

## Flight behavior of targeted fishes depends on variables other than fishing

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### ABSTRACT

Behavioral changes due to human predation can affect the functional role of targeted fishes and has implications for ecosystem and fisheries management. Wariness of targeted fishes towards divers, often measured as flight initiation distance (FID), has been shown to increase in areas where spear fishing pressure is higher. Additional research is required to understand how these patterns vary among different species and places. To support such studies, there is a need to explore the relationship of approach starting distance (SD) and other variables that influence measures of fish wariness. We used stereo video to record FID, a new direct measure of minimum approach distance (dMAD), and escape responses of targeted reef fishes in a marine reserve and heavily fished area in Hawai'i. We investigated the role of SD and 15 other variables in influencing FID and dMAD and tested differences between the reserve and fished area. SD explained a large portion of the variability in FID and somewhat less variability in dMAD. FID and dMAD were higher when fishes were travelling (vs feeding), increased with fish body length, and decreased with depth. When including these co-variables in models of FID and dMAD of targeted reef fishes, we found significant differences between study sites for dMAD, though not for FID. We also found differences in escape responses between sites. Based on these results, we recommend using stereo video to conduct measures of dMAD as a complement or alternative to FID, while simultaneously measuring SD and collecting additional data such as escape response. Relative effect sizes of SD and, to a lesser extent, other co-variables were large in comparison to site. Studies that use similar methods and do not control for or incorporate SD may produce biased results with regard to the effects of fishing pressure on flight behavior of targeted fishes.

### 1. Introduction

Fishing alters the structure and function of fish communities, influencing trophic composition (Jennings et al., 2013), size structure (Robinson et al., 2016), biomass (Friedlander et al., 2018), abundance (Kelaher et al., 2014) and diversity (Mora et al., 2011), with consequences for food security and ecosystem function (Bridge et al., 2013; Brown and Mumby, 2014). However, there has been comparatively little research on the effects of fishing on fish behavior and the resulting implications for fisheries and ecosystem management. Behavioral changes can influence the functional role that fishes play in the ecosystem (Madin et al., 2011, 2010), and may affect sexual selection (Biro and Post, 2008) and habitat usage (Lindfield et al., 2014b). For

example, Rizzari et al. (2014) showed that the presence of a predator led to the localized cessation of macroalgae removal by herbivorous fishes, due to the perceived risk of predation. Fish behavior can also influence estimates of fish assemblage metrics as measured by underwater visual surveys (UVC) (Kulbicki, 1998; Pais and Cabral, 2017), especially across gradients of fishing pressure and when evaluating MPA effectiveness (Gray et al., 2016; Lindfield et al., 2014a). This potential source of bias could also influence other applications of UVC data such as studies of fish/habitat relationships and species distribution modelling (Monk et al., 2012).

Reef fish wariness towards divers has been estimated by measuring flight initiation distance (FID) in a limited number of studies (eg. Gotanda et al., 2009) using methods adapted from terrestrial

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experiments where the subject is approached directly until it flees (Cooper, 2005; Frid and Dill, 2002). Lindfield et al. (2014a,b) used a passive measure; minimum approach distance (MAD) to estimate reef fish wariness, where minimum distance was recorded for every fish encountered on a transect. These studies have documented differences in fish wariness between marine reserves and fished areas and along gradients of fishing pressure (eg. Januchowski-Hartley et al., 2015). Fish wariness has also been shown, in some circumstances, to be more sensitive to changes in management than measures of abundance, length, or biomass (Goetze et al., 2017). Measures of fish wariness have the potential to be used as proxies for fishing pressure and indicators of marine reserve compliance (Bergseth et al., 2015). However, there is a need for additional research to see if findings are consistent across geographies and species and to establish regional baselines.

Starting distance (SD) – the distance at which the observer begins the trial approach – has been shown to have a strong and consistent relationship with FID in terrestrial species (Samia et al., 2013). Nevertheless, SD has not been incorporated in studies of flight distance of harvested fishes (but see Tran et al., 2016). Previous studies of FID for coral reef fishes have standardized SD by setting a minimum range, however, it is necessary to understand the influence of SD on flight distance of fishes to support continuing research and aid interpretation. In addition, factors such as fish body size have been recognized to be important determinants of flight behavior (Gotanda et al., 2009; Januchowski-Hartley et al., 2011) and there is a need to explore additional variables that may explain variation in flight distance besides fishing pressure.

In order to fill these knowledge gaps and support future flight behavior research on marine fishes, we used stereo-video to conduct measurements of SD, FID, and a new direct measure of MAD (dMAD), and investigated the role of SD and other co-variables on targeted reef fish wariness in a marine reserve and heavily fished area in Hawai'i. In addition, we recorded escape (post flight) responses of targeted reef fishes. Our objectives were to: 1) investigate the role of SD and other variables in measuring flight distance in coral reef fishes, 2) compare measures of FID and dMAD, and 3) incorporate escape response data to explore how flight behavior changes under different levels of fishing pressure.

## 2. Material and methods

### 2.1. Site descriptions

Measurements of reef fish flight behavior were conducted at two locations in the main Hawaiian Islands: Ka'ūpūlehu-Kīholo on Hawai'i Island and around the island of Kaho'olawe. Ka'ūpūlehu-Kīholo, hereafter referred to as Ka'ūpūlehu, lies on the west coast of Hawai'i Island, approximately 20 km north of a main population center, Kailua-Kona. Surveys of fish behavior were carried out in September 2013 shortly before a regional ban on SCUBA spearfishing was implemented (DLNR, 2013) and well before the more recent enactment of a 10-year fishing moratorium that went into effect July 29, 2016. Based on previous underwater fish surveys, average biomass of targeted reef fishes in the area was low ( $27.1 \pm 1.6$  (SE)  $\text{g}/\text{m}^2$ , Minton et al., 2015) compared with statewide estimates among fished areas ( $50.0 \text{ g}/\text{m}^2$ , Friedlander et al., 2018). Combined estimates of spearfishing effort for this area prior to the ban equaled more than  $5000 \text{ hrs yr}^{-1}$ , making it among the highest of the 18 locations in the state with fisheries creel survey data (Delaney et al., 2017). Kaho'olawe is the smallest of the eight main islands of Hawai'i, it is located southwest of Maui and southeast of Lāna'i. Surveys of targeted fish flight behavior were conducted there in June 2015. The island was a *de facto* marine reserve during World War II, and since 1990, it has been under the administration of the state Kaho'olawe Island Reserve Commission, with extremely limited access and only limited take of marine life permitted for cultural and subsistence purposes at specific locations on the island (Friedlander et al.,

2014). Average biomass of targeted reef fishes on Kaho'olawe ( $92.0 \pm 13.7$  SE  $\text{g}/\text{m}^2$ , Minton et al., 2016) is over three times higher than at Ka'ūpūlehu, and it has been used as a near-unfished baseline for the main Hawaiian Islands (Friedlander et al., 2018). Targeted species of the main Hawaiian Islands nearshore fishery were defined as coral reef fishes having  $\geq 450$  kg of annual recreational or commercial harvest for the past 10 years (2000–2010), or otherwise recognized as important for recreational, subsistence, or cultural fishing (<http://dlnr.hawaii.gov/dar/fishing/hmrfs/>).

### 2.2. Sample design and methodology

Surveys of fish flight behavior were conducted using SCUBA at random locations on hard-bottom habitat at each site, pre-selected in ArcGIS. Survey locations were accessed by small boat and spaced a minimum of 60 m apart, though adjacent locations were rarely surveyed on the same day. Flight behavior surveys were carried out in parallel with fish population surveys, thus three divers were present at each survey location. Two divers worked together to conduct belt-transects of fishes and benthos, while the third diver carried out surveys of fish behavior. The fish behavior diver maintained visual contact with the other divers but kept a distance of at least 10 m. Diver operated stereo-video (DOV) was used to conduct surveys of fish flight behavior that were later analyzed in the lab. Fish flight behavior surveys were based on those of Gotanda et al. (2009). The fish behavior diver (hereafter 'observer') swam slowly about the site searching for any targeted reef-fish species that was foraging or moving slowly and in a position where it could be approached directly. When a suitable individual was located, the observer approached horizontally at the same depth as the fish and at a steady swimming speed. The approach was continued until the fish started to flee, as indicated by an increase in speed and often a change in direction, or until the observer could not get any closer to the fish as it moved away. About 20 min was spent at each survey location and the number of behavior trials varied based on the density of targeted species present, resulting in differing sample sizes by species/family and site.

### 2.3. Video analysis

EventMeasure software (SeaGIS) was used to analyze stereo-video data and enabled precise measurements of distance and fish length. Fish species, conspecific group size, and activity (feeding or travelling), was recorded at the beginning of each trial approach. Fish length was measured at the closest point where the fish was orientated perpendicular to the observer. SD was measured at the beginning of each trial approach. This was determined as the farthest point of the approach where the line of sight between observer and fish (and vice-versa) was unobstructed. Flight response was identified as a change in speed and often direction. FID was measured as distance from observer (DOV system) to the nearest part of the fish, usually the tail, immediately before the observed flight response. If there was no observable flight response, FID was recorded as the minimum distance between the observer and fish. dMAD was measured separately as the minimum distance from the observer to the fish at any time during the approach. Thus dMAD was always less than or equal to FID. Often dMAD coincided with FID, however sometimes it occurred before, or after, an observed flight response.

Escape response was classified into five categories, based on video observations. These can be roughly organized from most-wary to least-wary behaviors listed as follows: "spook" – large burst of speed, "shelter" – take shelter in the substrate, "evade" – evasive maneuvers side to side and/or in and out of structure, "flee" – increase speed and swim away in a single direction, usually toward deep water, and "none" – no visible escape response.

**Table 1**

Variables tested with potential influence on flight behavior. Ranges of continuous variables for this study are provided in parenthesis.

Variable	Type	Units	Description/justification
<i>Observer</i>			
Bubble	True/False	–	If flight response coincided with SCUBA exhale. A potential confounding variable.
Observer	Categorical	–	Most observations were conducted by a single observer, though a small number were conducted by a different observer. A potential confounding variable.
Starting distance	Continuous	m	The distance between the fish and the observer at the beginning of the trial approach (1.7 – 14.4).
<i>Fish</i>			
Activity	Categorical	–	Fish activity during trial approach, either travelling or feeding.
Family	Categorical	–	Previous research has shown differences in flight response by fish family.
Group size	Continuous	fishes	Predator theory predicts differences in flight response based on group size (1 – 48).
Length	Continuous	cm	Shown by previous research to influence flight response. Larger individuals have higher reproductive value, and thus are warier of predation (7.5 – 58).
Maximum size	Continuous	cm	Maximum recorded size of species. Larger bodied species tend to be more targeted by fishers (14 – 70).
Mobility	Categorical	–	Range of daily movements of fish species (Friedlander and Parrish, 1998). Transient: move rapidly over relatively large distances, semi-vagile type I: tens of meters – butterflyfishes and small wrasses, semi-vagile type II: potentially hundreds of meters – large surgeonfish and parrotfish.
Targeted	True/False	–	If species is targeted by spear fishing in the area (Koike et al., 2015).
Trophic level	Categorical	–	Primary, secondary, top predator (Froese and Pauly, 2017).
<i>Environment</i>			
Depth	Continuous	m	Deeper areas are less accessible to spear fishers (3.7 – 17.1).
Distance to shore	Continuous	m	Areas far from shore are less accessible to spear fishers (60 – 646).
Rugosity	Continuous	m	A measure of seafloor complexity. The length of chain lain along the seafloor surface profile corresponding to a 10 m transect. Fish wariness is thought to increase in areas with less shelter available (10.5 – 17.5).
Visibility	Continuous	m	Estimated from video. Furthest distance where objects/fishes can be distinguished from background (5.3 – 21.7).
Wave power	Continuous	kW/m	Areas with high waves have been shown to harbor targeted fish populations and are thought to provide a refuge from fishing pressure (1,459 – 3,073).

## 2.4. Data analysis

### 2.4.1. Data cleaning

The full suite of variables influencing flight behavior, excluding fishing pressure, were investigated using the dataset from the fished area (Ka'ūpūlehu). This was the larger of the two datasets and had data for all variables of interest. Families with very small sample sizes ( $N < 5$ ) were removed, as were all soldierfishes (Holocentridae) due to their close affinity to shelter. To investigate the effect of SD on FID and dMAD and examine differences in targeted reef fish flight behavior related to fishing pressure, data from the reserve and fished area were combined. To ensure a robust comparison, data for families with  $N < 10$  for either site were removed. Species that were not sampled at both sites were also removed.

### 2.4.2. Variables influencing flight behavior

Previously tested and novel variables that potentially influence flight behavior were identified based on a review of the literature and grouped into three main categories: aspects of observer/observation trial, aspects/attributes of fish under observation, and environmental factors (Table 1). Influence of these variables on measures of FID and dMAD in the fished area were investigated using distance-based linear models (DistLM) (Anderson et al., 2008). DistLM is based on a resemblance matrix and we used Euclidean distances so the resulting  $F$  ratio and  $R^2$  values are equivalent to those obtained from traditional multiple linear regression. However, an important distinction of the DistLM routine is that the  $P$ -values are obtained by permutation, thus avoiding the traditional assumption that errors be normally distributed (Anderson et al., 2008). Distributions of continuous variables were examined to ensure they were not heavily skewed or contained extreme outliers and collinearity between variables was evaluated. Group size was 4th root transformed. Marginal tests were performed to evaluate

the independent influence of each predictor on FID and dMAD. Final combined models were identified using a step-wise selection procedure with AIC model selection criteria and models were run with 9,999 permutations.

The relationship of SD with FID and dMAD was analyzed using quantile regression on the combined dataset. Due to the constraint that  $FID/dMAD \leq SD$  (escape cannot occur before the experiment starts), the relationship could not be modeled using ordinary least squares (OLS) linear regression as it violates the assumption of homoscedasticity and a spurious positive relationship is likely to be produced (Chamaillé-Jammes and Blumstein, 2012). Quantile regression overcomes problems with the estimation of regression models that exhibit heteroscedasticity (non-constant variance) and is robust to outliers. The natural rate of leaving ( $\lambda$ ) is a critical determinant of the slope of the FID/dMAD-SD relationship. As animals become more likely to leave when approached, FID/dMAD become closer to SD and the slope increases towards 1. Thus, conducting flight distance experiments is difficult on mobile species because false escapes will be recorded (Chamaillé-Jammes and Blumstein, 2012). When the value of  $\lambda$  is unknown one must assume that the likelihood of the animal leaving before the observer reaches FID/dMAD is negligible. Under this assumption, the most robust approach is to test whether the slope of the lowest quantiles differs significantly from zero (Chamaillé-Jammes and Blumstein, 2012). In addition, the use of quantile regression on upper quantiles can provide information as to the relative value of  $\lambda$  (Chamaillé-Jammes and Blumstein, 2012). The relationship of water visibility and SD was visualized using OLS linear regression. Distributions of SD, water visibility, and depth for each site were compared using one-way Analysis of Variance (ANOVA) tests. SD was  $\ln(x)$  transformed to meet assumptions of normality, while water visibility did not require transformation.

### 2.4.3. Fishing effects on flight behavior

In order to incorporate the variation among survey locations and fish species, the effect of fishing on flight behavior was determined using linear mixed models where survey location and species were included as random factors. Key variables identified using the DistLM analysis were included as fixed factors. These were SD, length, depth, group size, family, activity and site (fishing level). Visibility was also included as a fixed factor. While shown to be significant variables in the DistLM models, maximum species size and mobility guild were not included in the linear mixed models because the variability associated with these variables relates directly to species level differences. Preliminary models indicated that observer was a significant factor, so observations by the secondary observer (n = 43) were removed. FID and dMAD were ln(x) transformed prior to modeling to meet assumptions of normality. Continuous variables were centered and scaled prior to modeling. A significance test of fixed factors was performed with a type III F-test, a marginal test that asks how much variation a predictor explains after the other predictors are accounted for. Degrees of freedom were estimated using the Kenward-Roger approximation.

### 2.4.4. Escape response

Due to larger sample sizes, observations of three families: Acanthuridae, Mullidae, and Scarinae (subfamily of Labridae) were selected for analysis of flight response. A Chi-squared test of independence of escape response by site and family was conducted and a mosaic plot was built based on these results. The plot shows relative occurrences of each escape response category by family and site and shows which combination of factors are significantly associated.

## 3. Results

Measures of flight behavior were recorded for a total of 760 fishes comprising 58 species from 15 families at 40 independent locations in the fished area (Ka'ūpūlehu) and 23 independent locations in the reserve (Kaho'olawe). Variables influencing flight behavior were investigated for the fished area that, after cleaning, resulted in a total of 446 observations of 43 species from 9 families (Table A.1). The influence of fishing on flight behavior of targeted species was tested on a combined dataset from the reserve and fished area that, after cleaning, made up 489 observations of 14 species from five families (Table A.2).

### 3.1. Variables influencing flight behavior

DistLM marginal tests showed that all variables tested, with the exception of SCUBA bubbles, observer, and group size, were significant independent predictors of FID. Final combined DistLM results showed that SD had a disproportionately large effect on FID, accounting for 51% of total variation, followed by family (4.1%), fish length (3.4%), and activity etc. (Table 2). Whether a species was targeted by spear fishers was a significant predictor accounting for 1.3% of total variation. SCUBA bubbles, distance to shore, group size, observer, rugosity,

trophic level, visibility, and waves were not significant predictors of reef fish FID. Marginal tests for dMAD indicated that only SCUBA bubbles was not a significant independent predictor. Final combined DistLM results for dMAD also showed a large effect of SD, though it explained less variation (43%) compared to the FID model (Table 3). Length accounted for more variation in this model (5.5%), compared to the FID model and group size was a significant predictor, while other predictors showed similar results (Table 3). SCUBA bubbles, distance to shore, observer, rugosity, trophic level, visibility, and waves were not significant predictors of reef fish dMAD.

#### 3.1.1. Starting distance

Distributions of SD did not differ statistically between sites ( $F_{1,487} = 0.74, p = 0.4$ ), though there were more high values in the fished area. Quantile regressions revealed that the slope of fitted lines increased with higher SD (corresponding to higher FID and dMAD) (Fig. 1). Slopes for dMAD were slightly lower for all quantiles compared to FID. The slope for the lowest (0.1) quantile was significantly different from zero (Fig. 1). This result, however, was mainly driven by scarids which predominated in the dataset and did not hold for the other families measured (Fig. A.2). The slope for the highest (0.9) quantile was significantly < 1 for scarids and mullids, though not for acanthurids, labrids, or lethinids (Fig. A.2), though the small sample size for the latter two families urges caution in interpretation. In addition, the scarids and mullids are largely represented by a single common species (Table A2), which likely drive these results.

Visibility had a significant positive relationship with SD (Fig. A.1A) and the fished area had significantly higher visibility ( $F_{1,487} = 4.00, p < 0.05$ ) (Fig. A.1B). Average depth of sample sites was greater in the fished area ( $F_{1,476} = 17.89, p < 0.001$ ).

### 3.2. Fishing effects on flight behavior

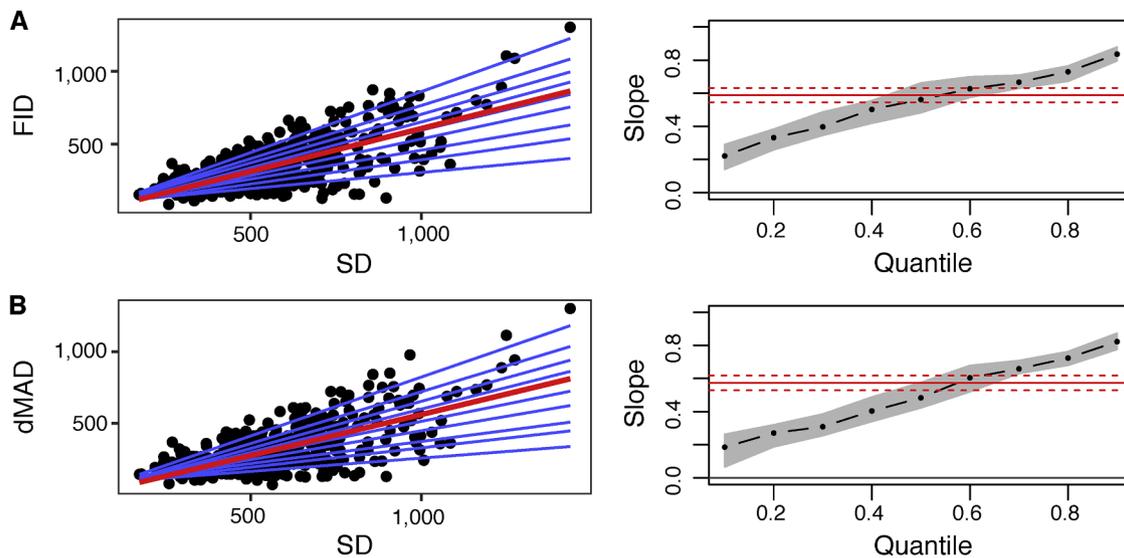
In the linear mixed effects model of FID, SD, activity, length, and depth were significant. Group size, visibility, site, and family were not significant (Table 4). In the linear mixed effects model of dMAD, SD, activity, depth, length, site, and group size were all significant (Table 5). Effect of SD was smaller compared to FID. More variability was attributed to site, and site was a significant factor in this model. Visibility and family were not significant (Table 5). SD, length, visibility, and group size all had a positive relationship with dMAD while depth had a negative relationship (Fig. 2). dMAD was lower when fishes were feeding. While dMAD by family did not differ significantly, lethinids had the largest average dMAD and labrids had the lowest (Fig. 2). Average dMAD for acanthurids, mullids, and scarids were very similar. Overall, targeted species in the fished area had significantly higher dMAD compared to in the marine reserve (Fig. 2). Mean modeled family level differences in dMAD between sites ranged from 90.3 cm for lethinids to 16.5 cm for scarids (Fig. 3).

**Table 2**  
DistLM results for FID, showing predictors identified as significant.

Predictor	AIC	SS (trace)	Pseudo-F	P	Prop.	Cumul.	res.df	regr.df
Start dist.	6322.7	6.61E+08	463.1	< 0.001	0.511	0.511	444	2
Length	6292.9	4.37E+07	32.8	< 0.001	0.034	0.544	443	3
Activity	6270	3.20E+07	25.3	< 0.001	0.025	0.569	442	4
Family	6241.8	5.27E+07	5.7	< 0.001	0.041	0.610	434	12
Targeted	6229.1	1.64E+07	14.6	< 0.001	0.013	0.622	433	13
Depth	6217.3	1.49E+07	13.5	< 0.001	0.011	0.634	432	14
Max size	6211.9	7.88E+06	7.3	0.006	0.006	0.640	431	15
Mobility	6206.3	9.90E+06	4.6	0.013	0.008	0.648	429	17

**Table 3**  
DistLM results for dMAD, showing predictors identified as significant.

Predictor	AIC	SS (trace)	Pseudo-F	P	Prop.	Cumul.	res.df	regr.df
Start dist.	6379.6	5.44E+08	335.0	< 0.001	0.430	0.430	444	2
Length	6336.6	6.91E+07	47.0	< 0.001	0.055	0.485	443	3
Family	6312	5.67E+07	5.2	< 0.001	0.045	0.530	435	11
Activity	6290.7	3.03E+07	23.3	< 0.001	0.024	0.554	434	12
Targeted	6277.8	1.85E+07	14.7	0.001	0.015	0.568	433	13
Depth	6268.6	1.36E+07	11.0	0.001	0.011	0.579	432	14
Max size	6259.4	1.32E+07	10.9	0.002	0.010	0.589	431	15
Mobility	6246.4	1.94E+07	8.3	0.002	0.015	0.605	429	17
Group size	6242.1	6.95E+06	6.0	0.015	0.006	0.610	428	18



**Fig. 1.** Quantile regression of SD vs A) FID (cm) and B) dMAD (cm). Left hand plots show regression lines fit to each of 9 quantiles of FID and dMAD (0.1 – 0.9) with the OLS fit in red included for reference. Right hand plots show the slope of each fit with 95% confidence intervals. The slope of the ordinary least squares fitted line and confidence intervals are shown in red. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

**Table 4**  
Linear mixed effects model – FID.

	Sum Sq	Mean Sq	Num DF	Den DF	F	Pr(> F)
<b>Start dist.</b>	8.366	8.366	1	475.603	109.765	< 0.001 ***
<b>Activity</b>	1.284	1.284	1	473.462	16.848	< 0.001 ***
<b>Length</b>	1.020	1.020	1	472.903	13.388	< 0.001 ***
<b>Depth</b>	0.598	0.598	1	59.939	7.843	0.007 **
<b>Group size</b>	0.133	0.133	1	453.373	1.746	0.187
<b>Visibility</b>	0.131	0.131	1	49.917	1.716	0.196
<b>Site</b>	0.098	0.098	1	72.959	1.281	0.261
<b>Family</b>	0.206	0.052	4	7.813	0.677	0.627

**Table 5**  
Linear mixed effects model – dMAD.

	Sum Sq	Mean Sq	Num DF	Den DF	F	Pr(> F)
<b>Start dist.</b>	8.203	8.203	1	475.460	92.339	< 0.001 ***
<b>Activity</b>	1.130	1.130	1	474.605	12.723	< 0.001 ***
<b>Depth</b>	1.125	1.125	1	60.974	12.668	0.001 ***
<b>Length</b>	0.909	0.909	1	469.711	10.227	0.001 **
<b>Site</b>	0.617	0.617	1	74.325	6.943	0.010 *
<b>Group size</b>	0.508	0.508	1	456.892	5.713	0.017 *
<b>Visibility</b>	0.212	0.212	1	48.833	2.384	0.129
<b>Family</b>	0.309	0.077	4	7.855	0.870	0.522

3.3. Escape response

Analysis of escape response showed that surgeonfishes (Acanthuridae) had a significantly lower incidence of evasive flight in the fished area (Fig. 4). Goatfish (Mullidae) and parrotfish (Scarinae) had a significantly higher incidence of “spook” in the fished area (Fig. 4). Surgeonfishes predominately exhibited a ‘flee’ response. Overall, ‘evade’ and ‘flee’ were the most common escape responses across all three family groups. Taking shelter was relatively uncommon, but most common among parrotfish.

4. Discussion

We found significant relationships between SD and both measures of flight behavior. SD explained a large portion of the variability in FID and somewhat less variability in dMAD. Other key variables were fish length, activity, and depth. When including these co-variates in models of FID and dMAD of targeted reef fishes, we found significant differences between a marine reserve and heavily fished area for dMAD though not for FID. Relative effect sizes of SD and, to a lesser extent, other co-variates were large in comparison to site. While analogous research in different systems is needed, studies that use similar methods and do not control for or incorporate SD may produce biased results with regard to the effects of fishing pressure on flight behavior of reef fishes.

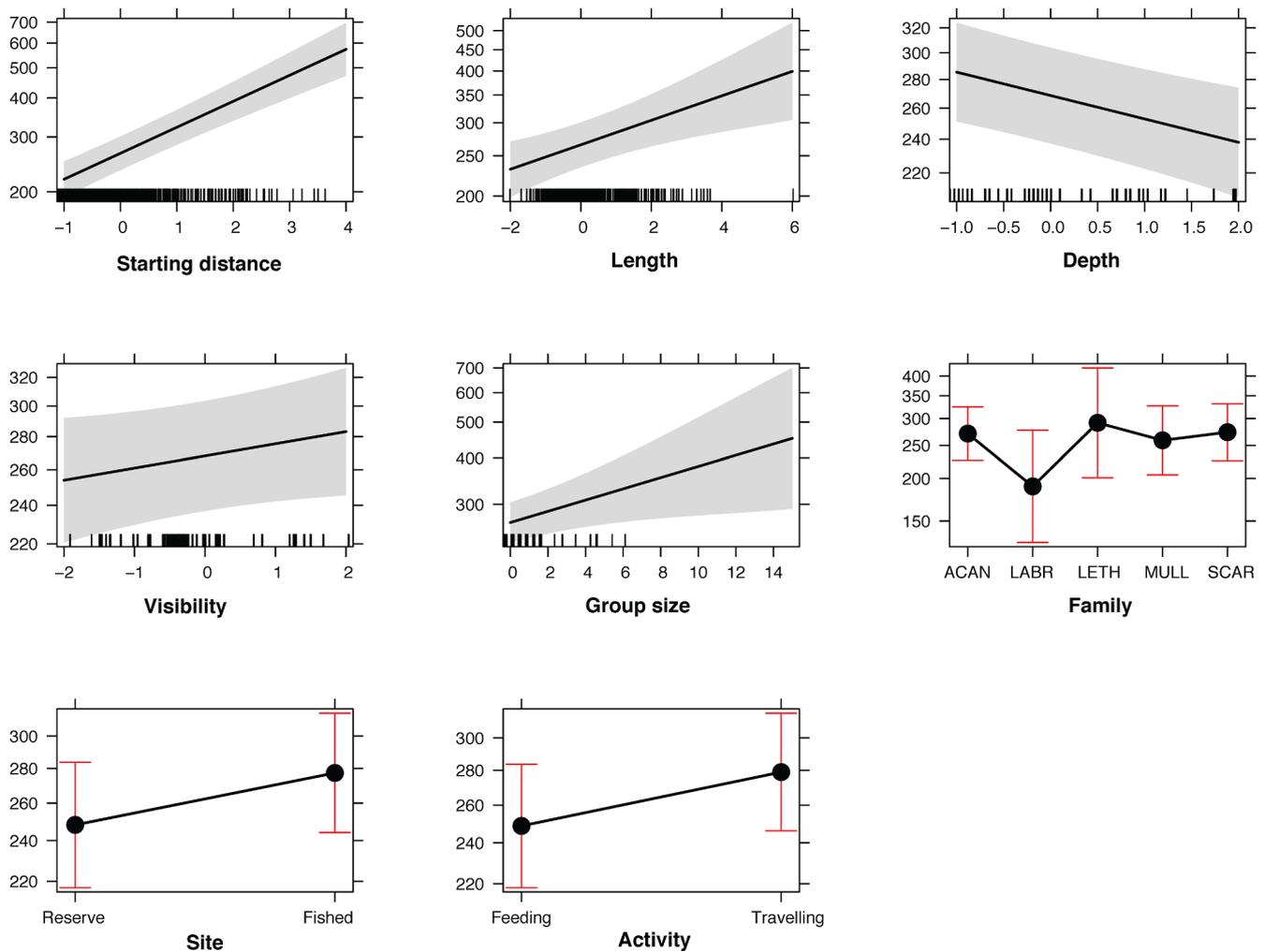


Fig. 2. Fixed effects for dMAD linear mixed effects model. Y-axis is dMAD in cm (log scale), x-axis represents each fixed effect, units shown in Table 1. All continuous variables were centered and scaled prior to modeling. Family codes are as follows: ACAN – Acanthuridae, LABR – Labridae, LETH – Lethrinidae, SCAR – Scarinae.

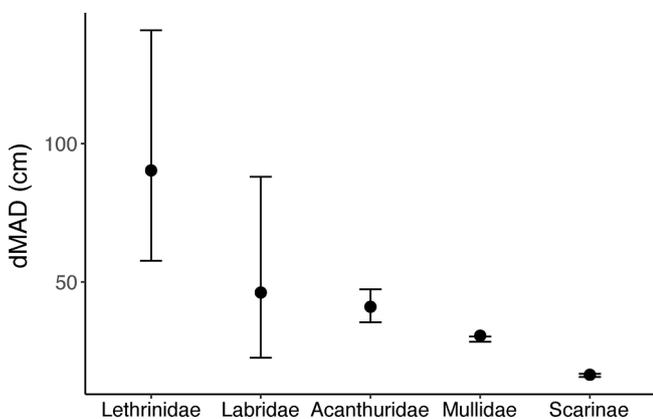
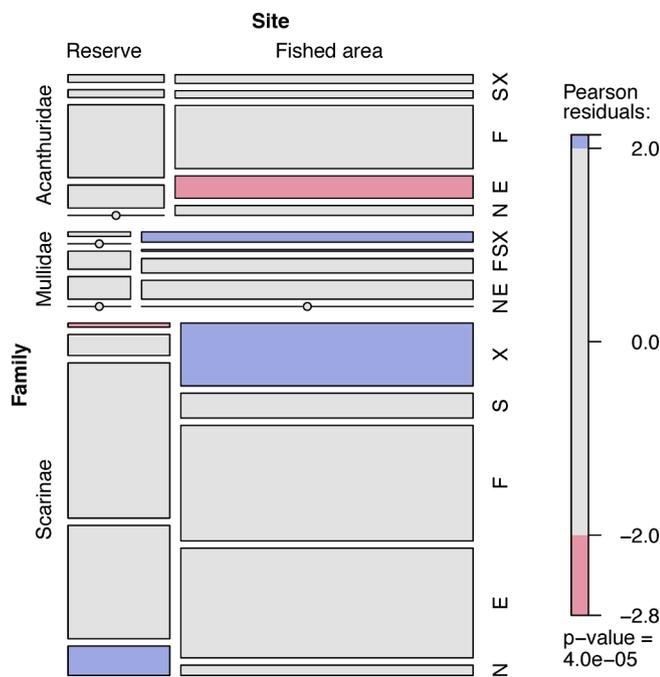


Fig. 3. Differences in effect size between sites by family: Fished area (Ka’ūpūlehu) minus reserve (Kaho’olawe). Effect size differences are shown in centimeters, error bars represent 0.95 confidence intervals.

#### 4.1. Starting distance

Behavior trials were conducted using a large range of SD, which enabled a robust evaluation of the relationship with measurements of flight behavior. By definition, an approached fish cannot initiate flight from a distance longer than SD. This constraint can potentially create an artefactual relationship between the variables if the variance increases with distance (Dumont et al., 2012). Nevertheless, there is support for a general rule of anti-predator behavior based on the relationship between SD and FID in other taxa, where animals should initiate flight soon after they detect a predator to minimize monitoring costs – the ‘flush early and avoid the rush’ hypothesis (Blumstein, 2010; Samia et al., 2013). Our quantile regression results suggest that SD has a significant effect on FID and dMAD of scarids that is not artefactual, though this was not the case for the other families tested (Chamaillé-Jammes and Blumstein, 2012). Our results indicate a low natural rate of leaving for scarids and mullids (Chamaillé-Jammes and Blumstein, 2012). This was not the case for acanthurids, labrids, or lethrinids,



**Fig. 4.** Mosaic plot of fish escape response by site for families with the greatest number of observations. From least wary to most wary: N = none, E = evade, F = flee, S = shelter, and X = spook. The size of the cells represents the frequency of occurrences for each combination of levels. Cell colors represent the residual levels corresponding to the legend. Blue colors mean there are more observations than would be expected under the null model (independence), red colors mean there are fewer. Overall this plot shows which cells are contributing to the significance of the Chi-squared test result. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

suggesting a higher natural rate of leaving. Data for all families were largely composed of a single species, so additional studies are needed to confirm these patterns. Tran et al. (2016) demonstrated a positive relationship between SD and FID in a non-targeted coral reef fish (*Ctenochaetus striatus*). We show this relationship holds across a number of targeted reef fish families and appears to be artefactual, except in the case of scarids. An important implication of these findings is that FID/dMAD of fishes (as in other taxa) is dynamic and depends to a large degree on SD. Previous studies on flight behavior of coral reef fishes have controlled for SD by maintaining a minimum value or narrow range of SD (eg. Bergseth et al., 2016; Feary et al., 2010; Januchowski-Hartley et al., 2011, 2015, 2013). However, visual estimates of distance are prone to error and may differ among observers (Harvey et al., 2004). Furthermore, in our study SD was correlated with water visibility which can be variable. Because it is difficult to standardize SD for behavior trials of fishes in the field, we recommend that future studies measure SD so that it may be accounted for in the analysis.

#### 4.2. Other variables

In addition to SD, we found large and consistent effects on flight behavior from depth and activity, two variables that to our knowledge have not been previously tested for fishes. Depth had a negative relationship with flight distance. This could be because deeper areas are

more difficult for spear fishers to access, however, our models did not show a significant interaction between site and depth. Additionally, distance to shore also relates to accessibility to fishers and was not shown to be a significant predictor of flight behavior. Many fishes in our study fled towards deep water, thus perceived risk may increase in shallow water (where there is greater distance from potential depth refuge) leading to increased flight distances (Stankowich and Blumstein, 2005). Fishes that were actively foraging prior to or during a trial approach had significantly lower flight distance, likely due to reduced ability to detect and react to the human predator while feeding (Krause and Godin, 1996).

Fish length and group size were significant predictors of flight behavior. Fish length had strong positive relationships with both FID and dMAD. This is supported by optimal fitness theory (Cooper and Frederick, 2007) and previous flight behavior research on coral reef fishes (Bergseth et al., 2016; Gotanda et al., 2009; Januchowski-Hartley et al., 2011, 2015; Miller et al., 2011). In our study, group size had a significant positive effect on dMAD but not FID. Previous studies have failed to find an effect of group size on FID (Benevides et al., 2016; Gotanda et al., 2009; Nunes et al., 2016) with the exception of Januchowski-Hartley et al. (2011) who found group size to be important for acanthurids, but not for other families. Our findings do not follow the theory that there is a dilution of risk with larger fish groups, leading to smaller flight distances (Godin, 1986; Krause and Godin, 1994). This may be because the coral reef fish species included in this study rarely form large schools and may use conspecific behavior as cues of predation risk and thus flee at greater distances when in larger groups (Owens, 1977).

Fish attributes of maximum size and mobility were shown to have positive relationships with flight distance, while trophic level was not a significant predictor. Larger-bodied species are generally more targeted by spear fishers (Pavlowich and Kapuscinski, 2017), and thus more likely to have experience with human predation, leading to longer flight distances (Stankowich and Blumstein, 2005). Fishes with higher mobility are more likely to be found farther from potential refuges, also leading to increased flight distances (Gotanda et al., 2009; Miller et al., 2011). Spearfishers caught the most diverse array of species across all trophic levels, compared to users of other fishing gear at Ka'ūpūlehu (Koike et al., 2015). It is, therefore, not surprising that trophic level did not significantly influence flight behavior.

Environmental variables of rugosity, visibility, and waves were not found to be significant predictors of flight behavior. Rugosity is an index of structural complexity that relates to refuge availability and thus might be expected to influence flight behavior. In contrast to our results, Januchowski-Hartley et al. (2015) and Nunes et al. (2015) showed a significant effect of structural complexity on parrotfishes and two labrid species, respectively. Likewise, visibility did not have a direct effect on flight behavior, though it did have indirect effects on flight behavior as we showed it to mediate SD. The limiting factor in terms of visibility in this study was the video resolution, which is less sensitive than both human and fish vision. Nevertheless, it is likely that visibility does have some effect on fish flight behavior, as fishes are less likely to detect predators under very low visibility. Waves have been shown to promote targeted fish biomass and abundance and are thought to provide a refuge from fishing pressure (Stamoulis et al., 2016). The lack of a significant effect of waves on flight behavior in this study could be due to the low range of wave power among Ka'ūpūlehu sites, and future investigations would benefit from sampling across a larger gradient.

All behavior trials were conducted using SCUBA. Based on observations of fishes reacting to the diver exhalation/bubbles, we tested if FID and dMAD were significantly influenced by the timing of diver exhalation (i.e., did FID/dMAD coincide with diver bubbles), and found no significant effects. Nevertheless, in order to avoid this potential factor, we recommend that observers on SCUBA measuring flight behavior take care to regulate their breathing. The majority of trial observations in our study were conducted by a single observer, however, a small subset (43) were conducted by an alternate observer. While observer was not a significant variable in DistLM models for the fished area dataset, when included in LMM models for the combined dataset it was a significant predictor of both FID and dMAD, and thus data from the second observer was excluded for the final models. Januchowski-Hartley et al. (2012) found small but significant differences in FID between observers using both SCUBA and free diving methods in a no-take marine reserve. Because the differences were not consistent in direction and did not occur between the same observers, they were considered a random source of error. Based on this previous work and our results, we recommend that observer effects be considered in future studies and care taken to standardize approach speed, diver behavior, and gear, to minimize these effects.

#### 4.3. dMAD vs FID

We introduce dMAD as a compliment or alternative to FID. Video analysis procedures are very similar to MAD calculated from stereo-video transect surveys (Goetze et al., 2017; Lindfield et al., 2014a), though fishes were actively approached using the same methodology used to measure FID. Importantly, dMAD was significantly affected by differences in fishing pressure while accounting for other key variables, but FID was not. While the relationships of dMAD to most variables were very similar to FID, we found dMAD to be less dependent on SD. Another advantage of using dMAD as an alternative to FID is that flight responses in fishes are not always evident. For instance, a large proportion of parrotfishes showed no flight response within the reserve. In these cases, FID was assumed to be equal to dMAD. In addition, dMAD may solve a potential source of error in FID. Spontaneous movement could produce an artefactual effect of SD on FID where probability of spontaneous movement increases with SD (Cooper, 2005). In contrast to most other taxa for which FID has been studied, fishes rarely stop moving. Aggressive or evasive movements of fishes in response to other fishes may be mistaken for a flight response. Because it ignores these fine-scale movements, dMAD may tend to minimize this potential source of error.

#### 4.4. Fishing effects on flight behavior

Studies of flight behavior of coral reef fishes have focused on the effects of (spear) fishing pressure as the primary variable of interest. Establishing a relationship between fishing pressure and flight behavior could provide useful applications for management of coral reef fisheries such as assessing compliance in no-take marine reserves (Bergseth et al., 2015). We show that four variables (SD, activity, depth, fish length) have larger effects on FID than fishing pressure, and only by considering an alternate measure of flight distance did we find a

significant effect of fishing. Nevertheless, our results are consistent with previous studies showing higher flight distance of targeted species in fished areas compared to protected areas (Bergseth et al., 2016; Feary et al., 2010; Gotanda et al., 2009; Januchowski-Hartley et al., 2011, 2015, 2014). Species included in our analysis are known to be targeted in Hawai'i and have been shown to be components of spearfishing catch in the fished area (Table A.1, Koike et al., 2015).

We found no significant differences in FID or dMAD between reef fish families. Nevertheless, differences in mean effect size suggests that some families may be more sensitive to fishing pressure than others. Emperors (Lethrinids – represented by a single species in this study) had the largest mean effect size, suggesting that *Monotaxis grandoculis* could be a potential indicator species for spearfishing pressure in Hawai'i where this species is highly prized by spearfishers. In contrast, parrotfishes (Scarinae) had the lowest mean effect size and surgeonfishes (Acanthuridae) had intermediate effect sizes. This is supported by a previous study that showed flight behavior of surgeonfishes to be more sensitive to differences in fishing pressure compared to parrotfishes (Januchowski-Hartley et al., 2014).

#### 4.5. Escape response

Escape response behaviors of parrotfishes and goatfishes support the dMAD results. Parrotfishes and goatfishes had significantly higher proportion of 'spook' behavior at the fished area and parrotfishes had significantly higher proportion of 'no flight' behavior at the reserve. Spook behavior is an energetically costly flight response in which the fish suddenly flees at high speed. For parrotfishes, this involves body and caudal fin swimming as opposed to using pectoral fins only (Miller et al., 2011). 'No flight' reflects a low level of perceived threat, where fishes are not seeking cover or increasing speed. Surgeonfishes showed a significantly lower proportion of 'evade' at the fished area and relatively higher proportion of 'no flight'. This seems to contradict the dMAD results and suggests that escape response may not be a reliable indicator of perceived threat for acanthurids. Guidetti et al. (2008) showed that two species of sea breams more frequently sought shelter on protected reefs and more often escaped to open water on fished reefs in the Mediterranean. Our findings did not reflect this pattern, as frequencies of shelter behavior were consistent between sites for each family. Nunes et al. (2015) reported that 'run away' behavior was the most common escape response in labrids. This is equivalent to 'flee' behavior in this study which was the most common escape behavior among acanthurids and scarids. Conversely, for labrids, 'shelter' was the most common escape response and 'flee' was among the least common. This could be due to differences between labrid species studied. We suggest including escape response as a compliment to flight distance in studies of flight behavior to help understand if the patterns described here are consistent across geographies and species and determine if escape response is a reliable indicator of fishing pressure for some fish families. The escape response categories developed for this study were refined over many repeated observations of the experimental trial video recordings. They represent consistent escape behaviors for coral reef fish and we recommend their use in future studies.

### 5. Conclusions

We show that SD, feeding activity, depth, and length have significant effects on flight distance which outweigh the effects of fishing pressure. While our results are unique to our Hawai'i study sites, we believe that future studies investigating fishing effects on flight distance in other regions should aim to include these variables in the analysis. SD in particular should be recorded to control for its impact on flight distance. Furthermore, we recommend using dMAD as a complement or alternative to FID. Stereo-video provides a means to accomplish these objectives with high precision and minimum effort in the field and can yield a variety of complementary data such as escape response. Research is needed to understand if incorporating fish behavior can improve measures of targeted fish assemblages such as abundance and biomass. This has implications for evaluating MPA effectiveness, studies of fish-habitat relationships, species distribution modelling, as well as other applications. How flight behavior impacts ecosystem function of

targeted fishes is another important area for study. In addition, flight distance is a potential indicator of spear fishing pressure that could be used as a tool to measure and monitor compliance in marine reserves. To address these topics, further research is needed to quantify flight distance of targeted species along gradients of fishing pressure, while controlling for key co-variables.

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### Appendix

- Fig. A.1
- Fig. A.2
- Table A.1
- Table A.2

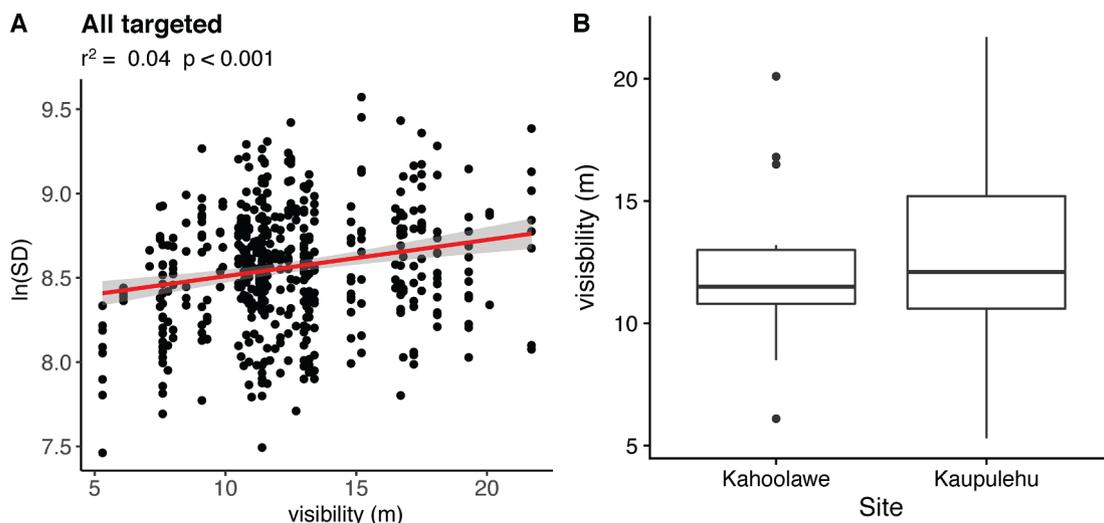


Fig. A.1. A) Relationship between visibility (m) and ln(x) transformed starting distance. B) Comparison of visibility (m) between sites.

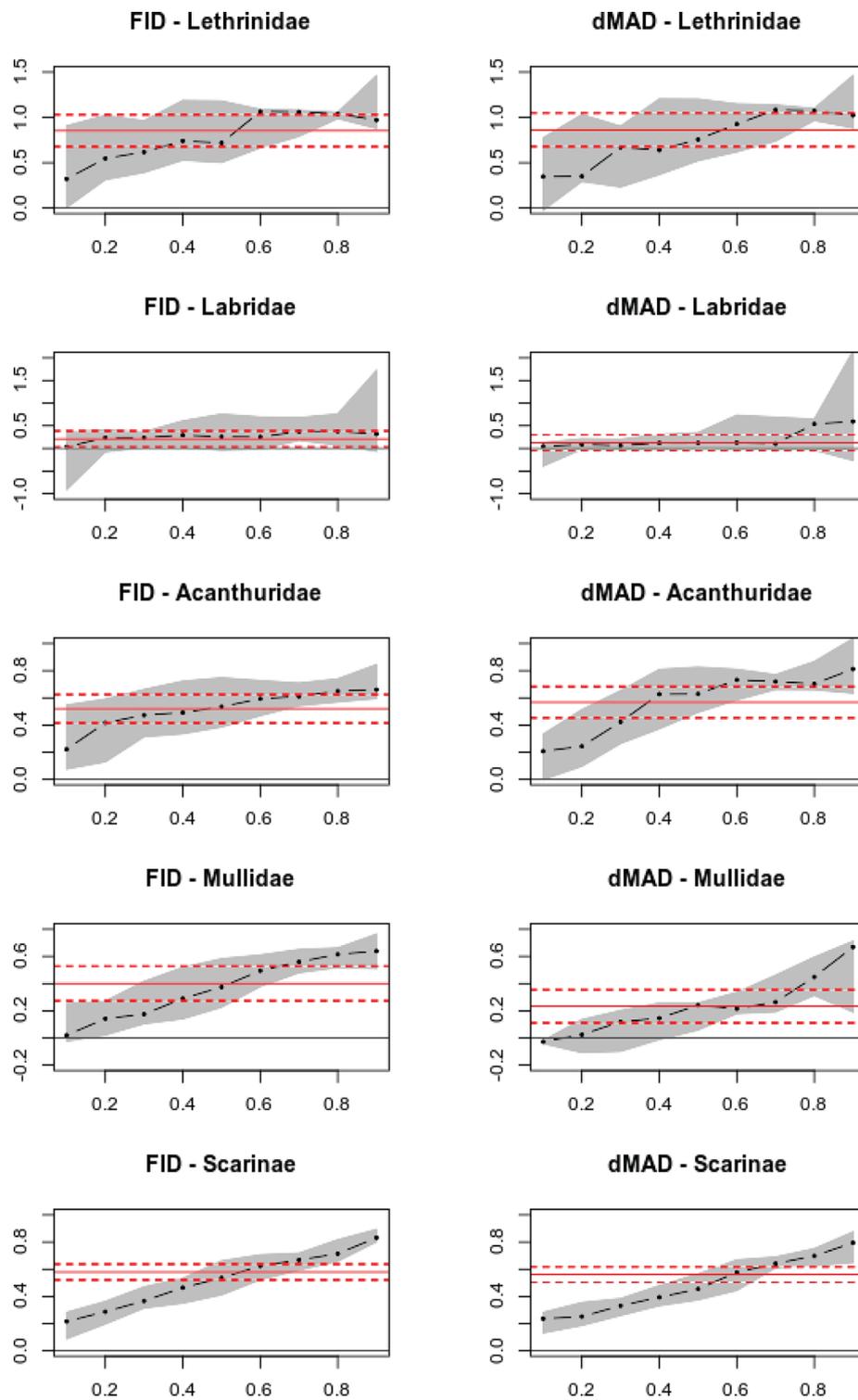


Fig. A.2. Slopes of quantile regressions of SD vs FID and dMAD by family. X-axis is quantile, y-axis is slope. The slope of the ordinary least squares fitted line and confidence intervals are shown in red. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

**Table A.1**

Details of dataset for fished area (Ka'ūpūlehu) used for DistLM analysis of variable influence on fish flight behavior. Numbers refer to sample size by species/family. Non-targeted families/species are identified with \*.

Family/species	Count	Family/species	Count
Acanthuridae	93	Labridae	20
<i>Acanthurus achilles</i>	4	<i>Bodianus bilunulatus</i>	6
<i>Acanthurus blochii</i>	2	<i>Oxycheilinus unifasciatus</i>	10
<i>Acanthurus dussumieri</i>	3	<i>Thalassoma duperrey</i> *	4
<i>Acanthurus leucopareus</i>	3	Lethrinidae	12
<i>Acanthurus nigroris</i>	1	<i>Monotaxis grandoculis</i>	12
<i>Acanthurus olivaceus</i>	36	Lutjanidae	6
<i>Naso brevirostris</i>	1	<i>Aphareus furca</i>	1
<i>Naso hexacanthus</i>	1	<i>Lutjanus fulvus</i>	3
<i>Naso lituratus</i>	37	<i>Lutjanus kasmira</i>	2
<i>Naso unicornis</i>	5	Mullidae	54
Balistidae*	27	<i>Mulloidichthys flavolineatus</i>	4
<i>Melichthys niger</i>	5	<i>Mulloidichthys vanicolensis</i>	1
<i>Melichthys vidua</i>	6	<i>Parupeneus cyclostomus</i>	1
<i>Rhinecanthus rectangulus</i>	1	<i>Parupeneus insularis</i>	2
<i>Sufflamen bursa</i>	10	<i>Parupeneus multifasciatus</i>	43
<i>Sufflamen fraenatum</i>	5	<i>Parupeneus pleurostigma</i>	1
Chaetodontidae*	19	<i>Parupeneus porphyreus</i>	2
<i>Chaetodon lunula</i>	1	Scarinae	207
<i>Chaetodon lunulatus</i>	1	<i>Calotomus carolinus</i>	1
<i>Chaetodon multicinctus</i>	1	<i>Chlorurus perspicillatus</i>	3
<i>Chaetodon ornatissimus</i>	10	<i>Chlorurus sordidus</i>	145
<i>Chaetodon quadrimaculatus</i>	1	<i>Scarus psittacus</i>	21
<i>Chaetodon unimaculatus</i>	1	<i>Scarus rubroviolaceus</i>	37
<i>Forcipiger flavissimus</i>	2	Serranidae	8
<i>Forcipiger longirostris</i>	2	<i>Cephalopholis argus</i>	8

**Table A.2**

Details of final combined dataset used for linear mixed effects models. Numbers refer to sample size by species/family for each study site.

Family/species	Kaho'olawe	Ka'ūpūlehu
Acanthuridae	29	75
<i>Acanthurus blochii</i>	4	1
<i>Acanthurus dussumieri</i>	3	3
<i>Acanthurus olivaceus</i>	8	30
<i>Naso lituratus</i>	10	36
<i>Naso unicornis</i>	4	5
Labridae	16	5
<i>Bodianus bilunulatus</i>	16	5
Lethrinidae	18	11
<i>Monotaxis grandoculis</i>	18	11
Mullidae	10	46
<i>Mulloidichthys flavolineatus</i>	2	4
<i>Parupeneus insularis</i>	4	2
<i>Parupeneus multifasciatus</i>	4	40
Scarinae	77	202
<i>Chlorurus perspicillatus</i>	1	2
<i>Chlorurus sordidus</i>	33	143
<i>Scarus psittacus</i>	2	21
<i>Scarus rubroviolaceus</i>	41	36
<b>Grand Total</b>	<b>150</b>	<b>339</b>

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