# Trait-mediated foraging drives patterns of selective predation by native and invasive coral-reef fishes

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**Abstract.** As the geographic ranges of species are increasingly altered by forces such as biological invasion and climate change, when and where will strong biotic interactions arise within reassembling communities? Prey selectivity data are often of limited use for predicting future consumptive interactions because they are specific to the identity and relative abundance of species in past assemblages. Here, we investigate whether the strength of consumptive interactions can be predicted based on a priori knowledge of behavioral traits that are hypothesized to affect the predation process and recur across species. To test this approach, we conducted multi-species foraging trials with coral-reef fishes in the Bahamas, a diverse, trait-rich fauna for which interactions are likely shifting rapidly due to the introduction of predatory Indo-Pacific lionfish. We evaluated predictions about the combined effects of three behavioral traits—water column position of both predator and prey, anti-predator aggregation behavior of prey, and hunting strategy of predators—on successive phases of the predation process and ultimately the strength of predator–prey interactions. Tracking predator and prey behaviors revealed that inter-specific variation in traits mediated relative encounter, attack, and capture rates between different predators and prey. Behaviorally driven bottlenecks at different stages of the process underpinned selective consumption by each predator species, resulting in large differences in total mortality rates among prey species. Our analysis also suggests that unique behaviors exhibited by invasive lionfish, rather than naïve responses by prey, mediate their high foraging success relative to native predators. Our results illustrate how incorporating a priori knowledge about foraging and anti-predator traits can improve predictions of the strength of emergent consumptive interactions caused by global change.

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## INTRODUCTION

Biotic interactions shape the structure and function of ecological communities. However, interactions in many systems are changing in thus far unpredictable ways due to human-induced stressors such as biological invasions, climate change, and over-exploitation that, in combination, shift the geographical ranges and abundances of species (Mainka and Howard 2010, Chen et al. 2011, Pecl et al. 2017). These effects alter the combinations and relative abundances of species that interact with one another in local communities. Shifts in predator–prey interactions may have particularly large consequences for ecosystem structure and function because predation is a major source of mortality in many systems, influencing patterns of biomass, productivity, and diversity within and among food webs (Salo et al. 2010, Freestone et al. 2011, Blois et al. 2013). When and where will strong predator–prey interactions arise within reassembled communities, and how will these interactions further alter the structure and function of the system? Optimal foraging theory predicts that predators should consume prey in a way that maximizes energetic gain while minimizing both energy expended and risk assumed throughout the predation process (Pyke et al. 1977). When all prey types are equally valuable to a predator, consumptive interactions should track changes in prey species composition and relative abundances (e.g., Beukers-Stewart and Jones 2004). However, predators often consume prey types selectively, that is, in quantities disproportionate to their relative environmental abundance (e.g., Ryabov et al. 2015).

A large body of research is devoted to documenting patterns of diet selectivity observed in nature through analysis of stomach contents and observations of prey capture (e.g., Karanth and Sunquist 1995, review by Pettorelli et al. 2011). However, understanding the contexts in which strong predator–prey interactions will arise requires more than such observations to identify the mechanisms that generate patterns of selective predation. A variety of behavioral and morphological traits have been theoretically proposed and empirically demonstrated to affect the predation process, that is, the sequential steps

of encountering, attacking, capturing, and handling prey items. For example, behaviors affecting encounter rates between predator and prey include relative patterns of habitat use, predator strategy for approaching and attacking prey (e.g., active stalking vs. sit-and-wait ambush), and prey vigilance at maintaining a minimum distance from potential predators (Beukers and Jones 1997, Pressier et al. 2007, Andriskiw et al. 2008, Gorini et al. 2012). Predator and prey morphology also affect the likelihood of encounter (e.g., cryptic; Broom and Ruxton 2005, Norton 1991, Dukas and Clark 1995), attack (e.g., physical or chemical defense; Moitoza and Phillips 1979), and consumption (e.g., body shape; Clements et al. 2016, Juanes 2016).

Understanding how morphological and behavioral traits influence the predation process, and ultimately patterns of selective predation, could help in forecasting the strength of novel biotic interactions that emerge when species encounter one another for the first time. Empirical work on foraging traits has primarily focused on the effects on patterns of consumption of intra-specific or inter-specific variation in behavioral traits exhibited by predators or prey, either experimentally (e.g., Cooper et al. 1985; reviewed by Boukal 2014 for aquatic systems) or observationally (e.g., in fishes [Green and Côté 2014], birds [Dehling et al. 2016], and mammals [Spitz et al. 2014]). Yet little work has quantified the combined effects of multiple traits exhibited by predators and prey on successive phases of the predation process, and ultimately the strength of consumptive interactions within assemblages. However, this understanding is essential for developing mechanistic predictions regarding how characteristics shared by predator and prey species affect patterns of predation.

We conducted a series of multi-species laboratory foraging trials with Caribbean reef fishes to help address these gaps. Specifically, we (1) constructed hypotheses regarding how multiple behavioral traits of predator and prey species combine to influence each stage in the predation process, (2) measured prey and predator behavioral traits during interactions within the multi-species assemblages, (3) evaluated patterns of predation among potential predators and prey,

(4) linked trait responses to interaction outcomes across stages of the predation process, and (5) evaluated the consequences of trait-based prey selection for interaction strength among species.

## Methods

### Study system, hypothesis, and predictions

Our study focused on a subset of species within a system where predator–prey interactions are likely shifting as a result of a major biological invasion. Coral-reef fish communities are the most diverse vertebrate assemblages on Earth, with predators and prey exhibiting a broad array of morphologies and behaviors (Hixon 1991). Caribbean coral-reef fish communities have recently been invaded by predatory Indo-Pacific lionfish (*Pterois volitans* and *P. miles*; Côté et al. 2013, Wilcox et al. 2018). Thus, this system provides an excellent model for studying

how variation in behavioral traits mediates the strength of consumptive interactions (Fig. 1).

To isolate the effects of behavior on predatory interactions, we selected predator and prey species within the coral-reef fish assemblage that share similar body shapes and sizes (factors which strongly affect rates of capture success in fishes; Lundvall et al. 1999, Green and Côté 2014), but differ in key behavioral traits (predators: water column position and foraging strategy, prey: water column position and aggregation behavior) that are also hypothesized to affect successive stages in the predation process (Fig. 1). We predicted that midwater roving predators—whose behavior is typified by constant traversing of the environment—would encounter all prey types approximately equally, regardless of prey position in the water column or prey aggregation size, and thus exhibit relatively non-selective patterns of prey
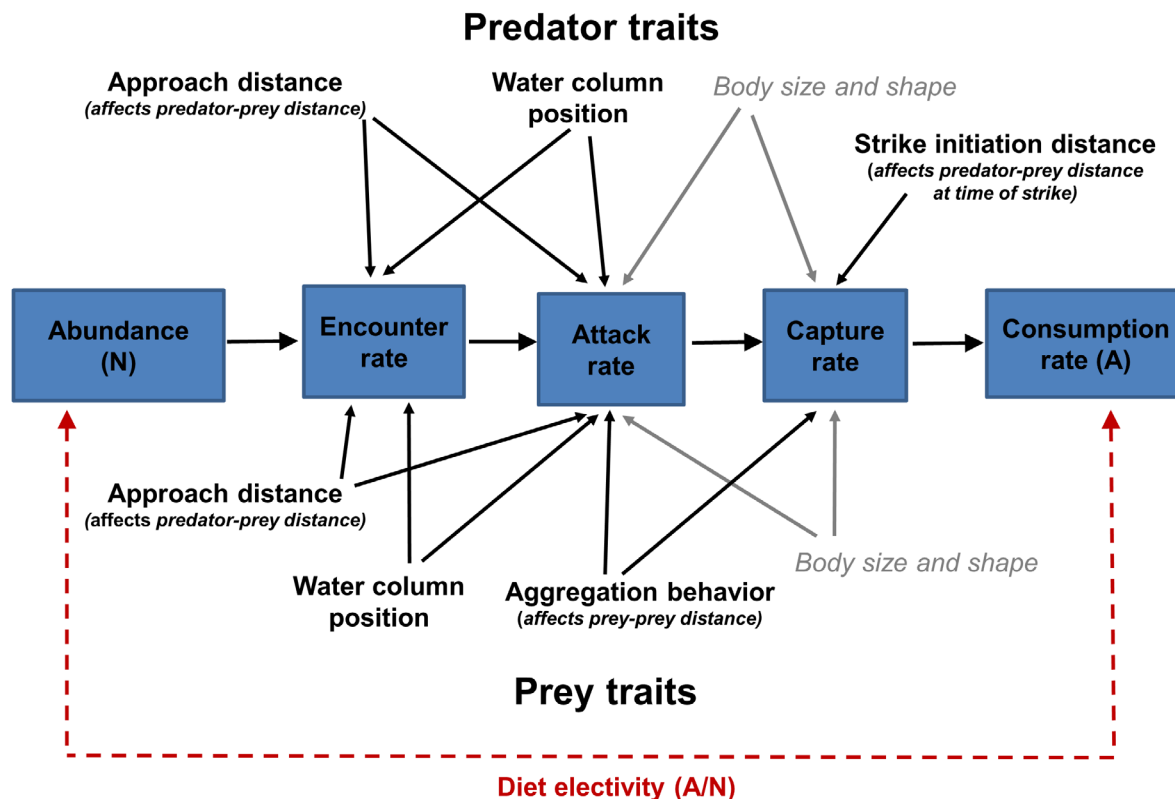


Fig. 1. Predator and prey traits hypothesized to affect successive stages of the predation process. Body size and shape are dimmed (gray lines and text) because they were held constant in this study.

consumption. In contrast, we predicted that demersal stalking predators—whose behavior is typified by singling-out and closely following an individual prey before a strike—would have relatively low encounter rates with midwater prey and low capture success with schooling prey, and therefore would primarily consume solitary benthic prey. Finally, we predicted that ambush predators—whose behavior is typified by resting motionless on the bottom—would most readily locate and capture prey passing in the water column rather than benthic prey that sit on the bottom, regardless of prey aggregation size.

To test these predictions, we selected as predators invasive lionfish and two similarly shaped native reef piscivores that co-occur on Caribbean reefs: the schoolmaster snapper (*Lutjanus apodus*) and the graysby grouper (*Cephalopholis cruentata*). All three species consume small-bodied reef fishes (Randall 1967, Morris and Akins 2009), but use different visual hunting strategies (McFarland 1991) and typically forage in different positions relative to the water column (Table 1). We predicted that the water column position and hunting strategy used by each predator would result in different encounter and capture rates of prey fishes in different water column positions and the extent to which the prey aggregate (i.e., polarized school, unpolarized shoal, or solitary) as a predator avoidance strategy (Parrish and Edelstein-Keshet 1999, Parrish et al. 2002; Fig. 1). We therefore focused on three coral-reef prey fishes that are similarly shaped but exhibit different water column positions and schooling behaviors: the tomtate grunt (*Haemulon aurolineatum*), the yellowhead wrasse (*Halichoeres garnoti*), and goldspot goby (*Coryphopterus glaucofraenum*; Table 1).

## Fish collection and husbandry

Predator and prey fish were collected from shallow coral reefs around the southern tip of Eleuthera, Bahamas (24°50′2.53″ N, 76°19′37.89″ W), by SCUBA divers using barbless hook-and-line or hand nets and transported back to the laboratory in 45-L coolers with air stones within an hour of collection (separate collecting trips for predators and prey). Predator fishes ranged in size from 20 to 30 cm total length (TL) while prey fish ranged from 3 to 5 cm TL, with size ranges similar among predator and among prey species. Between foraging trials, predators and prey were kept in separate 2-m diameter, 1600-L circular tanks at the Cape Eleuthera Institute (CEI) containing three $20 \times 20 \times 40$ cm cinderblocks as habitat structure (maximum 6 individuals per predator tank and 48 individuals per prey tank). To increase the likelihood and frequency of predatory behavior during trials, predators were not fed for 48 h preceding a trial. Predators were kept in captivity between one and two weeks, while prey were kept for up to one week, and each predator was used in 2–4 trials (Table 2) to minimize the number of individuals kept in captivity, and because we had no expectation that foraging behavior would systematically change across trials in a way that altered the likelihood of encounter, strikes, or capture by the predator species on the three prey types. After trials were complete, native predator species and all surviving prey were released at nearby coral patch reefs. Lionfish are a highly invasive species in the region and were thus euthanized according to approved protocol (Oregon State University Institutional Care and Use Committee, permit number 4351 and with permission of the Department of Marine Resources of The Bahamas).

Table 1. Water column position and hunting or anti-predator strategy of study fishes.

| Role | Species | Position | Strategy |
|---|---|---|---|
| Predator | Schoolmaster snapper (*Lutjanus apodus*) | Midwater | Roving: wanders until locates and strikes at prey |
| | Lionfish (*Pterois* sp.) | Demersal | Stalking: slowly approaches prey with pectoral fins flared |
| | Graysby grouper (*Cephalopholis cruentata*) | Benthic | Ambush: remains motionless (sit-and-wait) until sudden predatory strike |
| Prey | Tomtate grunt (*Haemulon aurolineatum*) | Midwater | Schooling: tight, polarized formations |
| | Yellowhead wrasse (*Halichoeres garnoti*) | Demersal | Shoaling: relatively loose group that breaks and re-forms intermittently |
| | Bridled goby (*Coryphopterus glaucofraenum*) | Benthic | Solitary: individuals that do not swim in groups |

Table 2. Sample sizes, prey consumption rates, and mean behavioral responses for each predator–prey combination.

| Predator type | No. trials | No. indivs. | Prey type | Prey consumed/ prey offered | | Predator–prey distance at strike initiation (cm) | | Prey–prey distance at strike initiation (cm) | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | No. | Percentage | Max. | Mean ± SD | Min. | Mean ± SD |
| Midwater roving | 10 | 5 | | | | 8.2 | | 8.9 | |
| | | | Midwater schooling | 10/40 | 25.0 | | 2.86 ± 1.50 | | 42.65 ± 5.40 |
| | | | Demersal shoaling | 8/40 | 20.0 | | 1.53 ± 100 | | 70.61 ± 5.04 |
| | | | Benthic solitary | 9/40 | 22.5 | | 6.64 ± 3.59 | | 55.68 ± 15.40 |
| Demersal stalking | 16 | 4 | | | | 6.0 | | 11.9 | |
| | | | Midwater schooling | 4/64 | 6.2 | | 2.5 ± 1.34 | | 11.9 ± 2.16 |
| | | | Demersal shoaling | 15/64 | 23.4 | | 2.9 ± 1.39 | | 49.48 ± 22.22 |
| | | | Benthic solitary | 23/64 | 35.9 | | 3.46 ± 1.70 | | 48.13 ± 13.06 |
| Benthic ambush | 14 | 4 | | | | 7.5 | | 20.2 | |
| | | | Midwater schooling | 2/56 | 3.6 | | 5.55 ± 2.89 | | 81.38 ± 3.41 |
| | | | Demersal shoaling | 10/56 | 17.8 | | 6.76 ± 2.10 | | 25.73 ± 5.15 |
| | | | Benthic solitary | 2/56 | 3.6 | | 5.38 ± 1.78 | | 32.48 ± 6.39 |

*Note:* Predator–prey distance is a proxy for the combined effect of prey avoidance and predator pursuit, while prey–prey distance is a proxy for aggregative behavior.

## Foraging arena design

We observed fish behavior and prey selection in large flow-through tanks (2 m diameter; 1600 L) located at CEI from June to August 2014 (Appendix S1: Fig. S1). Mesocosms are most appropriate for observing realistic predator–prey interactions for predators with small home and foraging ranges, which is true of the reef fishes we studied. Smaller reef fishes in general are known to have very limited home ranges on the order of meters (review by Green et al. 2015). Regarding our study species, tagged *L. apodus* of sizes overlapping the range we studied and inhabiting shallow habitats off Jamaica (Munro 2000) and Curaçao (Verweij et al. 2007) similar to our mesocosms typically roam only a few meters over a matter of days. Tagged and untagged lionfish (*Pterois* sp.) at low densities show very high site fidelity on small patch reefs where we conducted our study (Tamburello and Côté 2015, Benkwitt 2016a). Tagged *C. cruentata* of the sizes we studied and inhabiting shallow patch-reef habitat in Barbados exhibited virtually no movement, being captured repeatedly in the same traps over 3 months (Chapman and Kramer 2000).

Preliminary field observations and tank trials indicated that shelter is an important feature used by *C. cruentata* in their ambush hunting activities. One 20 × 20 × 40 cm cinderblock was placed in the tank to provide sufficient structure to elicit hunting behavior from *C. cruentata* during preliminary trials (Appendix S1: Fig. S4). The cinderblock remained in the tank across all trials regardless of predator species. We did not provide sand, gravel, or other rock substrates in the tank so that we could more clearly examine the influence of aggregation tightness, water column position, and avoidance distance on predator–prey encounters in the absence of shelter-seeking behavior, which may have dominated prey response under conditions of high-structure availability. Water temperature, salinity, and dissolved oxygen were maintained at ambient levels during trials (averages 8.52 mg/L $O_2$, 38.2 ppt salinity, 30.7°C; ranges 6.89–13.17 mg/L $O_2$, 37–39.2 ppt salinity, 28.7–38.9°C). GoPro Hero 3 Silver cameras were mounted above the tank and underwater to observe predation events, as well as aggregation behavior and water column position of prey fishes, all in the absence of human observers to minimize potential observer effects on fish behavior (Appendix S1: Figs. S1, S2 and S4).

## Foraging trial design

During each trial, one predator and four individuals of each of the three prey species (12 prey individuals per trial) were present in the tank over 4.5 h. Offering these prey species at equal

densities is justified given that the three species are all found in similar densities on small patch reefs in the area from which the fish were collected (Benkwitt 2016b; C. E. Benkwitt, *unpublished data*). Furthermore, the prey densities used in the tanks are within the range of densities observed on patch-reef habitat similar to the scale of the mesocosms, with the maximum natural density of these species exceeding the densities used in the foraging trials (Forrester and Steele 2000, Overholtzer-McLeod 2005). All three predator species used for this study forage most actively during crepuscular periods (see Helfman 1986) and therefore all trials coincided with either sunrise or sunset. At the start of each trial, the tank was split in half using a netted partition (Appendix S1: Fig. S2). The focal predator was placed on one side of the partition for at least 1 h before the trial was initiated. Next, the 12 prey fish were introduced to the opposite side of the partition and allowed to acclimate to tank conditions for 10 min before the partition was removed to start the trial. Top- and side-view cameras were set to record high-definition video footage of the tank from when prey fishes were introduced until trial termination (Appendix S1: Figs. S1 and S2). At the end of each trial, all remaining non-consumed prey were counted and identified.

### Foraging trial data collection

For each trial, we identified all predator strikes, both unsuccessful (prey escaped) and successful (prey captured), and the species identity of predator and prey involved in each interaction. We used these data to calculate prey selection by each predator type (see *Prey selection* below). Next, we analyzed footage from our recordings of each trial to obtain metrics for the predator and prey behaviors that we hypothesized would affect successive steps in the predation process (Fig. 1; approach distance, avoidance distance, strike initiation distance, and aggregation tightness). Specifically, for each successful predation event (for which we also noted prey species identity), we extracted two frames from the top camera's footage: one at 15 s before the predator's strike at the focal prey (hereafter referenced as T-15) and the last frame before the predator's strike (T-0). From each trial's T-15 and T-0 images, we used ImageJ

software (1.48v; Schneider et al. 2012, see Appendix S1) to measure (1) distance (in cm) between the focal prey fish and the predator (i.e., predator–prey distance), and (2) distances (in cm) between each prey fish and the three closest prey fish of any species (i.e., prey–prey distance), noting which prey was the focus in the interaction (i.e., consumed) and those that were not consumed. Prey–prey distance is a proxy for the tightness of aggregative behavior by each prey fish and was calculated by taking the average of the three nearest-neighbor distances. We considered predator–prey distance at the frame before the predator's strike (i.e., T-0) to be the strike initiation distance and predator–prey distance at 15 s before the predator's strike to result from a combination of the prey's avoidance of the predator and the predator's approach to the prey.

Next, we estimated encounter rates between predator and prey types. We defined an encounter as any instance in which a potential prey was positioned anteriorly to the predator and closer than the maximum strike initiation distance for successful prey captures across all trials (i.e., the prey was within the predator's danger zone; see Table 2 and Appendix S1: Fig. S5). We quantified encounter rates by conducting continuous observations of each trial video and recording all instances in which potential prey were within the predator's danger zone, as well as the species identity of the prey. We used the side-view camera footage to confirm both the general water column positions of each predator and prey species during all strike events, and whether or not the interaction resulted in consumption.

### Data analysis

*Diet electivity.*—To assess the extent to which predators selectively consumed the three prey types offered, we calculated Jacobs' second selection index ($D_i$; Manly et al. 2004), which accounts for prey depletion (i.e., no replacement of consumed prey during a trial) for each prey type ($i$) per predator type:

$$D_i = \frac{r_i - p_i}{(r_i + p_i - 2r_ip_i)} \qquad (1)$$

where $r_i$ is the relative abundance of prey type $i$ in the diet of the predator, and $p_i$ is the relative

abundance of the prey type $i$ in the environment. In our study, $r_i$ was calculated as the relative abundance of prey type $i$ in the diet of the predator at the end of a trial, and $p_i$ is the relative abundance of the same prey type in the foraging arena at the start of the trial. Because all trials began with four individuals of the three prey types, $p_i$ had the same value in all trials (0.3333). $D_i$ ranges from +1 to −1, where positive values indicate consumption of a particular prey type by the predator greater than expected based upon $p_i$ (i.e., preferred), a value of 0 indicates no selection or random foraging by the predator, and a negative value indicates that prey were consumed less than would be expected by $p_i$ (i.e., avoided). We then calculated mean and 95% confidence intervals across trials for each predator type.

*Effects of behavioral traits on the predation process.*—To examine how successive steps in the predation process differed between predator and prey in relation to their foraging and anti-predator behaviors (Fig. 1, Table 1), we first calculated encounter rate (i.e., step 1 in the predation process) as the number of times potential prey of each type entered the danger zone (see above in *Foraging trial data collection*) of each predator type across all trials, divided by the total number of danger zone entries for all three prey types across all trials for that predator type. We then calculated strike probability (i.e., step 2) for the three prey types as the proportion of danger zone encounters with each predator type that resulted in a strike. Finally, we calculated capture probability (i.e., step 3) for the three prey types as the proportion of strikes by each predator type that resulted in successful captures.

*Effects of behavioral traits on consumption.*—We evaluated the extent to which prey aggregation and avoidance behavior (quantifying the proxies of prey–prey distance and predator–prey distance, respectively) differed between prey that were and were not consumed. To do so, we first calculated the mean values and standard deviations of predator–prey distance and prey–prey distance for consumed and non-consumed individuals of each predator and prey species combination across all trials. We then subtracted the mean distance for consumed prey from the mean distance for non-consumed prey to obtain the difference in response. We calculated the difference in response between groups 1000 times

using Monte Carlo simulation, drawing values from a normal distribution of each group's response characterized by the mean and standard deviation, and then calculating the mean and 95% confidence intervals of the resulting distribution of values. Finally, we evaluated whether the mean distance from the simulation varied among prey types, predator types, and time period (i.e., lack of overlap of 95% confidence intervals indicated significant difference).

## RESULTS

We observed a total of 83 predation events across 40 foraging trials, with all predator types using typical hunting strategies (Table 1) and consuming at least one individual of each of the three prey types by the end of the study (Table 2).

### Diet electivity

The midwater roving and demersal stalking predators consumed greater proportions of the prey offered to them (22.5% and 21.9%, respectively) compared with benthic ambush predators (8.3%). Patterns of prey selection varied greatly among predator types (Fig. 2A). In particular, benthic ambush predators selectively consumed demersal shoaling prey, but avoided midwater schooling and benthic solitary prey (Fig. 2A). In contrast, demersal stalking predators selectively consumed benthic solitary prey but far fewer midwater schooling prey than expected based on their relative abundance. Finally, midwater roving predators consumed all prey types approximately equally (i.e., non-selective foraging; Fig. 2A). Patterns of prey electivity suggest that demersal shoaling and benthic solitary prey types are likely to experience greater total mortality compared with midwater schooling prey when interactions with all three predators are considered (Fig. 2B).

### Effects of behavioral traits on the predation process

All three predator types encountered benthic prey at greater rates than demersal or midwater prey (Fig. 3). However, there was substantial variation in strike and capture rates among predator and prey combinations. In particular, benthic ambush predators were far more likely to strike and capture demersal shoaling prey (Fig. 3F)
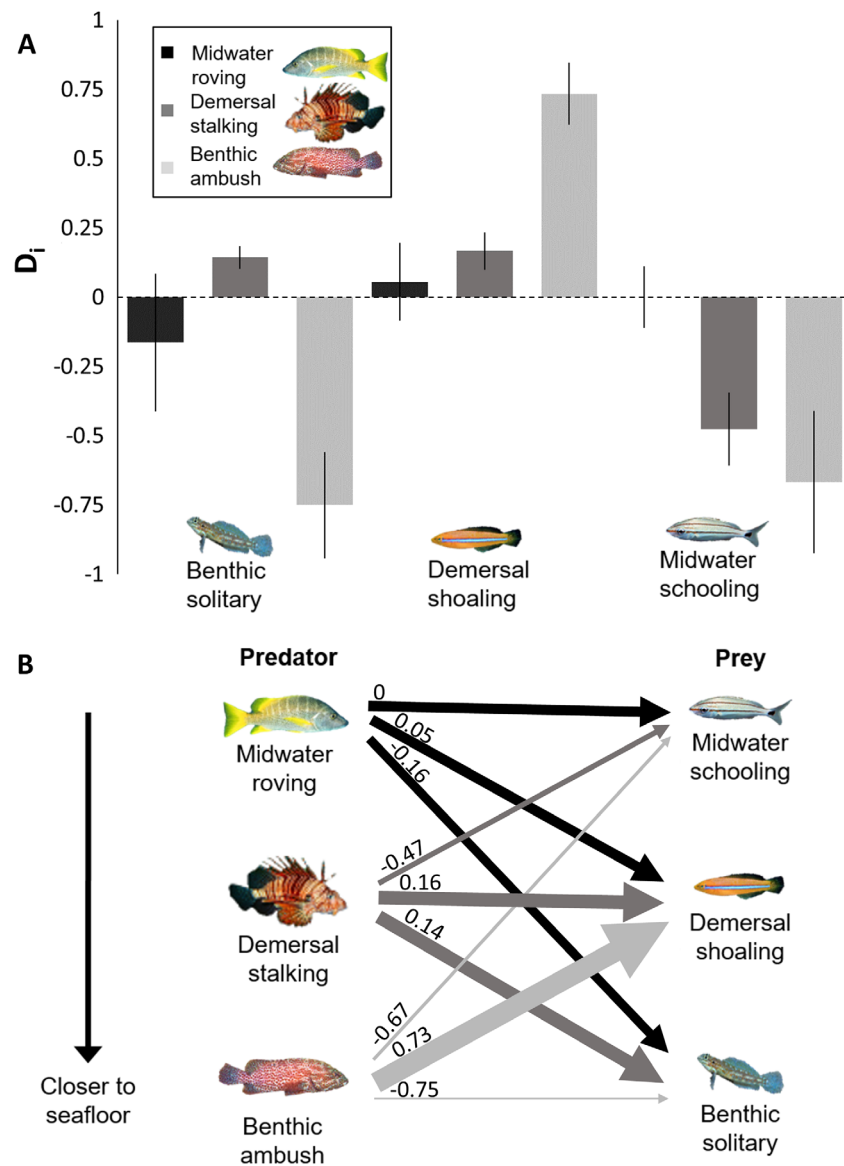
Fig. 2. (A) Consumption (measured as Jacobs' diet selectivity index $D_i$) of the three prey types by the three predator types. During laboratory trials, a single individual of each predator type was exposed to all three prey types simultaneously in equal abundance. Positive values indicate prey that were selectively consumed by a given predator type, while negative values indicate prey that were avoided. Bar heights represent means bounded by 95% confidence intervals. (B) Relative level of selectivity for each predator–prey. Arrow thickness is proportional to Jacobs' selectivity index score. Photo credit for fish images: New World Publications. Photographs of fishes are not to scale.

compared with other prey types (Fig. 3C, I), resulting in high selectivity for demersal shoaling prey (Fig. 2). In contrast, demersal stalking predators had high rates of success in capturing all three prey types (Fig. 3B, E, H), but the rates at which they encountered and made strikes on benthic prey (Fig. 3B) were greater than for demersal and midwater prey (Fig. 3E, H), patterns that explained their selective consumption of the benthic prey type (Fig. 2). Finally, whereas
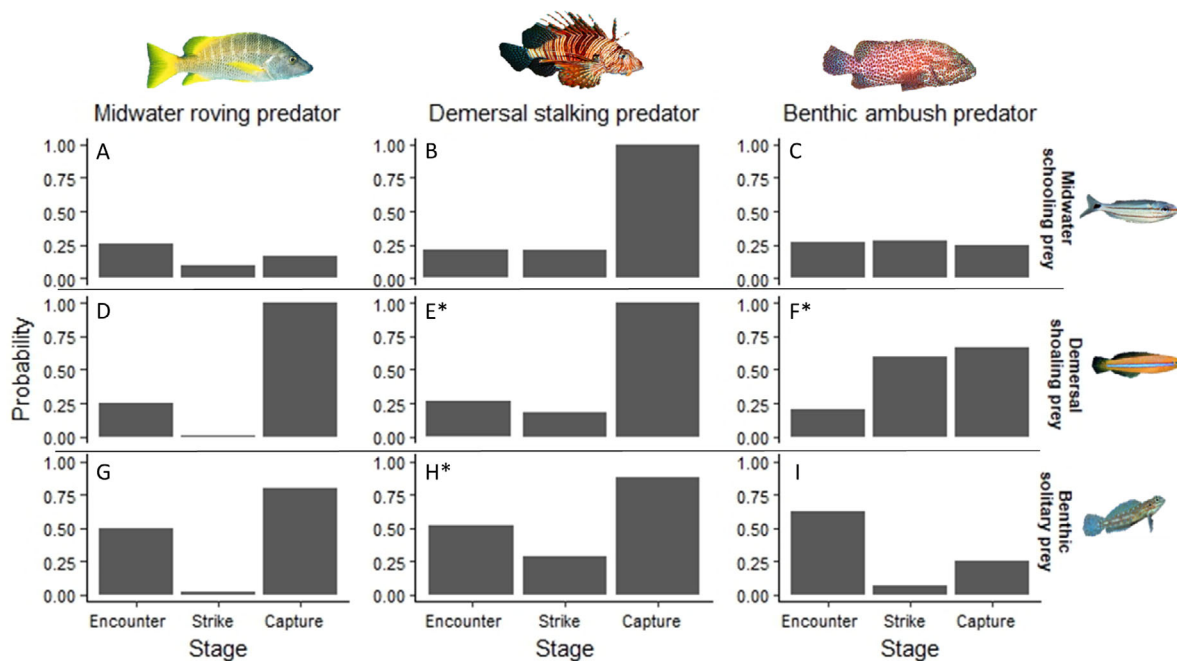
Fig. 3. Probability of encounter (A–C), strike (D–F), and capture (G–I) for each of the three prey types by the three predator types. Asterisks denote prey types that were selectively consumed by the given predator (i.e., at rates above that predicted by their abundance alone).

midwater roving predators had lower attack rates on all prey types compared with the other two predators, midwater schooling prey were the most likely target of their attacks (Fig. 3A, D, G). Unexpectedly, midwater roving predators were substantially more successful at capturing benthic solitary and demersal shoaling prey, but attacked these two prey types at lower rates compared with midwater schooling prey (Fig. 3A, D, G). As a result of differential attack and capture rates between the prey types, midwater roving predators consumed all three prey types at approximately equal rates (Table 2, Fig. 2).

*Effects of prey behavioral traits on likelihood of consumption*

All strikes occurred when predators were in close proximity to prey, with average strike initiation distances similar among predator–prey combinations (Table 2; Appendix S1: Fig. S5). Maximum strike distance varied slightly among predator types (Table 2). At the moment of all successful strikes (T-0), focal prey (i.e., those

consumed) were significantly closer to the predator than were non-focal prey (i.e., those not consumed; Fig. 4A–C). Fifteen seconds prior to strike events (T-15), prey that would be consumed by predators were also typically closer than individuals that were not consumed, but the magnitude of this pattern differed by predator type (Fig. 4A–C). In particular, consumed individuals of all three prey types were closer to demersal stalking predators than were their surviving conspecifics ahead of strike events (T-15; Fig. 4C). In contrast, while all three prey types were in close proximity to midwater roving predators at the time of successful strikes (Fig. 4; T-0), this pattern did not persist 15 s ahead of predation events for two of the three prey types (Fig. 4C; T-15). We found that consumed prey were also more isolated from other prey (i.e., greater prey–prey distance) at the moment of predation events (T-0) and also 15 s prior to being captured (T-15) than prey that survived (Fig. 4D–F). Of notable exception were predation events involving benthic solitary prey, in which consumed prey were no more aggregated than
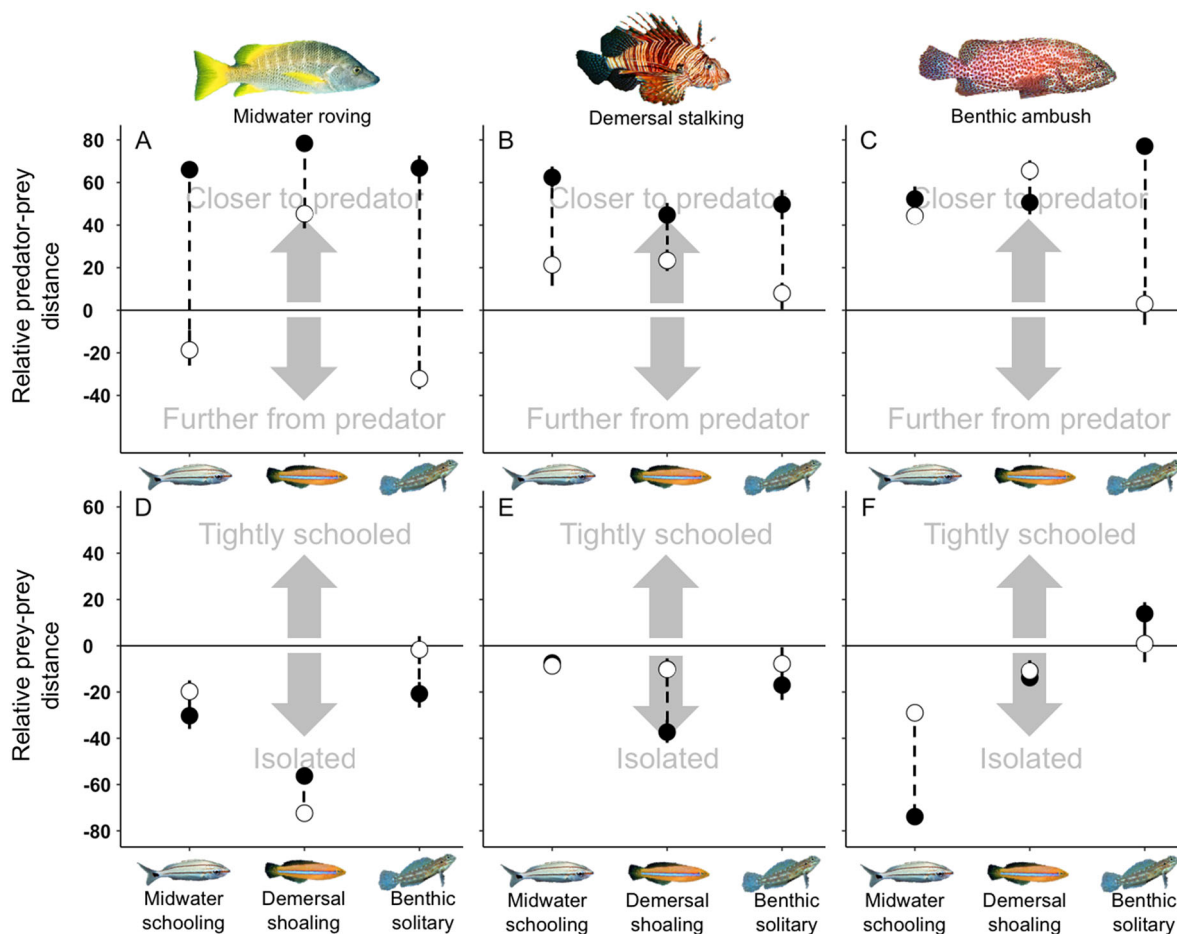
Fig. 4. Difference in response (A–C: predator–prey distance, proxy for the combined effect of prey avoidance and predator pursuit; D–F: prey–prey distance, a proxy for aggregative behavior) between prey that were and were not consumed by predators in laboratory trials (mean ± 95% bootstrapped confidence intervals). Black circles represent behavior at the initiation of the predator strike, while open circles represent behavior 15 s before a strike event.

individuals that were not consumed (i.e., remained solitary; all points below zero in Fig. 4D–F).

## DISCUSSION

Our multi-species foraging trials confirmed many of our predictions about the influence of predator and prey behavioral traits on the relative strength of consumptive interactions between species. In particular, tracking behaviors throughout the predation process shed light on how inter-specific variation in trait forms mediated patterns of selective predation. For example,

while the roving predator consumed all prey types non-selectively, behaviorally driven bottlenecks in rates of success at different stages of the predation process underpinned this result. Roving predators were relatively unsuccessful at capturing midwater schooling prey, yet were more likely to strike at this prey type compared with prey that were less aggregated and lower in the water column. This pattern is in line with substantial empirical evidence for the effect of aggregation behavior on predator success (Magurran 1990, Parrish and Edelstein-Keshet 1999, Parrish et al. 2002). Demersal stalking predators selectively consumed benthic solitary prey because,

although they had high rates of success in capturing all prey types, they encountered benthic solitary prey at far greater rates compared with species that occupied the water column, that is, within a distance at which a successful strike could be made. Our calculations of encounter rate relied on measured predator–prey distance, which results from some combination of prey avoidance and predator pursuit. Our observations from the video data of the demersal stalking predator, lionfish, showed them slowly pursuing benthic prey in a head down manner and blowing jets of water at motionless benthic prey, causing the prey to re-orient head-on to the predator prior to striking (described in detail by Albins and Lyons 2012).

Our observations also allowed us to evaluate assumptions about behavioral mechanisms that may have facilitated the success of invasive Indo-Pacific lionfish in the broader Caribbean region. In particular, many authors have surmised that the naïve prey hypothesis—in which native species do not recognize the threat posed by the lionfish's unique appearance and stalking behavior and fail to evade approaches by them— explains the high rates of native prey consumption by lionfish in the invaded range (Albins and Hixon 2013, Côté and Maljković 2010, Cure et al. 2012, Côté et al. 2013a, Marsh-Hunkin et al. 2013, Black et al. 2014, Kindinger 2015, Anton et al. 2016, Eaton et al. 2016, Benkwitt 2017). However, our observations suggest that prey respond as appropriately to this non-native predator as they do to native piscivores, given that encounter rates (i.e., prey within a distance at which a successful strike could be made) with lionfish across prey types were quite ordinary in comparison with the two native predators we observed (All prey species we studied have been identified in lionfish's diet in the invaded range; Albins and Hixon 2013, Morris and Akins 2009, Muñoz et al. 2011, Layman and Allgeier 2012, Côté et al. 2013a, b, Dahl and Patterson 2014, Eddy et al. 2016, Harms-Tuohy et al. 2016). Instead, lionfish were very successful in capturing individuals of all prey types once they were encountered. This result suggests that high rates of prey consumption are likely due to the effectiveness of the combination of unique stalking behavior, buccal suction, and forward momentum generated during strike events, behavioral

traits that are unlike native fish predators and highly successful in capturing prey that occupy habitat on or near the bottom (Albins and Lyons 2012, Green and Côté 2014).

Tracking interactions throughout the predation process also allowed us to evaluate why some of our predictions about prey electivity were not borne out. In particular, while benthic ambush predators were very likely to encounter bottom-dwelling prey (counter to our prediction), they were more likely to strike and successfully capture prey that occupied the water column (in line with our prediction). However, this pattern held only for loosely aggregated shoaling prey, not polarized schooling prey, suggesting that aggregation tightness and behavior in addition to water column position affect the probability of strikes and captures by ambush predators. These interactions also suggest that, in addition to predator–prey distance, the angle of encounter (a metric that we were not able to reliably assess with the orientation of cameras in our study design) is also an important influence on whether strikes or captures are likely to occur, potentially due to the effects of predator visual acuity and eye placement on their field of vision (McFarland 1991). Because we equalized the abundance of prey types in our experiment, we also were not able to examine the effect of prey density either on aggregation behavior by each prey species or on risk of consumption. The latter is owing to trade-offs between lower risk of capture for any one individual (e.g., Hamilton 1971) vs. prey being more conspicuous and predators preferring to attack larger aggregations (Botham and Krause 2005, Maury 2017).

Food web models are a main tool used to understand the effect of environmental perturbations on the flow of energy through ecosystems over time and space (McCann 2011, Polis and Winemiller 2013, Moore et al. 2017). Yet, the majority of interaction webs upon which these models depend are data poor, with linkages between taxonomic groups based on patchy diet data often derived from populations other than those being modeled (McCann 2011, Polis and Winemiller 2013, Chagaris et al. 2016, Moore et al. 2017). In particular, the majority of studies of diet selection by predatory reef fishes (including those associated with our focal predators) have focused on gut contents (e.g., Nagelkerken 1979, Rooker 1995, Beukers-Stewart and Jones

2004, Nunn et al. 2012, Peake et al. 2018) or tissue stable isotope analysis (e.g., Curtis et al. 2017, Matley et al. 2017). While these approaches demonstrate the identity of prey species and reveal patterns of diet breadth and variability, they fall short of providing insights into the behavioral mechanisms generating diet patterns, in particular, the important influence of relative prey availability and the selection process on observed patterns of consumption. Our study suggests that observable traits can be used to constrain estimates of interaction strength within food webs for which there is little empirical information on pairwise interactions. A behavioral trait lens could also provide insightful predictions regarding the strength of consumptive interactions that emerge as food webs are reassembled by anthropogenic and environmental stresses such as biological invasions, climate change, and extirpations. For example, this study confirms the importance of key behavioral and morphological traits in conferring susceptibility to predation by invasive lionfish (Green and Côté 2014) and further corroborates the hypothesis that native species exhibiting this suite of traits are likely to face greater predation mortality as the invasion progresses (Albins and Hixon 2013, Green et al. 2012, Côté et al. 2013a, Albins 2015). However, we also show that accounting for differential patterns of selective prey consumption by multiple predators is essential for assessing how the magnitude of total mortality may shift among prey species as a result of the invasion. While benthic solitary prey were preferred by invasive lionfish, demersal shoaling prey faced greater total mortality from the entire suite of native and non-native predators.

Finally, this study highlights opportunities and requirements for further research into the role that predator and prey traits play in predicting foraging outcomes within communities. In particular, evaluating whether similar patterns of interaction emerge across unrelated species that exhibit similar trait forms is essential for evaluating the generality of our results. For example, we selected candidate species with similar body shapes and sizes in order to account for key behavioral traits that are known to influence foraging success. However, other species-specific traits may contribute to predation outcomes beyond the behavioral characteristics for which we made predictions. A key challenge for testing mechanistic predictions about foraging through observations and experiments is the logistical effort required to conduct studies that realistically capture the required depth of detail across a breadth of species. This study required months of field and laboratory work to repeat standardized foraging trials with multiple sets of species, as well as hundreds of hours analyzing the resulting video products. Technological advances in the precision and accuracy of tracking data that can be automatically obtained from video imagery are likely to improve the ability to observe foraging interactions among an increased range of species and in more challenging habitats. Moreover, while the spatial scale of our foraging arenas and relative densities of prey offered are comparable to a subset of conditions under which predatory fishes forage on small patch reefs, these conditions inevitably limit the range of anti-predator strategies that can be employed by prey (e.g., limits on predator avoidance distance and spacing between conspecifics, and reduced habitat variability limit opportunities for sheltering or camouflage). A likely consequence of this limited environment is that the magnitude of inter-specific variation in the anti-predator behaviors we observed may be far less than would be observed in situ. Thus, our approach likely yields conservative estimates of the influence of inter-specific trait variation on interactions along the foraging process. In any case, our results indicate that developing and testing mechanistic predictions about the trait basis of foraging interactions is a worthwhile endeavor because they provide a means to anticipate how consumptive interactions—and ultimately flows of energy and biomass throughout a community—may be altered by ongoing change in species distributions and abundance globally.

## Acknowledgments

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## Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2752/full

**Ecosphere**

**Trait-mediated foraging drives patterns of selective predation by native and invasive coral reef fishes**

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**Appendix S1. Supplementary information about foraging trial design and analysis**

**Figure S1** Tank, camera rack, and observer blind cover (opened) at the Cape Eleuthera Institute in the Bahamas.

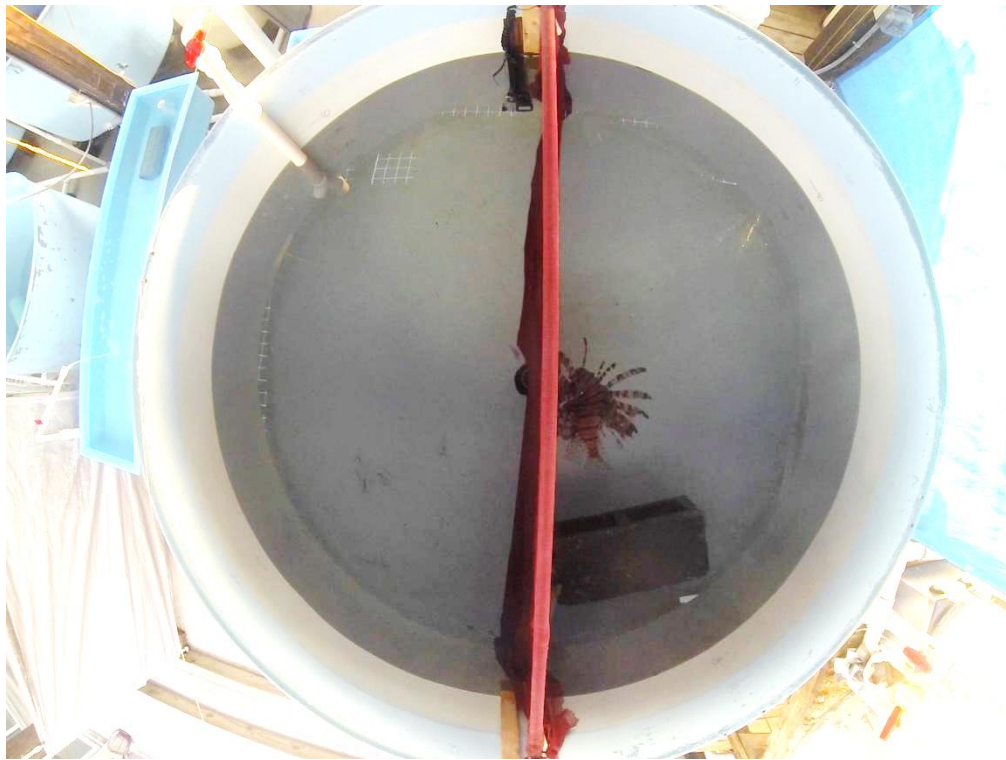**Figure S2** Tank with the underwater camera and acclimating lionfish from the perspective of the top-view camera.

**Figure S3** Image from the top-view camera with lines drawn to measure distances between fish using ImageJ software.
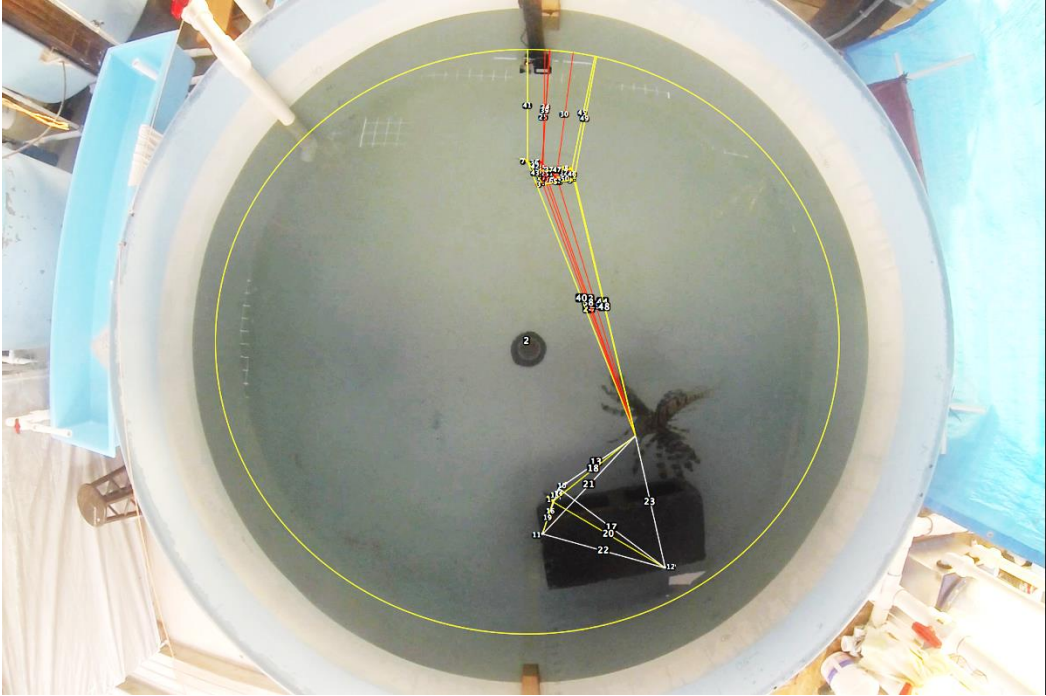
**Figure S4** View from underwater side camera of the foraging arena during a trial with the demersal stalking predator (lionfish). The cinderblock shelter was present for all trials.
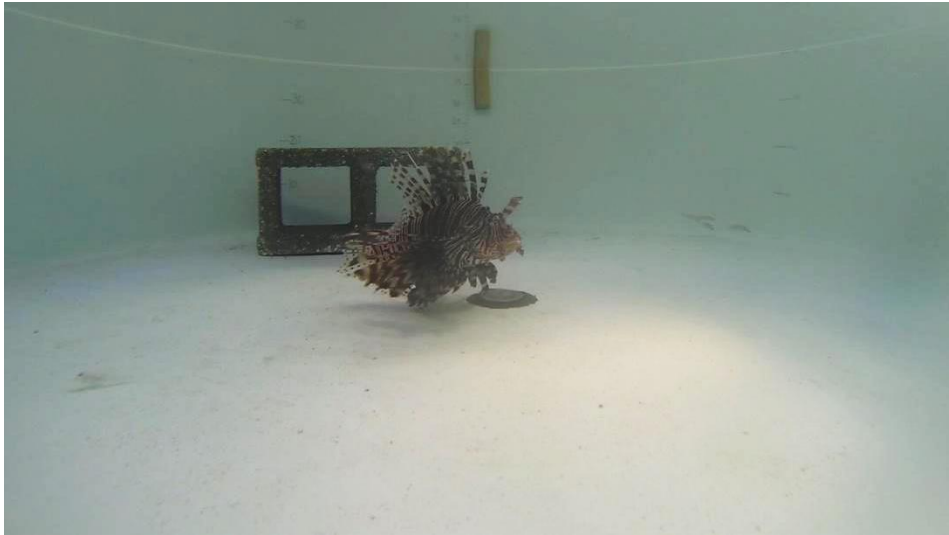
**Figure S5.** Mean (± 95 % confidence intervals) predator-prey distance (A & B) and prey-prey distance (C & D) at the moment of a successful strike (T-0) by predator type for prey that were and were not consumed.