

Preference of Invasive Lionfish and Native Grouper Between Congeneric Prey Fishes

Preferencia de Pez León Invasor y de Mero Nativo Entre Congéneres Presas Peces

Préférence de Lionfish Envahissantes et Mériou Natif Entre Poissons Proies Congénères

TYE L. KINDINGER* and EMILY R. ANDERSON

Department of Integrative Biology, Oregon State University, 3029 Cordley Hall, Corvallis, Oregon 97331 USA.

*kindingt@science.oregonstate.edu.

ABSTRACT

To gain insight about how an invasive predator influences native prey, we performed a series of controlled experiments in aquaria to characterize and compare the prey preferences of the invasive red lionfish (*Pterois volitans*) and an ecologically-similar native mesopredator, the graysby grouper (*Cephalopholis cruentata*). Preference for native congeneric fishes, the fairy and blackcap basslets (*Gramma loreto* and *G. melacara*, respectively) were tested. We observed behavior of predators in response to two individual prey consisting of cross-factored combinations of species (fairy and blackcap basslets) and size (small and large). Upon initial exposure to prey, lionfish first hunted fairy basslet and graysby hunted blackcap basslet first, and both predators initially preferred large over small fish. Overall predatory behavior quantified from the entire duration of observation indicated both predators lacked a preference between basslet species based on total number of strikes and hunting time. Despite essentially identical size ranges of predators studied, graysby overall preferred large basslet across all graysby sizes, whereas the overall preference of lionfish between prey size varied with lionfish size. Importantly, the initial preferences of predators were least affected by the unnatural setting in aquaria and thus more likely reflected true predatory behavior. This study demonstrates aspects of prey preference that are either different or similar between invasive and native predators. The combination of these predators could at one extreme enhance coexistence within and between basslets, or at the other extreme, deplete local basslet populations via increased overall predation.

KEY WORDS: Predation, prey preference, invasive species, coral reefs, lionfish, grouper, basslets

INTRODUCTION

Invasive predators typically have effects on native prey that are more severe than the effects of native predators (Salo et al. 2007), which often includes causing substantial declines in native species (Pitt and Witmer 2007). These predators often have generalized diets and in extreme cases, can drive native species to local or global extinction (Clavero and Garcia-Berthou 2005). Therefore, accurately predicting the effects of invasive predators on native prey populations and communities is important for informing management and conservation strategies.

A key mechanism underlying predatory effects is prey preference. Predators may have a preferred prey which is disproportionately consumed, or they may exhibit prey switching behavior (sensu Murdoch 1969) where the predator switches to other available prey once the preferred prey becomes rare. Because the predator population is not dependent on the abundance of the preferred prey, this switching behavior exhibited by an invasive predator can ultimately lead to the extinction of native prey once they become sequentially preferred (e.g., Savidge 1987). Further, if the invasive predator has the same or opposite prey preference than that of a native predator, then the addition of invasive predation to a system is likely to enhance or complement native predation, respectively. And, if both predators have a preferred prey in common, then the invasive predator could also potentially moderate native predation by acting as a novel competitor to the native predator. Overall, understanding the prey preference of an invasive predator and comparing it to that of a native predator can reveal potential mechanisms underlying the overall effects of an invasion on native communities.

By performing a series of controlled experiments, we characterized the prey preference of an invasive marine predator, the Pacific red lionfish (*Pterois volitans*), and compared this preference to that of an ecologically-similar mesopredator that is native throughout the Atlantic, the graysby grouper (*Cephalopholis cruentata*). Invasive lionfish are commonly found invading coral reefs throughout the tropical and subtropical Western Atlantic and greater Caribbean region (Schofield 2010), and like the native graysby, are considered to be generalist predators (e.g., Morris and Akins 2009). This voracious predator can cause large reductions in the abundance and richness of small native fishes that scale-up from smaller patch reefs (e.g., Albins & Hixon 2008) to large coral reefs (Albins 2015).

Marine piscivores often preferentially distinguish among prey by species (e.g., Almany et al. 2007) or by size (e.g., Floeter and Temming 2003). Because native graysby and invasive lionfish are both generalist mesopredators, we hypothesized that they have similar prey preferences. We predicted that neither predator would display a strong preference for either basslet species, but would both exhibit shifts in preference from smaller- to larger-sized basslets with increasing predator size, because graysby and lionfish are gape-limited predators.

METHODS

Study Area and Fish Collection

We conducted this study during August 2014 at the Cape Eleuthera Institute on Eleuthera, the Bahamas where we investigated the preference of predators for two native coral-reef fishes, the fairy and blackcap basslets (*Gramma loreto* and *G. melacara*, respectively). These congeners are popular aquarium fishes that differ in appearance primarily by coloration (Figure S1) and are commonly found under ledges (rock overhangs) throughout Caribbean reefs (Böhlke and Randall 1963,

Starck et al. 1978). SCUBA divers collected basslets from reefs in the Exuma Sound at maximum depths of 15 m with small aquarium hand nets and the fish anesthetic quinaldine. We collected graysby and lionfish from shallow patch reefs (< 5 m deep) in Rock Sound with the respective use of hand fishing lines while snorkeling and hand nets on SCUBA. We collected 15 lionfish ranging in size from 10.2 - 20.9 cm total length (TL) and 15 graysby with a size range of 10.0 - 20.3 cm TL. All fish were maintained in outdoor tanks with continuous flow-through saltwater systems and fed daily; predators were fed live silverside fish and basslets were fed live brine shrimp (*Artemia* sp.).

Experimental Design

We conducted all experimental trials in 50-gallon acrylic aquarium tanks (91.5 x 38 x 51 cm) with continuous flow-through seawater systems. Food was withheld from predators 24 hours prior to observation to ensure predator response to the presence of prey. Tanks were divided in half with a removable central barrier of solid aluminum (Figure 1). We released a single predator into one side of the tank and placed two basslets in the other side. Basslets were held in identical small glass containers (~500 ml) with mesh covers (one basslet per container) positioned in each corner of the tank. With these prey containers, predators were able to receive both visual and chemical cues from basslets, but could neither make physical contact nor consume any basslets.

To determine whether the preference of predators for basslets was driven by basslet species (fairy and blackcap) and/or basslet size (small: 1.7 - 2.5 cm TL and large: 3.5 - 5.2 cm TL) we presented pairs of basslets in cross-factored combinations of the two variables, resulting in the following treatments:

- i) Small fairy and large fairy,
- ii) Small blackcap and large blackcap,
- iii) Small fairy and small blackcap,
- iv) Large fairy and large blackcap,
- v) Small fairy and large blackcap, and
- vi) Large fairy and small blackcap.

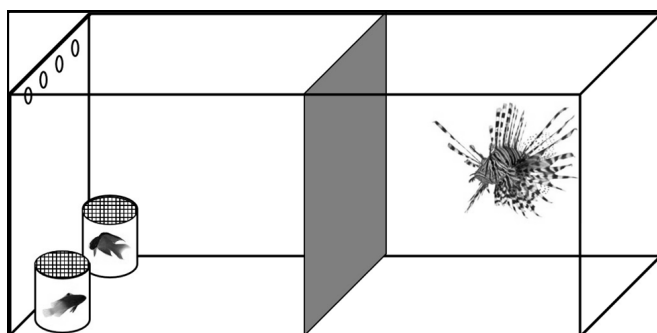


Figure 1. Experimental tank setup, consisting of a 50-gallon acrylic aquarium tank, divided by a removable aluminum central barrier separating basslets (in ~500 ml glass containers with mesh covers) from a predator (lionfish shown here). After a 20-minute acclimation period, the central barrier was removed and predator-prey behavior was observed.

In addition to randomizing the order of basslet treatments presented to each predator, we also randomized which corner of the tank basslets were placed every time a treatment was presented.

Once the predator and basslets were in their respective sides of the tank, we allowed them to acclimate for 20 minutes, after which we removed the central barrier and observed the predator's behavior for 10 minutes. Observations were performed either in-person or filmed with a digital video camera (16 lionfish trials; 17 graysby trials) positioned outside of the tank. During each 10-minute trial, we recorded (1) which basslet the predator hunted (defined below) first (initial hunting preference); (2) the number of times the predator's mouth made physical contact with each glass container (number of strikes); and (3) the amount of time the predator hunted each basslet (hunting time). We defined the hunting behavior of lionfish as occurring when an individual directly faced a basslet with flared pectoral fins and/or blew pulsed jets of water towards a basslet (Cure et al. 2012). We characterized graysby hunting behavior as occurring when an individual positioned itself near a basslet (< 10 cm in this experiment) while directly facing the basslet (Webster 2004).

At the conclusion of the 10-minute trial, we separated the predator from the basslets and placed the central barrier back in the tank. A new combination of basslets were placed in the glass containers, and all fish were allowed to acclimate for 20 minutes before removing the barrier and observing predator response for another 10 minutes. This procedure was repeated until all six basslet treatments had been presented to each predator in random order.

Statistical Analyses

When testing for significant differences in predator response between fairy versus blackcap basslets, we analyzed only the four treatments where predators were presented with two different basslet species (lionfish: $n = 11$, graysby: $n = 11$). Similarly, we analyzed the four treatments where we presented predators with two basslets differing in size (small versus large) when comparing predator response between basslet sizes (lionfish: $n = 13$, graysby: $n = 12$). If a predator did not display any predatory behavior during any of the four treatments described in the treatment groupings above, then the individual was dropped from that respective group prior to analysis (resulting in the final sample sizes reported above).

To test whether initial hunting preferences between basslet species (fairy and blackcap) and basslet sizes (small and large) significantly differed between predators (lionfish and graysby) and/or among predator sizes (continuous variables), we fit Generalized Estimation Equations (GEEs) with binomial distributions and exchangeable correlation structures. GEEs are an extension to the generalized linear model approach that allow for correlations between observations from the same subject, thus allowing us to account for repeated measures. We fit a full model with an interaction between predators and predator size, and then compared the model fit to that of the reduced additive model by calculating quasi-likelihood values under the

independence model criterion (QIC; Pan 2001). If the initial hunting preference significantly varied between predators, we then performed a post-hoc McNemar test with a continuity correction for lionfish and graysby (separately) to test whether each predator had a significant initial preference.

We fit full GEEs with Poisson distributions and exchangeable correlation structures to test whether the number of strikes and hunting time of predators significantly depended on a three-way interaction among the type of predator, predator size, and basslet species. We compared the full and reduced additive GEEs with QIC. If the three-way interaction was significant, we fit GEEs for lionfish and graysby separately to determine whether each predator's response significantly differed among predator size and/or basslet species (or an interaction between the two). Again, final models (full versus reduced) were selected for each predator based on QIC values. We repeated this entire process, but with basslet size instead of basslet species as an explanatory variable in all the GEEs. All statistical analyses were conducted using *R* version 3.1.2 (*R* Core Team 2014) with the associated packages *geepack* (Halekoh et al. 2006) and *MESS* (Ekstrom 2014).

RESULTS

Invasive lionfish and native graysby exhibited clear initial hunting preferences for basslet species that significantly differed between predators (Figure 2A-B, GEE, Wald $\chi^2 = 25.5$, $p < 0.0001$), yet did not significantly differ among predator sizes (GEE, Wald $\chi^2 = 1.49$, $p = 0.22$). Upon initial exposure to both basslet species, lionfish first hunted fairy basslet significantly more often than blackcap basslet (McNemar test $\chi^2 = 96.01$, $p < 0.0001$), whereas graysby initially hunted blackcap basslet (McNemar test; $\chi^2 = 62.02$, $p < 0.0001$). However, these initial preferences were not maintained for the remainder of the observational periods. Across all predator sizes observed, there was no significant difference in the number of strikes or hunting time directed at each basslet species exhibited by either predator (Table 1).

When testing the initial hunting preference between basslet sizes, we found that despite the full GEE model having a lower QIC value than the reduced model (Table S1), the interaction between the predator species and predator size was not significant (GEE, Wald $\chi^2 = 2.60$, $p = 0.11$).

Initial preference between basslet sizes did not significantly differ between predator species (GEE, Wald $\chi^2 = 2.57$, $p = 0.11$) nor across predator sizes (GEE, Wald $\chi^2 = 1.01$, $p = 0.31$). Both lionfish and graysby had a significant initial preference for large basslet (Figure 2C-D, McNemar tests; $\chi^2 = 16.1$ and 29.0 , respectively; $p < 0.0001$ for both predators). This preference for large basslet remained consistent for graysby in terms of both the overall number of strikes (Figure 3A, GEE, Wald $\chi^2 = 13.19$, $p < 0.0003$) and hunting time (Fig. 3B, GEE, Wald $\chi^2 = 10.24$, $p = 0.0014$). This preference was also maintained across all sizes of graysby tested (number of strikes: GEE, Wald $\chi^2 = 0.65$, $p = 0.4202$; hunting time: GEE, Wald $\chi^2 = 0.01$, $p = 0.9433$). In contrast, both the overall number of strikes and hunting time of lionfish depended on a significant interaction between the size of lionfish and basslet size (Figure 4, number of strikes: GEE, Wald $\chi^2 = 8.42$, $p = 0.0037$; hunting time: GEE, Wald $\chi^2 = 11.53$, $p < 0.0007$). Predatory behavior directed at small basslet was greatest among smaller-sized lionfish sizes, and gradually decreased with increasing lionfish size (Figure 4A and 4C). We found the opposite trend in response to large basslet, with increasing levels of predatory response as lionfish size increased (Figure 4B and 4D).

DISCUSSION

The distinctiveness hypothesis postulates that invasive predators are expected to have similar effects on prey species that are taxonomically and functionally similar (e.g., Ricciardi and Atkinson 2004). Contrary to this prediction, we have provided evidence of an invasive marine predator having strong prey preferences that depend on both the species and size of prey upon initial exposure to a pair of congeneric coral-reef fishes.

Table 1. Results of full Generalized Estimating Equation (GEE) models of the number of strikes and hunting time of predators (graysby and lionfish) in response to two different basslet species (fairy and blackcap). Full models were selected for both response variables based on Quasi-Akaike Information Criterion (QIC) values (see Table S1).

Response variable	Explanatory variable (from full model)	Wald χ^2	p-value
Number of strikes	Predator size	0.780	0.380
	Basslet species	0.420	0.520
	Predator species	0.230	0.640
	Predator size x Basslet species	0.740	0.390
	Predator size x Predator species	0.720	0.400
	Basslet species x Predator species	0.560	0.460
	Predator size x Basslet species x Predator species	0.500	0.480
Hunting time	Predator size	0.35	0.556
	Basslet species	0.77	0.379
	Predator species	2.96	0.085
	Predator size x Basslet species	0.24	0.622
	Predator size x Predator species	0.18	0.672
	Basslet species x Predator species	2.92	0.088
	Predator size x Basslet species x Predator species	1.89	0.170

Lionfish first hunted fairy basslet more often than blackcap basslet, and initially preferred large over small fishes. In contrast, native graysby first hunted blackcap basslet, yet were consistent with lionfish in exhibiting an initial preference for large fish. Following these initial preferences, overall predatory behavior quantified from the entire duration of observations revealed that both the invasive and native predators hunted and struck about equally at both basslet species. In terms of overall preference between prey size, only the preference of invasive lionfish varied with predator size. Native graysby preferred large fishes across all predator sizes, yet smaller lionfish preferred small basslets and larger lionfish preferred large basslets.

We also observed additional variance in behavior between predators in response to basslets. Graysby typically performed strikes at basslets in quick succession, striking the glass containers up to as many as nine times in three seconds. In contrast, there was a minimum of two seconds between individual lionfish strikes. We also observed lionfish more often than graysby switching between which basslet were hunted within a single trial. A review of the trials we recorded with a digital camera revealed that lionfish switched which basslet were hunted a total of 31 times, whereas graysby switched only six times.

More than half of the observed switches by lionfish seemed associated with basslet movement, where immediately following the movement by the basslet not being hunted, we observed lionfish switch to hunting that basslet. None of the switches between basslets by graysby were associated with basslet movement.

The behavior of predators observed in this study suggest that invasive lionfish may have a slightly broader range of effects on basslets than native graysby, given that lionfish are seemingly more likely to hunt both small and large basslets, and even may exhibit switching behavior. However, the initial preferences of predators are of particular importance, because they were the observations that were least likely to reflect the unnatural setting used in this study. Predators in aquaria were unable to consume prey fishes, and the glass containers with basslets seemed to deter predators. Once a predator struck at the glass, there were often few subsequent strikes for the remainder of a trial, although predators did continue to display hunting behavior. If these initial observations of behavior are indicative of the true preferences of these predators on natural reefs, then the addition of invasive lionfish on reefs may promote coexistence between basslets by consuming the less-preferred species of the native predator. In

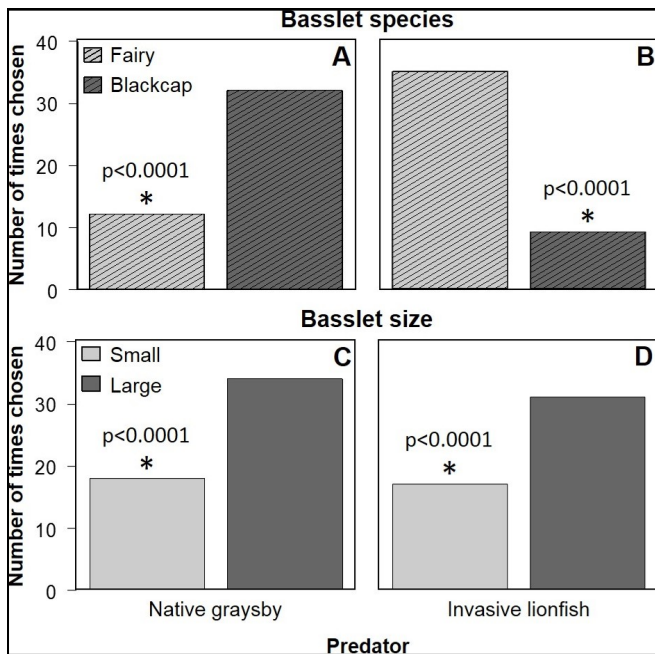


Figure 2. Initial hunting preference of (A, C) native graysby and (B, D) invasive lionfish between (A, B) fairy versus blackcap basslets (n = 11 graysby, n = 11 lionfish) and (B, D) small versus large basslets (n = 12 graysby, n = 13 lionfish). Bars represent the total number of times that each predator initially hunted each basslet during treatments consisting of two different basslet species (n = 4 per individual predator) and two different basslet sizes (n = 4 per individual predator).

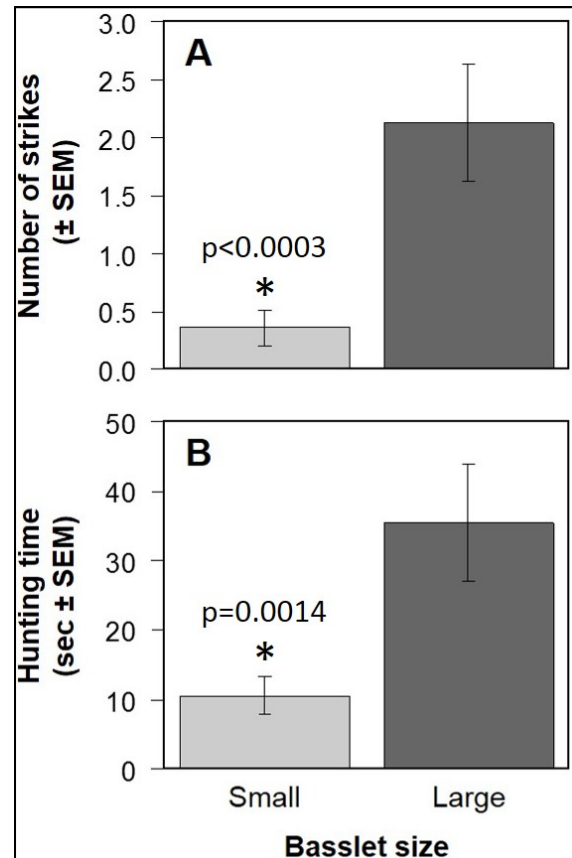


Figure 3. Mean (±SEM) number of strikes (A) and mean amount of time spent hunting (B) by native graysby (n=12) in response to small versus large basslets during treatments consisting of two different basslet sizes (n=4 per individual predator).

contrast, invasive lionfish may enhance overall predation of larger basslets.

The combination of invasive and native predation likely results in complex interactions with basslets. Basslets are found distributed among ledge positions in local populations based on a size hierarchy (Webster and Hixon 2000, Kindinger, in review). Under ledges, individuals compete both within and between species for feeding position, whereby larger individuals maintain coveted positions towards the fronts of ledges where the ability to obtain planktonic food is greatest. If both the invasive and native predators preferentially consume these larger fishes, the ability of smaller basslets to shift closer toward coveted feeding positions may increase. Interspecific competition between basslet species (Kindinger, in review) also may be altered by invasive lionfish via increased consumption of fairy basslet.

Alternatively, invasive lionfish may enhance predation of native basslets to the point where competition no longer exists within local populations. Indeed, previous field studies indicate that fairy basslet are faced with increased predation from the addition of lionfish to native reefs (Ingeman and Webster 2015), and invasive lionfish can even drive local populations of fairy basslet to extirpation (Ingeman, in review). In addition to these effects on fairy basslet, invasive lionfish may substantially affect both basslet species via elevated consumption rates of larger

individuals. Over time, this increased consumption of larger size classes of prey could cause shifts in the overall size distribution of basslets, or potentially even influence population growth rates via preferential targeting of adult basslets that are reproductively mature. Additionally, the enhanced depletion of prey fishes could also have potential indirect effects on native predators (including graysby) via apparent competition.

Our hypotheses about how the addition of invasive lionfish could potentially affect native communities all hinge on the main assumption that the initial preferences exhibited by predators in this study reflect the true preferences of these predators on natural reefs. Both in the experimental setting of this study and on natural reefs, recognition of basslet species by lionfish and graysby likely involves the use of visual and/or olfactory cues from prey (or combinations of both). Most reef-fish have acute color vision (McFarland 1991), so these predators may be able to interpret the differences in coloration between fairy and blackcap basslets. Preferences for a prey species could also be explained by varying activity levels between basslets. Anecdotally, fairy basslet appeared to be more active in the glass containers compared to blackcap basslet in this study, and our observations of lionfish often switching which basslet was being hunted seemingly in response to basslet movement further supports this hypothesis. Kindinger (in review) revealed that fairy basslet were more aggressive than blackcap basslet, which may indicate fairy basslet are also more conspicuous in a natural setting.

Consumption of basslets on reefs is also likely influenced by the respective antipredator response of each basslet species. Even though we focused on the behavior of predators in this study, we did find anecdotal evidence that suggests basslet behavior varied in response to predators. Both basslets became highly active as graysby approached the glass containers, and basslets rapidly darted around the container immediately following graysby strikes. In contrast, basslets rarely reacted to the predatory behavior of lionfish and typically remained hovering or resting within containers, even during lionfish strikes. This lack of response to invasive lionfish may indicate that basslets are naïve to this novel predator, due to a lack of shared evolutionary history (Cox and Lima 2006).

Our study demonstrates aspects of prey preference that are either different or similar between invasive and native predators. As a result, invasive lionfish may at one extreme enhance coexistence by preferentially consuming the less-preferred prey species of the native predator or by enhancing preferential predation on larger, competitively-dominant basslets. At the other extreme, increased consumption of basslets by invasive lionfish may deplete local basslet populations, especially if lionfish exhibit switching behavior following the reduction of preferred prey. Determining how the combination of invasive and native predation will ultimately affect native prey populations and communities is imperative for accurately predicting the extent of impact from an invasion, which can greatly inform management and conservation initiatives.

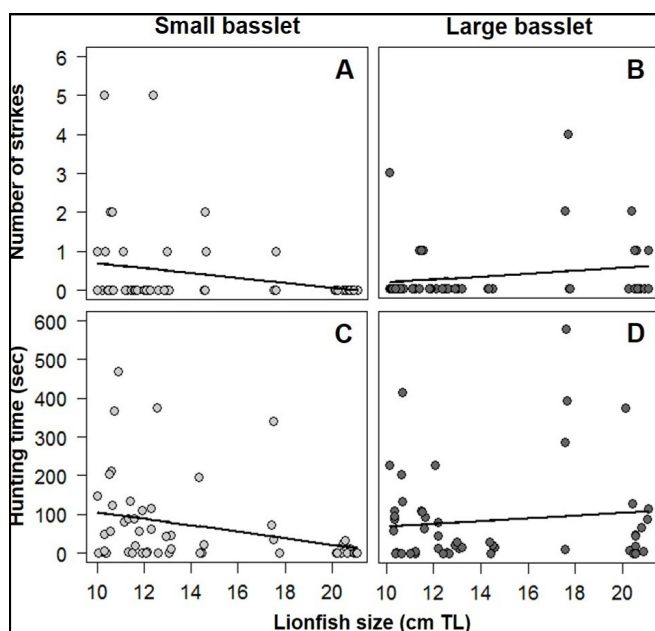


Figure 4. Number of strikes (A, B) and amount of time spent hunting (C, D) by invasive lionfish ($n=13$) throughout a range of lionfish sizes (cm total length) in response to small (A, C) and large (B, D) basslets during treatments consisting of two different basslet sizes ($n=4$ per individual predator). Regression lines are models with significant interactions between lionfish size and basslet size.

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Figure S1. Two native prey fishes used in experiment (left to right): fairy basslet (*Gramma loreto*) and blackcap basslet (*Gramma melacara*). Photo credits: Emily R. Anderson left and unknown (Google Images) right.

Table S1. Quasi-Akaike Information Criterion (QIC) values of full and reduced Generalized Estimating Equation (GEE) models, where full models include all interactions among explanatory variables and reduced models are additive models. QIC values in bold and asterisked (*) are the lower QIC values between the full and reduced models of each response variable.

Response variable	Full GEE model	QIC values	
		Full model	Additive model
Initial preference basslet species	~ Predator size x Predator species	103.324	101.286*
Initial preference basslet size	~ Predator size x Predator species	134.34*	135.98
Number of strikes basslet species	~ Predator size x Predator species x Basslet size	320.07*	321.91
Number of strikes basslet size	~ Predator size x Predator species x Basslet size	271.72*	303.74
Lionfish strikes basslet size	~ Lionfish size x Basslet size	148.41*	159.61
Graysby strikes basslet size	~ Graysby size x Basslet size	123.05	122.21*
Hunting time basslet species	~ Predator size x Predator species x Basslet size	-69559.80*	-68693.87
Hunting time basslet size	~ Predator size x Predator species x Basslet size	-65091.26*	-63650.07
Lionfish hunting time basslet size	~ Lionfish size x Basslet size	-54905.07*	-53933.97
Graysby hunting time basslet size	~ Graysby size x Basslet size	-10183.24*	-10142.15

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