

Body size and reserve protection affect flight initiation distance in parrotfishes

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Abstract Flight initiation distance (FID), the distance at which an organism begins to flee an approaching threat, is an important component of antipredator behavior and a potential indicator of an animal's perception of threat. In a field study on parrotfishes, we tested the predictions that FID in response to a diver will increase with body size, a correlate of reproductive value, and with experience of threat from humans. We studied a broad size range in four species on fringing reefs inside and outside the Barbados Marine Reserve. We used the Akaike's Information Criterion modified for small sample sizes (AICc) and model averaging to select and assess alternative models. Body size, reserve protection, and distance to a refuge, but not species, had strong support in explaining FID. FID increased with body size and generally remained two to ten times fish total length. FID was greater outside the reserve, especially in larger fish. Although we were not able to completely rule out other effects of size or reserve, this study supports predictions of an increase in FID with reproductive value and threat from humans.

Keywords Marine protected area · Reaction distance · *Scarus* · *Sparisoma* · Spearfishing

Fleeing from predators entails costs in time, energy, and lost opportunities to engage in other fitness-enhancing activities. Animals sometimes detect predators that are too far away to be a threat, so they should not necessarily flee

immediately. Rather, the timing of flight should be optimized according to the benefits and costs of both fleeing and remaining (Ydenberg and Dill 1986; Cooper and Frederick 2007). Thus, flight initiation distance (FID, the distance between the prey and a potential predator at which the prey starts to flee) should provide a measure of an animal's perception of the danger associated with a particular context and the risks it is willing to take. According to theory (Ydenberg and Dill 1986; Cooper and Frederick 2007), the variables predicted to influence FID are associated with the threat posed by the predator (e.g., predator species, size, and approach speed and prey group size), the capacity of the prey to escape (e.g., escape speed, distance to a refuge), fitness gains of an animal before it flees (e.g., quality of a currently exploited food patch), and expected fitness if it survives a given encounter (reproductive value; Clark 1994).

In many invertebrates and ectothermic vertebrates, size varies with age, and individuals varying by more than an order of magnitude in body size may be simultaneously present in a population. Size and age influence many fundamental biological and ecological characteristics of an organism, including metabolic rate, diet, swimming speed, sensory and defensive capabilities, reproductive potential, mobility, aggregation patterns, relative abundance of potential predators, and predator preferences (Peters 1983; Booth 1990; Sogard 1997; Glaudas et al. 2006). As a result, size may influence any or all of the general categories predicted by theory to affect FID. Previous studies have considered the effect of size on FID in insects (Scrimgeour et al. 1997), fishes (Webb 1981; Grant and Noakes 1987; Fuiman 1993; Abrahams 1995) and lizards (Burger and Gochfeld 1990; Burger et al. 1991; Bulova 1994; Martín and López 1995; Plasman et al. 2007). The results of these studies have been inconsistent, with FID unaffected by size

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(e.g., Bulova 1994), or greater for individuals of larger (e.g., Grant and Noakes 1987), smaller (e.g., Scrimgeour et al. 1997), or intermediate (e.g., Berger et al. 2007) size. Most of the studies of insects and fishes were done under laboratory conditions and with a limited size range of organisms. Except for Burger and Gochfeld (1990) and Martín and López (1995), the lizard studies treated size primarily as a potentially confounding variable and provided few results and limited discussion. Thus, there appears to be a need for additional field studies, especially where it is possible to examine a large size range.

FID should increase with risk posed by an approaching predator. The perceived threat of a stimulus, however, may be influenced by prior experience (Knight and Temple 1995; Brown 2003). Thus, FID is expected to vary in space and time. Mammals and birds that are hunted often show greater FID to humans than do animals in non-hunted populations, although the differences are not always large or consistent (Madsen and Fox 1995; Setsaas et al. 2007; Stankowich 2008). Conversely, animals learn to reduce responses to less threatening stimuli (e.g., Deecke et al. 2002), so frequent exposure to non-threatening humans should reduce FID to humans (Burger and Gochfeld 1990; Baudains and Lloyd 2007; Cooper and Whiting 2007; Stankowich 2008). Marine reserves protect fish from underwater hunting by spearfishers and are often used for ecotourism and recreational diving. Although divers anecdotally report decreased avoidance by fishes in reserves, we have not found any studies documenting the extent to which this protection and/or exposure to humans influences FID. The primary goal of our study was to examine how a broad range of body sizes influences FID in fishes in the field. Parrotfishes (family Scaridae), which are relatively common on Caribbean coral reefs, settle from the plankton at less than 1 cm long and grow to over 60 cm in some species, were selected as an appropriate family for investigation. In addition, the location of our study site adjacent to a marine reserve in Barbados allowed us to compare FID of fish in and outside the reserve.

Materials and methods

Study site

We measured FID in parrotfish on five sites distributed among four fringing reefs along the west coast of Barbados. We focused our sampling in the spur and groove zone, which is characterized by finger-like, seaward extensions of the reef separated by sand with depths of 4–8 m (Lewis 1960; Stearn et al. 1977; Rakitin and Kramer 1996). We collected data both within and outside the boundaries of the Barbados Marine Reserve established as a protected area in

1981. The sites within the Reserve were on the adjacent North Bellairs (13°11'32" N; 59°38'30" W) and South Bellairs (13°11'28" N; 59°38'31" W) reefs. Outside the reserve, we used two sites on Sandy Lane reef (13°10'17" N; 59°38'20" W), 210 m and 280 m south of the southern boundary of the reserve and about 50 m from each other. The other non-reserve site was on Bachelor Hall reef (13°11'58" N; 59°38'35" W), 670 m north of the northern boundary and separated from the reserve by another non-reserve reef. In the spur and groove zone outside the reserve, fish traps and spearfishing are regularly observed (Gotanda and Turgeon, personal observations). Although we observed occasional violations of the ban on fishing within the reserve, fishing pressure is lower as indicated by the greater size and abundance of fishes (Rakitin and Kramer 1996; Chapman and Kramer 1999; Tupper and Juanes 1999). Snorkeling and SCUBA diving not associated with spearfishing occur on all reefs, but are much more frequent on the two reefs within the reserve because they are relatively closer to a park and to dive shops. We are not aware of any quantitative data on the frequency of spearfishing or diving on any of the reefs.

Study species

Parrotfishes are common herbivores that maintain a strong association with solid reef substrates and play an important role in reef ecosystems by reducing algal biomass (Mumby et al. 2007). We selected the striped parrotfish (*Scarus iseri*, often referred to as *S. iserti* or *croicensis*; see <http://www.itis.gov/index.html>), princess parrotfish (*Scarus taeniopterus*), queen parrotfish (*Scarus vetula*), and stoplight parrotfish (*Sparisoma viride*), based on their local abundance. *S. iseri* and *S. taeniopterus* reach a maximum size of about 35 cm; *S. vetula* and *S. viride* are considerably larger, reaching just over 60 cm (<http://www.fishbase.org/home.htm>). Parrotfishes are moderately sedentary after settlement. Average home ranges of adult *S. iseri* range up to about 100 m² and those of *S. viride* up to about 200 m² (Mumby and Wabnitz 2002), while those of juvenile *S. viride* are much smaller (Overholtzer and Motta 1999). In a mark-recapture study in Barbados, median recapture and resighting distances of several of these species were 0–27 m and the longest observed movements were 57–127 m, with fish almost never moving between different reefs (Chapman and Kramer 2000). Thus, fish tested at locations separated by 50 m or more will almost always be different individuals.

In parrotfishes, three distinct life history stages, juveniles, initial phase adults, and terminal phase adults, are readily distinguished on the basis of color pattern. Terminal phase individuals are always male and are the largest individuals in the population. Initial phase individuals may be male or female. All species are protogynous hermaph-

rodites, changing sex from female to male (Robertson and Warner 1978). Terminal phase individuals predominate among parrotfishes captured by spearfishers (Turgeon, personal observations) and are relatively less common in locations with higher fishing pressure (Hawkins and Roberts 2004).

Data collection

We used a SCUBA diver as the stimulus for flight initiation. Humans are often used as stimuli in studies of flight initiation on terrestrial species ranging from small lizards and birds to large mammals (Frid and Dill 2002; Cooper 2005; Møller et al. 2008) and have been used in one previous study on fishes (Grant and Noakes 1987). A diver was an appropriate stimulus in this study because of our interest in the effect of protection from spearfishers.

Data were collected by the first author from 30 May to 16 August 2007. The observer, using SCUBA, swam slowly about the site searching for a parrotfish that was foraging or moving slowly and in a position where it could be approached directly. A dive buddy remained in the vicinity but did not move with the observer. Once a suitable individual had been located, the observer approached horizontally at about the same depth as the fish and approximately perpendicular to the fish's long axis at a speed of about 0.9 m/s. When the parrotfish started to flee, as indicated by an increase in speed, often accompanied by a change in direction, the observer dropped a weighted marker held at her waist. She then placed a second marker at the position of the parrotfish when it initiated flight. The distance between the two markers was measured with a graduated chain, and the distance between the observer's head and waist was subtracted so that the recorded FID was the distance between the fish and the closest part of the observer's body. Approaches were initiated as far away from the focal individual as possible to avoid starting from less than the FID of the focal individual while allowing the observer to correctly identify the individual and estimate its size. Because the large size variation affected the observer's ability to clearly see the fish, starting distance was shorter for small than for large individuals, ranging from approximately 1.5 m for the smallest juveniles to 7 m for the largest adults. To protect the reef, all approaches were conducted so that the first marker would not drop onto live coral. We abandoned trials in which the parrotfish was chased by damselfish or other species during the approach. Although the fish were not tagged, the observer used criteria of species, size, phase, and specific location within sites to avoid repeating trials on the same individual.

For each trial, the observer recorded the species, life history stage (juvenile, initial, or terminal phase), and total

length (to the nearest centimeter). Although not our primary interest, we recorded distance to a refuge and whether the focal individual was solitary or in a group because these variables influence FID in other species (Stankowich and Blumstein 2005). Species and life history stage identification followed illustrations in Humann and Deloach (2002). Distance to the nearest refuge, measured using the graduated chain, was the distance between the location of the parrotfish at the start of the observer's approach and the closest ledge, hole, or vertical structure capable of providing visual isolation. A parrotfish was considered to be in the same group as a focal individual if it was within five body lengths and moving in the same direction. Before starting data collection, the observer practiced until she could reliably estimate length to the nearest centimeter. She trained by estimating the length of static objects underwater (e.g., sections of PVC pipe of varying lengths) then practicing on fish very close to the reef where reliable landmarks could be identified near the snout and tail of a fish to permit checking of the estimate with a ruler. Accuracy was confirmed every 2 weeks using static landmarks on the reef.

Data analysis and model selection

We tested fish species, body size, distance to refuge, reserve (in vs. out), and group (solitary vs. in a group) as potential predictors of flight initiation distance. Fish size and distance to refuge were log-transformed and *z*-standardized prior to analysis. *Z*-standardization removes non-essential collinearity between single and interaction terms (Montgomery and Peck 1982; Neter et al. 1985), facilitates comparison among predictors by converting variables to a similar scale, and makes single terms more interpretable in the presence of an interaction (Quinn and Keough 2002). We did not include life history phase as a predictor because it was highly correlated with body size. To visually examine the interaction between fish body size and reserve protection, we categorized fish as large (≥ 25 cm) or small (< 25 cm), estimating 25 cm as a reasonable threshold for parrotfish to be targeted by spearfishers in Barbados (Gotanda and Turgeon, personal observations). We tested for multicollinearity among the retained predictors by examining tolerance, which is the inverse of the variance inflation factor and a measure of the amount of variation unique to each predictor (Neter et al. 1985; Tabachnick and Fidell 2001). Tolerance ranges from 0.0 to 1.0, with 1.0 indicating no collinearity. All tolerance values in our models were > 0.89 . In a preliminary analysis, we tested a priori for the effect of site on FID by means of an ANCOVA with fish body size and distance to refuge as covariables and species, reserve, and site as effect predictors. Site was not significant (p value = 0.391), whereas all other predictors were significant or

nearly so. Thus, for model simplicity and parsimony, we removed the site effect from our final models and retained the reserve effect.

Because biases and shortcomings of stepwise multiple regression are well-established (Hurvich and Tsai 1990; Wintle et al. 2003; Johnson and Omland 2004; Stephens et al. 2005; Whittingham et al. 2006) and because the use of the null hypothesis significance test approach has been criticized in observational studies (Stephens et al. 2007), we used the information theoretic approach for model selection and assessment of model performance. For that purpose, we used generalized linear models with a normal distribution and an identity link function (GLZ module in STATISTICA 6.1©) to produce candidate models that examine the effects of predictor variables on FID. GLZ uses the maximum likelihood (ML) method to build models and to estimate and test hypotheses about effects. In the modeling process, we included the five single terms mentioned above and allowed all possible two-way and three-way interactions among these predictors. To select the best subset of models among the candidate models, we used the Akaike's Information Criterion modified for small sample sizes (AICc, Burnham and Anderson 2002). The AICc value for each model quantifies its parsimony (based on the trade-off between the model fit and the number of parameters included) relative to other models considered. Candidate models are ranked using ΔAICc values ($\Delta\text{AICc} = \text{AICc}_i - \text{AICc}_{\min}$; where AICc_{\min} represents the best model in the model subsets). The plausibility of each model is quantified by its relative likelihood ($L(\text{model}|\text{data})$), which is proportional to the exponent of $-0.5 \times \Delta\text{AICc}$ given our data. Then, for each candidate model, the normalized Akaike weights ($w_{im}; \exp(-0.5 * \Delta\text{AICc}_i) / \sum_{r=1}^R \exp(-0.5 * \Delta\text{AICc}_r)$) are compiled as evidence that model i is the best of a set (Burnham and Anderson 2002). As a general rule of thumb, the confidence set of candidate models includes all models for which w_i is within 10% of the maximum weight, suggesting that these models have substantial support in explaining the data (Burnham and Anderson 2002). Because the w_{im} values in our best models were <0.9 , indicating that the other can-

didate models had substantial support as explanation of FID (Anderson et al. 2001; Burnham and Anderson 2002), we performed model averaging. Model averaging provides unconditional model variances and more reliable parameter estimates for each predictor. To determine the reliability of the predictor estimates from averaging, we calculated the weighted unconditional standard error with its associated confidence intervals (95% CI). To assess the relative importance of each predictor, we also use the normalized Akaike weights (w_{ip}). To calculate w_{ip} , the Akaike weights calculated for each model (w_{im}) that contains the parameter of interest are summed.

Results

We measured FID of 107 parrotfish, distributed among the four species, and ranging in size from 1 to 53 cm (Table 1). Parrotfish initiated flight when the observer was 0.03 to 3.68 m away (Table 1, Fig. 1). Fish sampled inside the Barbados Marine Reserve averaged larger body sizes (Mean \pm SD; 24.15 \pm 12.90 cm) than fish sampled outside (17.10 \pm 11.90 cm), but the size ranges were comparable (Fig. 1). Group sizes varied from two to 11 individuals, with about 43% of smaller fish (<25 cm) in groups as compared to 27% of larger fish.

Seven candidate models were within 10% of the strongest potential explanation of FID (Table 2). All of the potential predictors except species appeared in some of these seven models. There was strong support for an increase in FID with body size. Body size appeared in all selected models, had the highest w_{ip} along with distance to refuge and had a high, positive parameter estimate that did not include 0 within the 95% CI (Fig. 1, Table 2). FID was quite variable at any particular size, but generally remained between two and ten fish body lengths (Fig. 1).

Whether fish were inside or outside the Barbados Marine Reserve also affected FID, with lower FID in the reserve. The reserve effect was included in five of the seven selected models and the 95% CI of the parameter estimate did not

Table 1 Flight initiation distance (FID), body size, distance from refuge and the number of focal individuals observed inside and outside the Barbados Marine Reserve and solitary or in a group for each parrotfish species and for all species together (Mean \pm SD; range in parentheses)

Variables	<i>S. taeniopterus</i>	<i>S. iseri</i>	<i>S. vetula</i>	<i>S. viride</i>	All species
Flight initiation distance (m)	0.73 \pm 0.65 (0.03–2.48)	0.75 \pm 0.48 (0.08–1.93)	1.50 \pm 0.89 (0.28–3.23)	1.16 \pm 1.16 (0.03–3.68)	1.08 \pm 0.92 (0.03–3.68)
Body size (cm)	15.8 \pm 9.9 (4.00–32.0)	14.5 \pm 7.3 (3.50–28.0)	26.6 \pm 12.0 (6.00–50.0)	18.9 \pm 14.8 (1.00–53.0)	19.1 \pm 12.5 (1.00–53.0)
Distance from refuge (m)	0.77 \pm 0.76 (0.00–3.00)	0.66 \pm 0.80 (0.00–2.50)	0.71 \pm 0.83 (0.00–2.40)	0.54 \pm 0.82 (0.00–2.70)	0.66 \pm 0.80 (0.00–3.00)
Reserve (inside/outside)	4/15	10/16	5/23	11/23	30/77
Group (solitary/group)	13/6	14/12	18/10	21/13	66/41
Sample size	19	26	28	34	107

Fig. 1 Flight initiation distance in relation to total length in four parrotfish species inside (dots) and outside (inverted triangles) the Barbados Marine Reserve. The solid and dashed lines represent the best fit linear regressions inside and outside the reserve, respectively. Dotted gray lines indicate FID values of two times and ten times fish body length. Both axes are power scaled (x -axis; $p=0.4$ and y -axis; $p=0.1$)

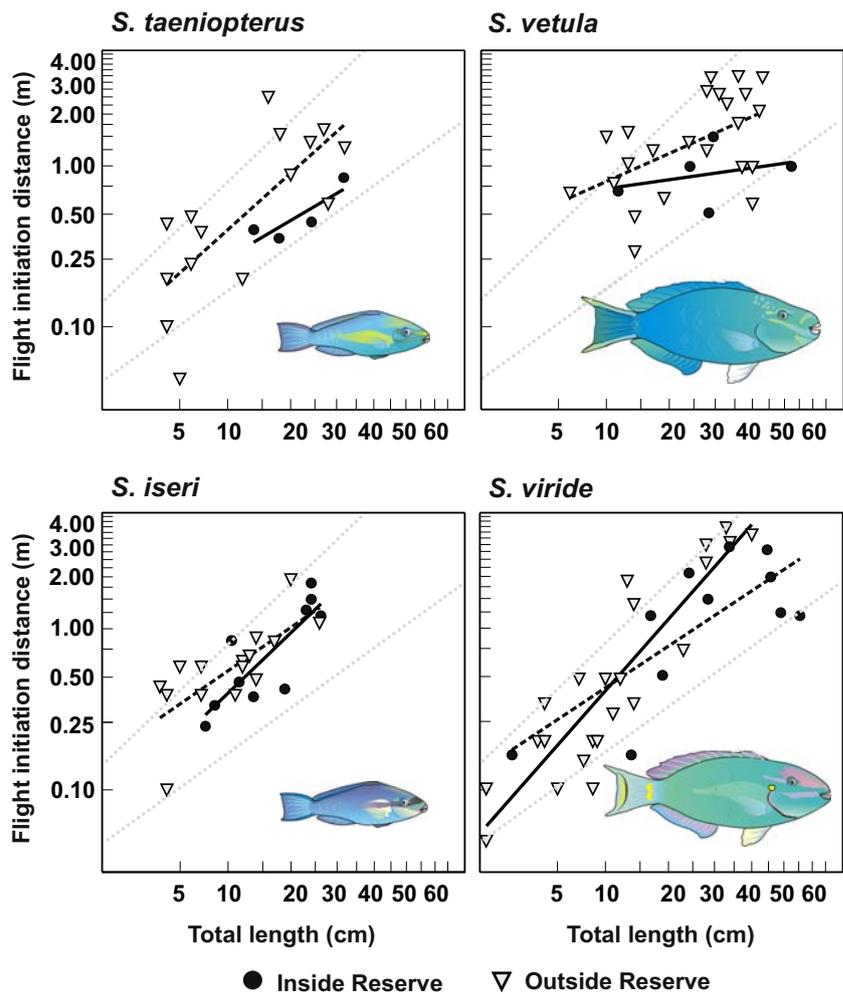


Table 2 Predictors and interactions terms included in the seven best models explaining variation in flight initiation distance (FID) of 107 parrotfish of four species

Predictors	Model rank							β	SE	95% CI	w_{ip}
	1	2	3	4	5	6	7				
Constant	■	■	■	■	■	■	■	-0.065	0.070	-0.202–0.072	
Body size	■	■	■	■	■	■	■	0.675	0.104	0.473–0.877	1.000
Distance to refuge	■	■	■	■	■	■	■	0.244	0.083	0.083–0.406	1.000
Reserve	■		■	■		■	■	-0.153	0.066	-0.282 to -0.025	0.727
Group				■	■			-0.058	0.175	-0.400–0.284	0.149
Reserve×size			■					-0.076	0.064	-0.200–0.049	0.104
Group×dist. to refuge					■			-0.033	0.061	-0.152–0.086	0.066
Size×dist. to refuge						■		-0.023	0.056	-0.132–0.086	0.056
Reserve×dist. to refuge							■	-0.016	0.064	-0.141–0.108	0.053
No. of parameters (K)	5	4	6	6	6	6	6				
AICc	208.5	210.0	211.3	211.8	212.2	212.6	212.7				
Δ AICc	0.00	1.46	2.85	3.30	3.74	4.08	4.18				
w_{im}	0.431	0.207	0.104	0.083	0.066	0.056	0.053				

Variables included in models are indicated with filled squares. The number of parameters (K) used in each model, the AICc, the Δ AICc (AIC of model _{i} –AIC of best model) and the w_{im} (normalized Akaike weights for each candidate models) are shown at the bottom of the table. Model-averaged estimates of parameters (β), unconditional standard errors (SE), 95% CI and the normalized Akaike weight for each predictors (w_{ip}) are shown as well. All models include a constant

include 0, although reserve protection was about 1.4 times less likely than body size or distance to refuge to explain FID, as indicated by the ratio of the sums of w_{ip} in the models that included body size and the models that included reserve (Burnham and Anderson 2002; Table 2). Furthermore, the interaction between reserve protection and body size was included in the third best model, suggesting that larger fish showed a stronger response to the reserve, as would be expected if they were more likely to be targeted by spearfishers. This interaction was at least 1.6 times more likely than any other interaction in the other candidate models, providing substantial evidence for an effect but was 9.6 times less likely than body size alone and 7.0 times less likely than reserve alone to explain FID. Larger fish (≥ 25 cm) fled at greater distances outside than inside the reserve (median outside, 2.33 m, inside, 1.33 m; Fig. 2). Smaller fish (< 25 cm) did not show this difference (outside, 0.48 m; inside, 0.53 m).

FID increased with distance to a potential refuge. This predictor was included in all seven selected models, and the 95% CI of the parameter estimate did not overlap 0 (Table 2). Distance to a potential refuge had an interaction with fish size in one selected model, with the reserve effect in another selected model, and with group size in a third selected model. To examine the relationship between distance to a refuge, body size, and reserve in more detail, we graphed the median response of large and small fish, inside and outside the reserve, in relation to distance from refuge. To facilitate the interpretation, we grouped distances from refuge into three classes of similar number of

observations: < 0.01 m, 0.01–1.5 m, and > 1.5 m. The graph suggested that the greater flight initiation distance of larger fish was particularly strong when they were farther from a potential refuge (Fig. 2). The interaction between distance to refuge and reserve was 18.8 times less likely than distance to refuge alone and 7.0 times less likely than reserve effect to explain FID. The interaction between distance to refuge and body size was 17.8 times less likely than distance to refuge or size alone to explain, but these two interactions nevertheless had some support. For some size class and reserve situations, the effect of distance from refuge was apparent only between the greatest and intermediate distance values. For others, the distance effect was stronger between the intermediate and closest distances (Fig. 2). It is important to note that not all individuals used refuges in the same way. Some individuals, especially smaller ones, sought refuge in holes or spaces between branches of live coral. Many individuals, especially larger ones, moved over sand along the grooves toward deeper water or crossed a spur.

Whether a fish was solitary or in a group may have influenced FID, as suggested by the inclusion of a group size effect in two of the seven selected models, and by an interaction between group size and distance to a potential refuge in one model (Table 2). Compared to body size, reserve protection, and distance to a refuge, the group size effect was relatively weak. In addition to the smaller number of selected models that included group size, the 95% CI of the parameter estimate overlapped 0. Whether a fish was in a group or not had 6.7 times less support than body length or distance to refuge in explaining FID and 4.9 times less support than the reserve effect. Overall, there was not a strong difference in FID for solitary fish (median, 0.81 m) compared to fish in a group (0.58 m).

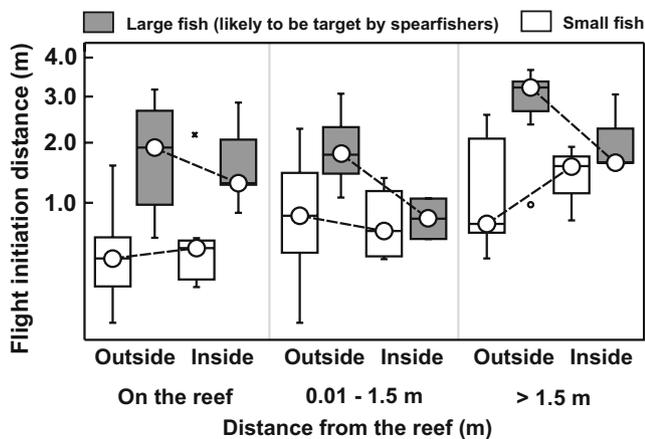


Fig. 2 Box plots showing flight initiation distance inside and outside the Barbados Marine Reserve in relation to the distance from a refuge for large fish (≥ 25 cm; shaded bars) and small fish (< 25 cm; white bars). White circles and horizontal bars show the median and the box represents the 25th and 75th percentile. The top whisker ranges from the 75th to the 90th percentile and the bottom whisker from the 25th to the 10th percentile. Asterisks and small circles indicate outliers. Dashed lines link plots for values from inside and outside the reserve to assist interpretation

Discussion

Body size

Life history theory predicts that as reproductive value (Fisher 1930; Grafen 2006) increases, risk-taking in general should decrease (Clark 1994) and FID in particular should therefore increase (Cooper and Frederick 2007). Reproductive value is likely to increase with size in parrotfishes because mortality rates generally decline with size in marine fishes, at least over the smaller size range (Sogard 1997), and reproductive potential increases (Wootton 1990). The increase in reproductive potential is especially strong in territorial, protogynous hermaphroditic species (Warner 1998; Rogers and Sargent 2001). Reinhardt (2002) developed a model for Pacific salmon that also predicted increasing risk avoidance with increasing size and reviewed

a number of previous studies showing increasing risk avoidance with larger size in fishes (see also Grant and Noakes 1987). Thus, increasing reproductive value with size is likely to explain the strong, consistent increase in FID with increasing body length in parrotfishes.

An alternative explanation consistent with FID theory is that the human stimulus is perceived as a greater threat by large than by small parrotfish. Many models of fish predator avoidance assume that larger predators present a stronger stimulus and a greater threat, leading to a greater reaction distance (Domenici 2002). Thus, we would expect the threat from a predator of constant size to decrease as the size of the focal fish increases. However, the threat could increase with size of the focal fish if large predators prefer larger prey and ignore smaller ones. This could explain the increasing response with size. Indirect support for this idea comes from the observation that studies reporting an increase in FID with size for fishes used a person as a stimulus (Grant and Noakes 1987; this study), whereas those finding no response or a negative one in fishes and aquatic insects used a predatory fish or fish model stimulus (Helfman 1989; Abrahams 1995; Helfman and Winkelman 1997; Scrimgeour et al. 1997). To distinguish the roles of reproductive value and predator size, it will be necessary to assess FID in relation to focal fish size for a range of predator sizes.

A second alternative explanation for size-related FID in parrotfishes is related to the observer starting distance. Several recent studies have discovered that starting distance correlates positively with FID in some mammals, birds, and lizards (Blumstein 2003; Cooper 2005; Stankowich and Coss 2006). This pattern is predicted from theory (more time spent in attention by prey during a longer approach; stronger evidence of a serious threat) but could also be a methodological artifact (start distances less than FID; more opportunity for prey to move spontaneously) (Blumstein 2003; Cooper 2005; Stankowich and Coss 2006; Cooper 2008). In our study, we used longer starting distances for larger than for smaller fish because we could not locate, identify, and estimate size of small subjects at distances greater than the FID of large individuals. We made a strong effort to start all trials beyond the FID and we could distinguish fleeing from spontaneous movements, so starting distance artifacts seem unlikely. In addition, for some lizards starting distance does not affect FID when approach speed is relatively slow (Cooper 2005) as it was in this study. However, we cannot rule out the possibility that some of the effect of size on FID might be related to an apparently greater threat from a longer approach.

Because the eyes of fishes increase in size as they grow while cone density decreases relatively little, larger fish are expected to have better visual acuity than smaller fish (McGill and Mittelbach 2006). Studies of foraging fishes

have shown that larger zooplankton-feeding fish can detect prey at greater distances than smaller fish (Breck and Gitter 1983), but we are not aware of any equivalent studies on predator detection. Although it is possible that large fish could see the diver from a greater distance, a visual constraint seems unlikely, given the clear water, large stimulus, and relatively small distances involved. The suggestion that FID is constrained by visual acuity is also incompatible with the observation that FID increased when parrotfish were out of the reserve and farther from a refuge.

The only previous field evidence for a size-related increase in FID in fishes is a study of responses by juvenile brook trout *Salvelinus fontinalis* to the approach of a wading observer (Grant and Noakes 1987). In a laboratory study of responses by staghorn sculpins *Leptocottus armatus*, a cryptic, benthic species, to a computer-generated, circular looming stimulus simulating an approaching object, there was an increase in the apparent distance of response as fish body size increased (Paglianti and Domenici 2006). In contrast, Helfman (1989) found that reaction distance to a model predator (not necessarily flight initiation) decreased with size in threespot damselfish *Stegastes planifrons*. Using a similar approach, Helfman and Winkelman (1997) found no effect of size on reaction distance in bicolor damselfish *Stegastes bicolor*. Our results also differ from laboratory studies indicating a negative relationship between FID and size in brook sticklebacks *Culea inconstans* and a lack of relationship in fathead minnows *Pimephales promelas* (Abrahams 1995). With eight- to 53-fold size variation, our study examined a much broader size range than previous studies, which ranged from as little as 1.5-fold (Abrahams 1995) to 5.7-fold (Paglianti and Domenici 2006).

As in fishes, the relationship between body size and FID is variable in other taxa. Some studies of lizard flight decisions that considered size primarily as a potentially confounding variable found no effect (Heatwole 1968; Burger 1991; Bulova 1994; Plasman et al. 2007). Other studies have reported a positive relationship (Burger and Gochfeld 1990; Martín and López 1995) or a maximum FID at intermediate sizes (Berger et al. 2007). A small size class of larval mayfly *Baetis tricaudatus* had greater FID values than a larger size class (Scrimgeour et al. 1997). Two recent studies have reported that FID in response to an approaching person increased with size in interspecific comparisons of birds (Blumstein 2006; Fernandez-Juricic et al. 2006). Perhaps the variation could result from differences in whether individuals are at higher or lower risk from a given threat stimulus as their size increases and the relative importance of changes in reproductive value, foraging activity, perception, and locomotion as size increases.

Reserve protection

Theory predicts that FID will increase as the danger posed by the predator increases (Cooper and Frederick 2007). Animals may gain information about the magnitude of a threat from experience or social learning, which can modify innate responses. The effect of the reserve on FID suggests that parrotfish respond to the threat of spearfishing or to exposure to non-threatening divers by increasing their FID outside the reserve or by decreasing it in the reserve. Although larger parrotfish have large home ranges, they rarely move between reefs (Chapman and Kramer 2000), so most fish are likely to have had post-settlement experience only in or out of the reserve. Testing in only one reserve and using a relatively small number of sites (two reefs in the reserve, three sites on two reefs outside the reserve) raises the possibility that the apparent reserve effect could be due to an environmental difference other than the level of spearfishing and habituation. Although the reefs do differ somewhat from each other in characteristics such as proportion of live coral and physical structure (Turgeon, K., unpublished data), there is no obvious, consistent difference associated with the reserve. Furthermore, a role for spearfishing rather than habituation is supported by the finding that the median FID in larger parrotfish, more likely to be targets of spearfishing, was 75% higher outside the reserve whereas for smaller parrotfish the median FID was actually 10% higher inside.

We are not aware of any other documentation of the effect of a marine reserve on FID in fishes. Other changes in antipredator behavior of fish, such as escaping to open water rather than refuging in shelters, have been reported as consequences of spearfishing in other species (Guidetti et al. 2008). Increases in FID as a consequence of hunting have been reported in some birds and mammals (Hutchings and Harris 1995; Thiel et al. 2007). Also FID to humans can decrease with increasing human exposure for other taxa, even when animals are not hunted in the area with lower exposure (e.g. Burger and Gochfeld 1990; Baudains and Loyd 2007; Cooper and Whiting 2007; Stankowich 2008). FID reductions as a result of human exposure, however, can be minor (Frid and Dill 2002), variable among individuals (Runyan and Blumstein 2004) or even increase with non-threatening exposure (Thiel et al. 2007).

Because fish often reach larger sizes in marine reserves (Halpern 2003; but see Mumby et al. 2006), including the Barbados Marine Reserve (Chapman and Kramer 1999), and because size has the opposite effect from protection, it is important to include size as a covariate in studies of reserve effects on FID. The effects of body size and protection on FID are also important because they could bias visual censuses by lowering counts of larger fishes outside reserves.

Other variables affecting flight initiation

The strong support for an effect of distance from a refuge on FID was not surprising because this pattern has a clear theoretical basis (Ydenberg and Dill 1986; Cooper and Frederick 2007) and is one of the most consistent patterns found in meta-analyses (Stankowich and Blumstein 2005). On the other hand, parrotfishes do not consistently enter refuges such as holes or branching coral colonies when threatened. Although they sometimes approach complex reef structure, they may also move quickly away from the reef and swim toward deeper water. This appeared to be more related to fish size than distance to the refuge but deserves further study. Our results suggest that distance to a potential refuge should be considered even in studies of species that do not hide in a hole or other refuge when threatened.

Conclusions

We have shown that body size has a large effect on FID, which we attribute to lower risk-taking associated with the higher reproductive value of large individuals. Although higher risk to larger fish from a large ‘predator’ and many other changes in state associated with size might also play a role, the strong size effect suggests that life history considerations may enhance our understanding of both antipredator tactics and the potential for human disturbance (Blumstein 2006). In future studies, it will be interesting to see whether individual changes in reproductive value, for example associated with changes in sex or mating status, influence FID. The lower FID in the reserve shows that fishes, like other vertebrates, can respond to protection and/or exposure to humans by changes in antipredator behavior. It should be possible to explore the relative roles of hunting and habituation by comparing species that are and are not targets of spearfishing.

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