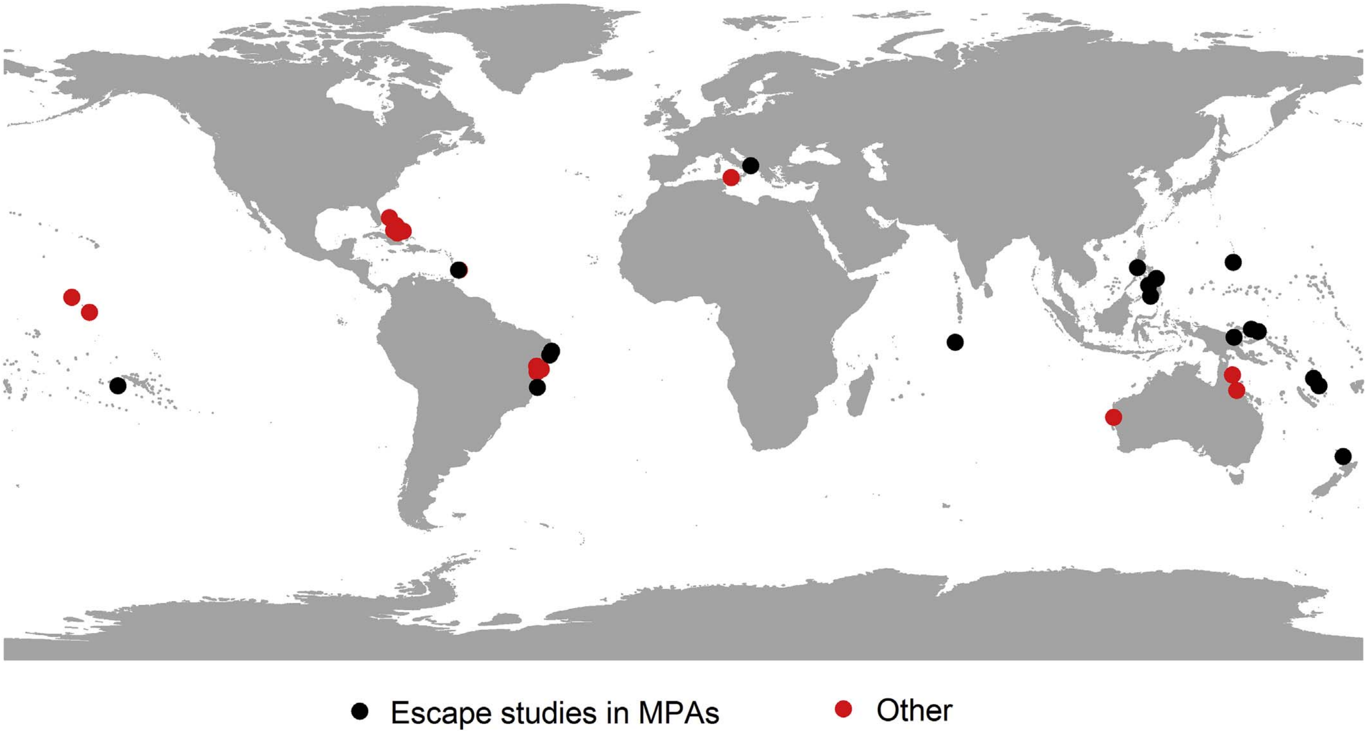

Fig. 1. Global distribution of studies conducted on reef fish ecology of fear using escape metrics. Black dots represent studies that investigated the effects of fishing pressure and protection (i.e., comparisons between inside and outside of marine protected areas) on FID. Red dots represent studies that focused on theoretical questions about escape behavior. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

3.4. Diving techniques employed

Most field studies aiming to measure FID *in situ* were conducted by snorkeling ($n = 12$). This was followed by the use of Self-Contained Underwater Breathing Apparatus (SCUBA, $n = 8$). One paper tested for differences in FID when measured by SCUBA and snorkel, but found none. Studies were conducted both in captivity ($n = 12$) and in the field ($n = 21$).

3.5. Spatial and temporal trends in FID studies

Most studies on FID were conducted on Indo-Pacific reefs (Fig. 1). By contrast, in Africa and on the Pacific coasts of the Americas (both North, Central and South) we found no reports of research studying aspects of escape behavior. In terms of temporal scale, the number of papers focusing on escape behavior of reef fishes is increasing annually, especially after 2010 (Fig. 2).

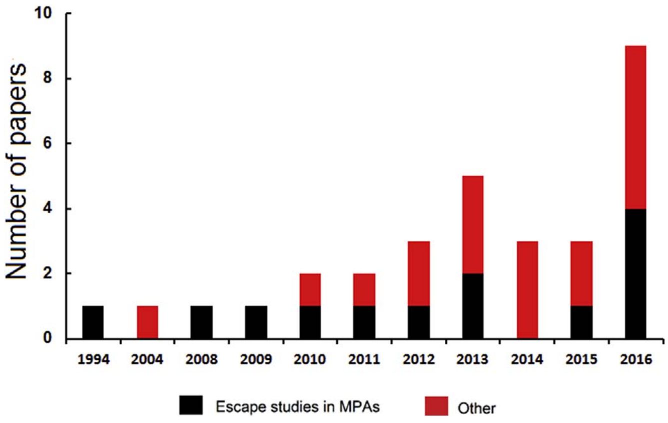

Fig. 2. Number of publications on reef fishes ecology of fear using escape metrics from 1994 to 2016.

3.6. Magnitude of the effect of MPAs on escape behavior

Overall, the results of our meta-analysis show that fish off MPAs had increased FID (Overall effect size = 1.3; Fig. 3; $p < 0.001$; diamond does not cross the non-effect line-Zero). However, there was some heterogeneity among the families; Labridae had a significantly higher effect size (Hedges $g = 1.65$; df = 10; $Q = 109.196$; $p < 0.001$). In addition, while five studies were conducted on the family Acanthuridae, no difference was found in FID effect sizes between MPAs and fished areas in one study. In the families Epinephelidae and Labridae, of all the studies conducted on the effects of MPAs on FID (three and seven studies, respectively) no effect was found in two and one (respectively; SM3).

4. Discussion

We examined global trends in the study of escape behavior involving reef fishes. While we showed that a variety of questions have been investigated using escape metrics, by far the effect of MPAs/NTZs was the focus of most research. While, to date, there have not been many of such studies, there has been a recent increase in using escape to study both fish behavioral ecology and to address questions of conservation concern. In terms of spatial occurrence, most studies on reef fish escape response were conducted in the Indo-Pacific region. Therefore, large geographical gaps exist in terms of where escape behavior studies were conducted. Two large spatial gaps include the Americas' West coast and all around Africa, as well as Mediterranean and Atlantic coast of Europe. FID studies can be further applied in a number of countries in both the Americas and Africa (e.g., United States of America, Panama, Costa Rica, Equator and Chile, Mauritania, Senegal, Guinea-Bissau, Cameron, Congo, South Africa, Mozambique, Madagascar and Somalia) where MPAs/NTZs are present. Studies that compared escape metrics inside and outside MPAs aimed to study the impacts of fishing on reef fish behavior. Such studies have shown that

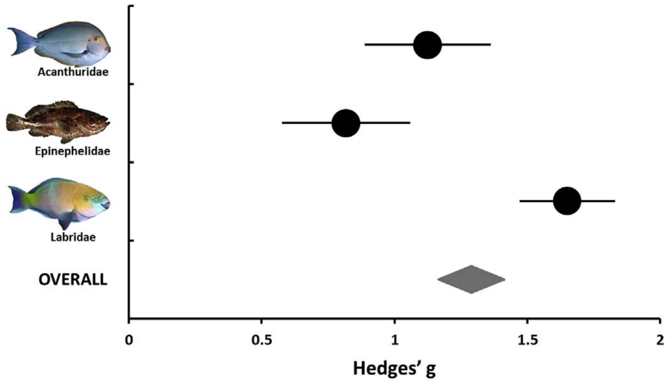

Fig. 3. Overall effects sizes (diamond) of the meta-analysis using standardized mean difference (black dots) and their 95% confidence intervals determined from the results of eleven studies (see SM1) comparing the flight initiation distances inside and outside marine protected areas for Acanthuridae (n = 5 studies; 354 FID samples, 172 in and 182 out MPAs), Epinephelidae (n = 3 studies; 300 FID samples, 140 in and 160 out MPAs) and Labridae (n = 8; 712 FID samples, 316 in and 396 out MPAs).

hunting pressure by humans can change behavior. Indeed, our meta-analysis suggests that FID typically increases along with fishing intensity (Januchowski-Hartley et al., 2011). While we do not expect there to be substantial differences because we found a universal increase in FID as a function of fishing, studies in these areas will include more diverse reefs structures (e.g., areas with low coral cover and rocky shores) and it will help develop a better understanding of variation in reef fishes FID living in different conditions.

Virtually several evaluations of MPA compliance focusing on fish use only abundance and species richness metrics (Bohnsack, 1998; Halpern et al., 2009; Guidetti et al., 2014; Goetze et al., 2017). A number of studies also investigate the effect on individual size, fish biomass (Guidetti et al., 2014, Edgar et al., 2014) and other focused on density/biomass of high trophic level species (e.g. Prato et al., 2017). Here, we show that FID can provide a useful tool to assess impacts of fishing that is complementary to other metrics (e.g., abundance, richness) because it is sensitive to differences in fishing pressure (Januchowski-Hartley et al., 2012), and may provide information about how well fishing regulations are enforced (Tran et al., 2016).

Employing FID metrics may also be cost effective. FID is a relatively simple procedure, which may be deployed with relative ease. In turn, the adoption of this methodological approach may provide important data to facilitate the adoption of adequate sampling designs with good predictive power (Januchowski-Hartley et al., 2012). Thus, we suggest that researchers and managers aiming to assess the relative compliance of MPAs should incorporate FID as an important behavioral metric to determine the relative level of fishing pressure occurring inside and outside of MPAs.

Additionally, it is important to realize that traditional uses of underwater visual censuses (UVC) to estimate the fish abundance and species richness inside and outside MPAs may be affected by increased FID of fishes in fished areas (Kulbicki, 1998). As fishing pressure increases, FID will increase, and this will reduce the probability that fishes will remain inside the observation distance of UVCs (Kulbicki, 1998). According to Feary et al. (2011) biases in UVC surveys may occur when visibility is reduced to < 6 m. In general, the studies we analyzed revealed greater FIDs associated with larger body size. Such a pattern is widely reported in other taxa (Blumstein, 2006; Møller, 2015) suggesting that larger-bodied fishes are more sensitive to human disturbance. Fishes, like other species, may compensate for benign disturbances (e.g., Samia et al., 2015), but this requires more research in aquatic systems.

For three fish families considered in our meta-analysis, the synthesis of results from all available studies confirmed the potential of FID as good estimator of compliance of fisheries control associated with MPAs. This result is most evident the Labridae family (Fig. 3). Studies of fishes in the Labridae family had reduced variation (i.e short confident intervals) in the overall effect size in our meta-analysis. Because these fishes are diurnal, and are found in relatively less dense aggregations, and because they are harvested globally (Nunes et al., 2016) they have been the subject of many studies. Species in this family may be found in any shallow reef around the world and thus subjected to intense fishing pressure (Bonaldo et al., 2014).

For instance, several species of the Epinephelidae family are crepuscular, which means that fish are associated with their burrows making it difficult to study FID during the day. Another reason is that this family was extensively exploited such that its abundance is almost null for several areas globally (Mitcheson et al., 2013). Species in the Acanthuridae family often swim in dense groups making it difficult to collect FID data, except for some species that swim in pairs or solitary. Yet, species in this family are heavily harvested globally (Benevides et al., 2016).

In spite of the fact that tourism is a frequent concern around and inside some MPAs, tourism was studied only in one paper (Benevides et al., 2018). More studies are required to make strong predictions about the influence of tourism in FID of fish. Albuquerque et al. (2015) showed that *in situ* human presence led to significant shifts in reef fish assemblage structure, resulting from short-term behavioral changes.

It is important to also consider the indirect effects that are created with fishing. For instance, fishing can behaviorally mediate trophic cascades and it can shape seascapes (Madin et al., 2010a, 2010b; 2011). In herbivorous fish, collective antipredator behavioral patterns were shown to change the distribution of vegetation and create grazing halos rings on a scale visible from space (Madin et al., 2011). Such ecology of fear studies contrast with the direct effects of predation on focal species and considers the effects prey behavior may have on its ecosystem. Nonetheless, such approaches could also be used for the conservation of target species considering larger spatial scales. In the case of grazing halos rings, monitoring the size of halos could be conducted by satellite, aerial photos and utilizing drones.

Visual census protocols (such as Atlantic and Gulf Rapid Reef Assessment (AGRRA) and Reef Check monitoring) were created to understand global variations in reef fish and coral assemblages (Lang et al., 2010; Freiwald et al., 2013). These protocols are commonly applied for monitoring of MPAs for protecting biota. If we want to understand the cumulative effects that MPAs may have on the performance of reef fishes, user-friendly protocols (including fear metrics) must be created and validated across a variety of spatial scales. Our review has shown that there is great promise in further development of these behavioral metrics.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.marenvres.2018.02.011.

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