Effects of predator hunting mode and prey anti-predator responses on prey selection by invasive Pacific red lionfish (*Pterois volitans*) and native Atlantic coral-reef piscivores

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Background & Hypothesis

The invasive Pacific red lionfish (*Pterois volitans*) is a voracious predator that poses a major threat to Caribbean coral reefs (Albins & Hixon 2013 *Env. Biol. Fish.* 96:1151-1157, Côté et al. 2013 *Biol. Cons.* 164:50-61). Predation by lionfish has been documented to reduce the abundance of small native fish on patch reefs by over 90% (Albins 2013 *Biol. Invas.* 15:29–43). Considering the unique hunting behavior of lionfish in comparison to native predators, how does predation by this invader differ from that by native piscivores in terms of prey anti-predator behaviors and prey selectivity (Fig. 1)?

A variety of predator and prey characteristics affect the predation process (Fig. 1). We hypothesized that different predator hunting strategies (stalking, ambushing, roving) will be differentially effective against different anti-predator aggregation behaviors (schooling, shoaling, and solitary). Regarding prey selection, we predicted that the stalking strategy of lionfish would be most effective against solitary benthic prey, resulting in high selectivity. Regarding prey behavior, we predicted that, because of their novel appearance, lionfish would be able to approach prey more closely than native predators before striking.
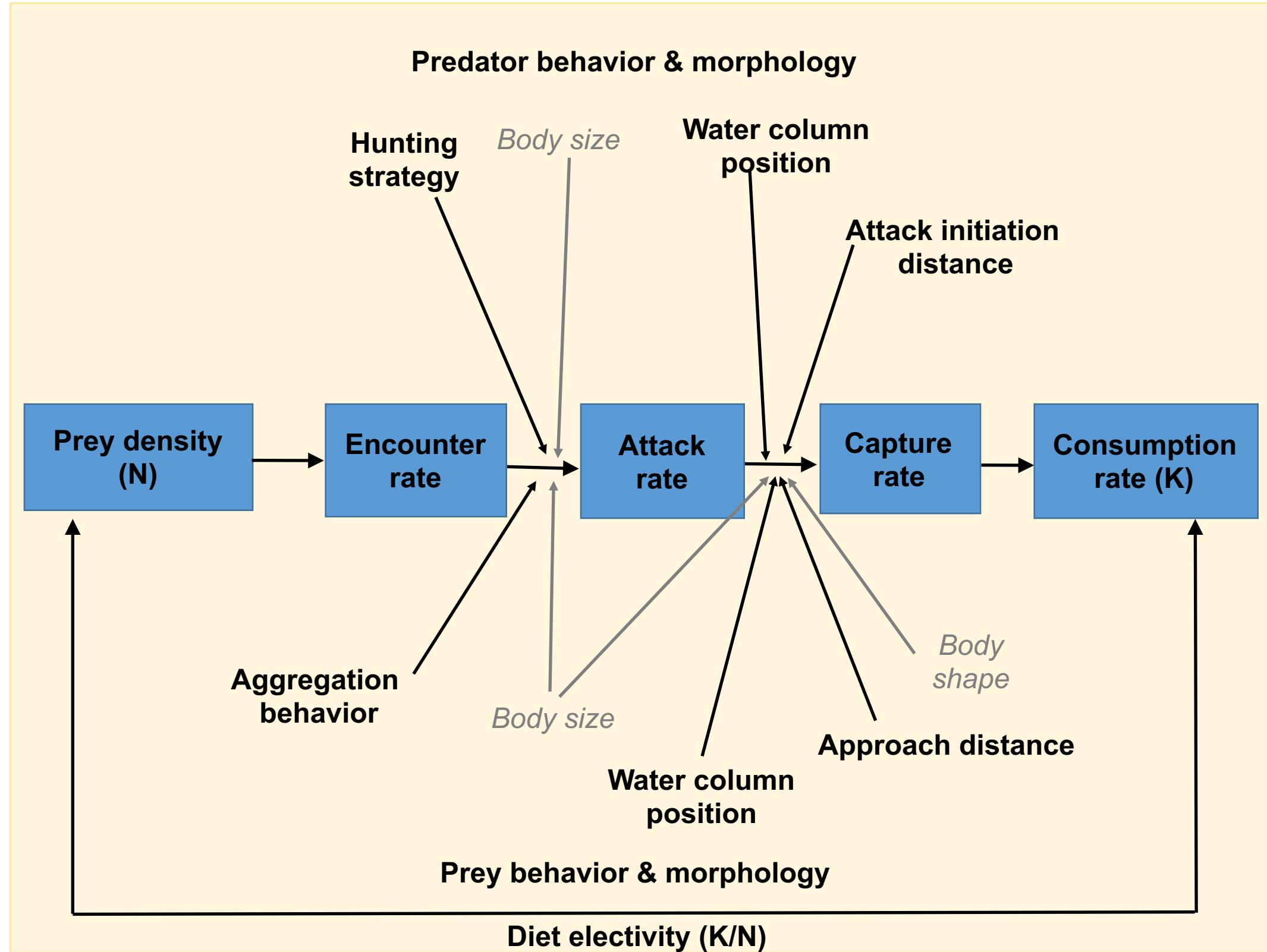

Fig 1. Predator and prey traits predicted to influence the probability of different rates in the predation process.
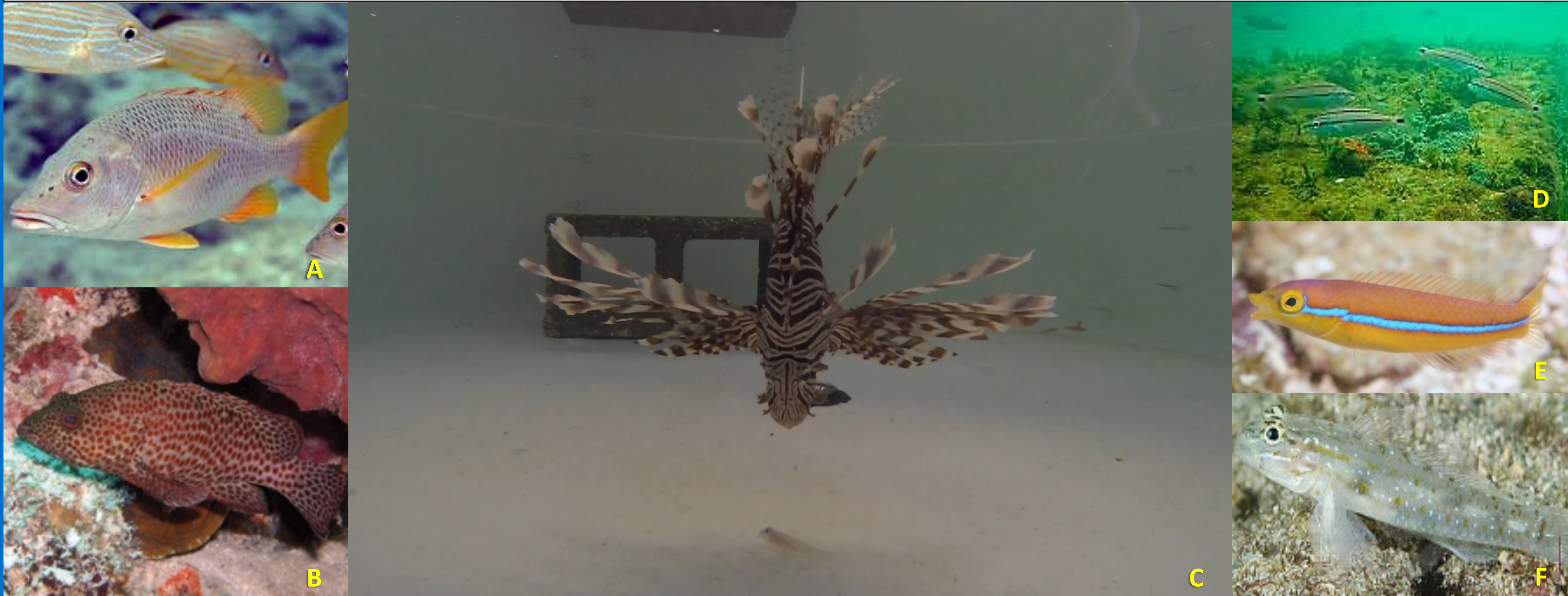
Study Species

Figure 2. Predators (A-C) and prey (D-F) study species. **A.** Roving native schoolmaster snapper (*Lutjanus apodus*). **B.** Ambushing native graysby grouper (*Cephalopholis cruentata*). **C.** Stalking invasive red lionfish (*Pterois volitans*) just before striking at a goby. **D.** Schooling midwater tomtate grunt (*Haemulon aurolineatum*). **E.** Shoaling demersal yellowhead wrasse (*Halichoeres garnoti*). **F.** Solitary benthic bridled goby (*Coryphopterus glaucofraenum*).

To determine how different combinations of predator hunting strategies and prey anti-predator behaviors affect the likelihood of predation events and prey selection, we conducted a lab study in the Bahamas. Three representative species each of predator (Fig. 2 A-C) and prey (Fig. 2 D-F) were studied. Predator hunting strategies included (A) roving snapper, (B) ambushing grouper, and (C) stalking lionfish. Prey behavior combinations included (D) schooling midwater grunt , (E) shoaling demersal (near seafloor) wrasse, and (F) solitary benthic (on seafloor) goby. Predators ranged from 20 to 30 cm TL (total length), and all prey were 3 to 5 cm TL.
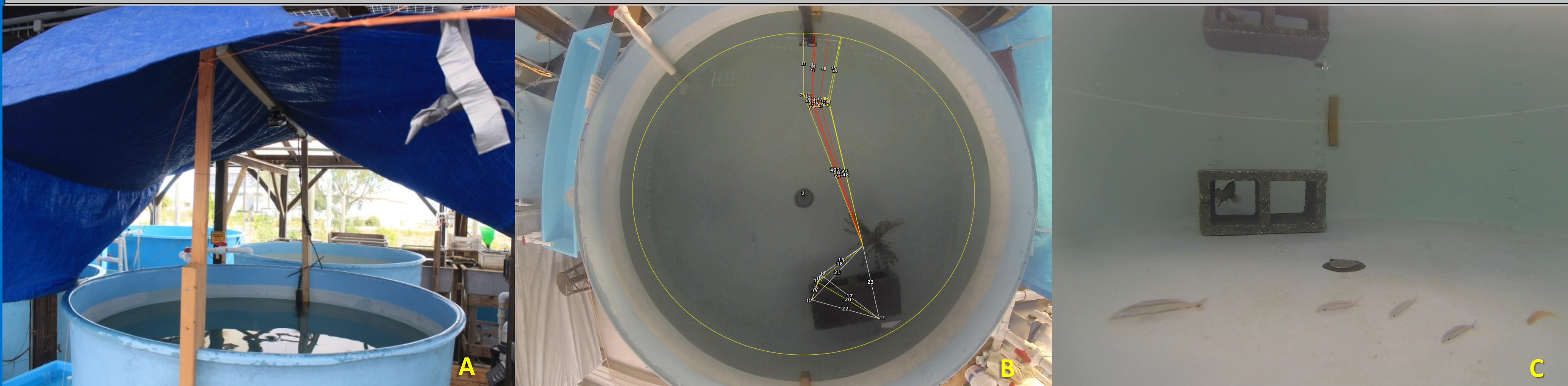
Methods

Figure 3. A. Side of mesocosm with GoPro camera rack and shading tarp. A blind shielded the mesocosm during each trial. **B.** Overhead camera image including lines drawn to measure distances between fish in *ImageJ* software. **C.** Underwater camera images used to help clarify water column position and orientation of predator and prey individuals.

Mesocosms
- We used 2-m diameter mesocosms with a water depth between 40 and 50 cm
- Mesocosms were fixed with a top-mounted camera rack, two GoPro cameras, and a cinderblock shelter for the predator (Fig. 3A-C).
- GoPro footage was captured from above the mesocosm (Fig. 3B) as well as underwater (Fig. 3C) providing a side-angle view for determining both vertical and horizontal position of fishes in the water column.
- An opaque central partition separated the predator and prey before the start of each trial.

Trials
- One predator was placed on side of the partition with the concrete block the night before each trial to acclimate to the mesocosm.
- Four prey of each species (12 fish total) were placed on side of the partition opposite the predator.
- Prey were given a 10-minute acclimation period before the trial began (with cameras recording).
- Partition was removed and each trial ran 4.5 hours (limit of GoPro memory).
- After each trial was complete, all prey fish remaining were counted and removed.
- Sunrise or sunset was included during each trial to capture the time of day when predatory fish are most active.

Video Data Collection
- We analyzed video frames at 15 and 0 seconds preceding each successful predatory strike.
- From each image, we measured the **distance between predator and prey** (to the nearest cm), **estimated aggregation tightness** as the average distance (in cm) between the prey that was consumed and its three nearest neighbors, and **estimated orientation of the prey relative to the predator** (categorized as either facing 'away' or 'toward' the predator)
- All images were evaluated using *ImageJ* (v 1.48) software.

Analysis and Results

Prey Selection
We calculated Ivlev's electivity index (E_i) for each prey type per predator as:

$$E_i = \frac{r_i - p_i}{r_i + p_i}$$

where r_i is the relative abundance of a prey item i in the diet of the predator, and p_i is the relative abundance of the same prey item in the environment. E_i ranges from +1 (selected above environmental abundance) to -1 (prey avoided; i.e consumed substantially less than predicted by their environmental abundance).

Ivlev's electivity index indicated that lionfish select gobies (solitary benthic prey) and grouper select wrasses (shoaling demersal prey), whereas snapper show little selectivity for any of the prey species (Figs. 4 & 5).
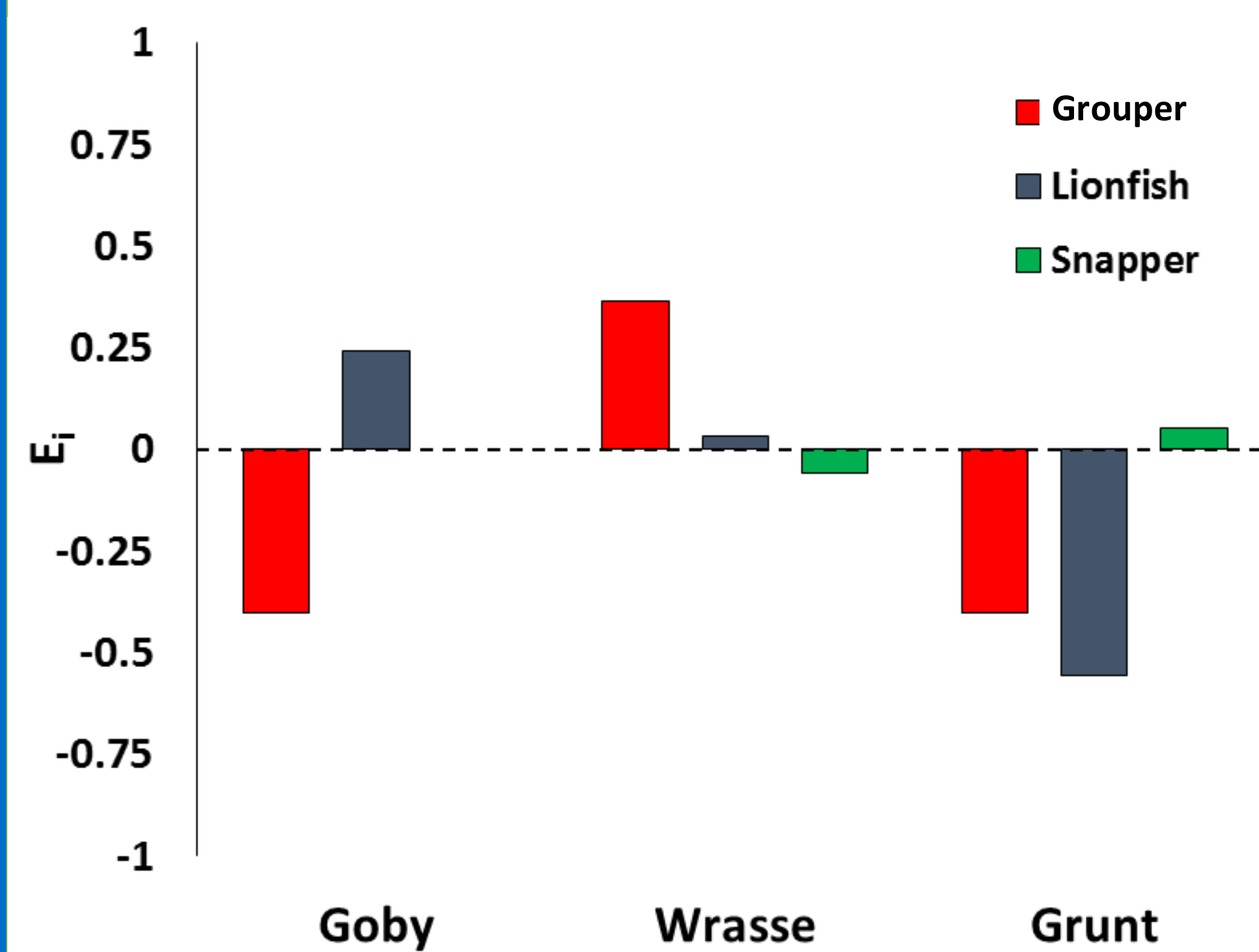
Predator (# individuals tested)	Prey (# predation events)	Number of trials (N_total = 40)
Grouper (4)	wrasse (10) grunt (2) goby (2)	14
Lionfish (4)	wrasse (15) grunt (4) goby (23)	16
Snapper (5)	wrasse (8) grunt (10) goby (9)	10

Figure 4. Prey selection (measured as Ivlev's electivity index [Ei]) of the three prey species by the three predator species. All prey species were present simultaneously and in equal abundance during mesocosm trials with a single individual of each predator species. Positive values (i.e. >0) indicate that prey were selectively consumed by a given predator type (bar color), while negative values (i.e. <0) indicate that the prey type was avoided.
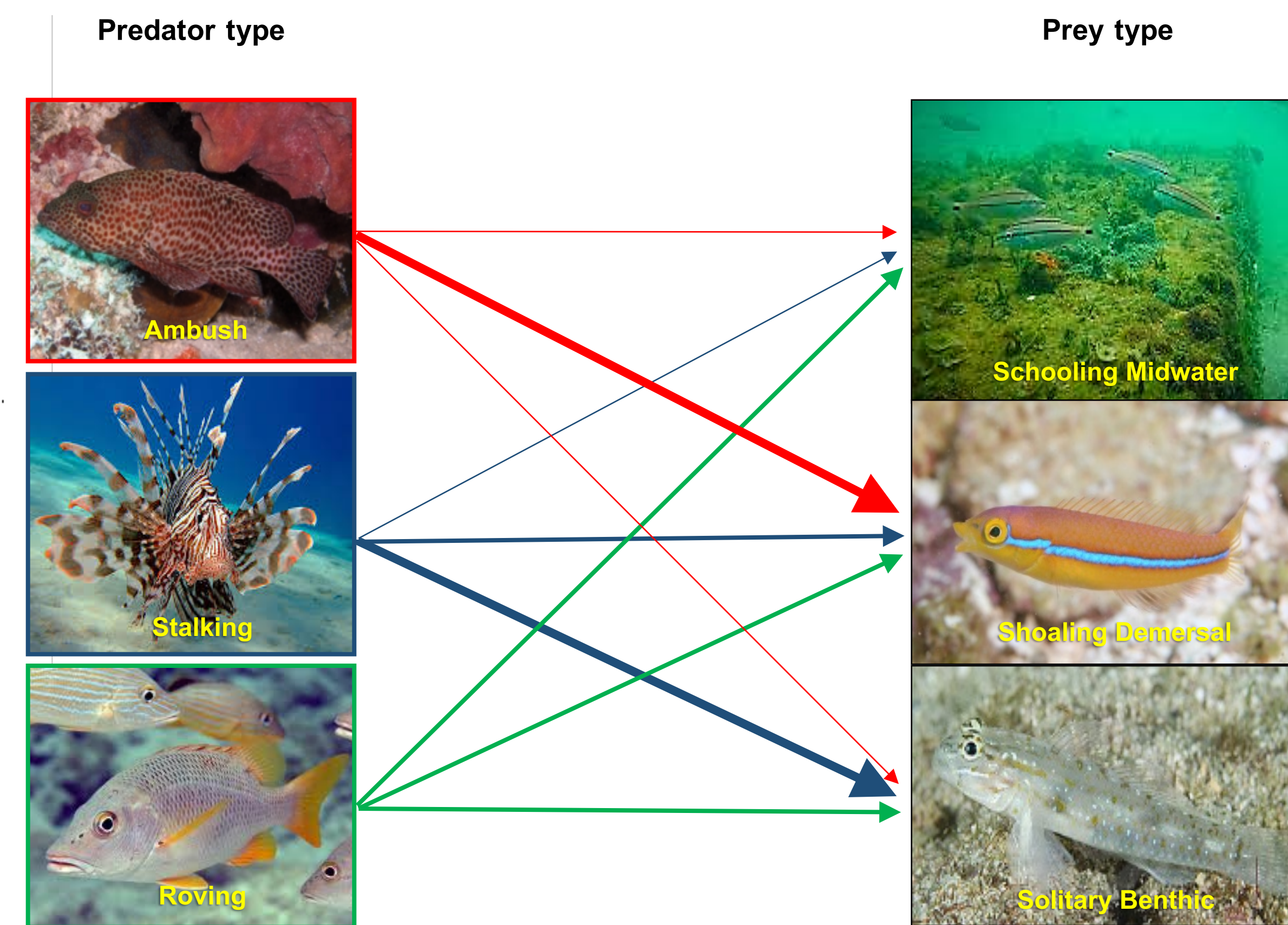

Figure 5. Prey selection for each predator-prey species pair. Predators are labelled based on their general hunting strategies while prey are categorized based on their general behavior and position relative to the seafloor. Arrow thickness represents the relative level of selectivity for each predator-prey pair based on Ivlev's electivity index [Ei].

Prey Behavior
For all three predators, consumption was more prevalent at low predator-prey distances, high prey dispersion, and high incidence of prey facing predators head-on (Fig. 6). Lionfish prey followed these trends for all three variables while grouper and snapper prey dispersion did not differ significantly between prey that were or were not eaten.
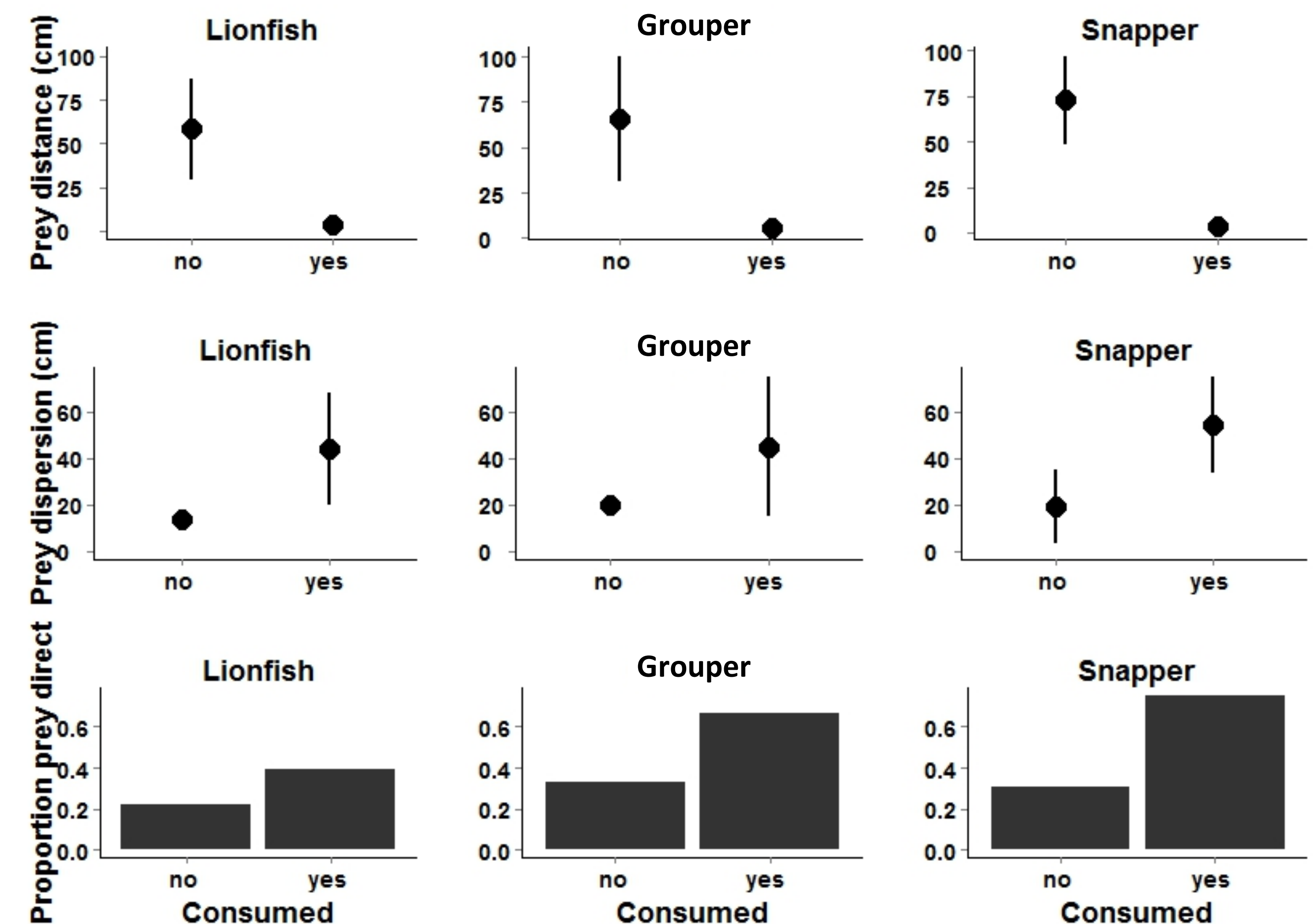

Figure 6. Three measured variables hypothesized to affect the likelihood of predation by the three predator species: average individual prey distance from predator (mean ± 95% CI), average individual prey distance to closest three prey individuals (prey dispersion; mean ± 95% CI) and proportion of prey with direct (head-on) orientation to the predator, all combined for all predation events. Results are by category such that the prey either was not eaten during the trial ("no") or was eaten ("yes").

Conclusions

Prey Selection
Lionfish stalk their prey in a way that is unique compared to native predators, which normally either ambush prey or rove into patches of prey. Given that this invasive predator differentially selects solitary benthic prey, such native species are likely to suffer disproportionate loss where lionfish are abundant. In fact, solitary benthic gobies are the most prevalent prey in lionfish stomach contents (Morris & Akins 2009 *Env. Biol. Fish.* 86:389-398), and show the greatest declines in abundance where lionfish are abundant (Albins 2015 *Mar. Ecol. Prog. Ser.* 522:231-243).

Prey Behavior
Invasive lionfish do not elicit anti-predatory behaviors from native prey that are any different from those behaviors in the presence of native predators. Similarities in the effect of aggregation tightness, distance to predator, and prey orientation between prey consumed by the three predators could be due in at least part to the constraints placed on interaction by conducting the study in a mesocosm environment (e.g. limited distance for predator avoidance). However, it may also be that position in the water column is one of the key factors that drives vulnerability to each of the hunting styles we analyzed. In future, we hope to assess a broader range of prey traits that are forecast to affect vulnerability to predation.

Acknowledgments