Coping with the lionfish invasion: Evidence that naïve, native predators can learn to help

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ABSTRACT

Invasive species often exacerbate global and local stresses on ecosystems, with animal invaders commonly experiencing a release from enemies, including predators. Release from predation helps explain the lionfish (*Pterois volitans/miles*) invasion of the western Atlantic, Caribbean and Gulf of Mexico, although the extent of biological control exerted by native predators is a topic of debate centered on the interpretation of spatial distributions of lionfish and those predators. In many places, control of lionfish numbers relies on people acting as predators via organized culls. In some cases, the resulting dead or injured lionfish are eaten by sharks and groupers, which may condition these naïve, native predators. This study complements existing field surveys by assessing the potential for predation on invasive lionfish at Little Cayman Island, BWI with tethering experiments. We tethered 132 live lionfish (52–220 mm total length) in three different habitats: seagrass beds, rarely culled reefs, and intensely culled reefs. Binary logistic regression indicated that, across all habitats and the size range tested, the potential for predation increased slightly (1.02×) but significantly with 1 mm increases in total length. In addition, lionfish tethered on intensely culled reefs were approximately 30× and 14× more likely to be taken by piscivores than fish tethered in seagrass or on rarely culled reefs. Overall, results suggested that native predators were capable of consuming healthy, tethered lionfish off Little Cayman Island and the naïveté of native predators was overcome by conditioning. Of course, conditioning designed to increase predation on lionfish, augment culling, and help control the invasion must be implemented without endangering people.

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1. Introduction

Invasive species often exacerbate problems caused by climate change, nutrient pollution, overfishing and other global and local anthropogenic stresses, with many negative outcomes impinging heavily on threatened and endangered species (Mack et al., 2000; Vitousek et al., 1997a). Once established, invasive species create direct, detrimental impacts via predation and competition for resources; indirect impacts by altering habitats and interactions among species; and disruptions of ecosystem structure and function by decreasing or homogenizing biodiversity (Mack et al., 2000; Pimental et al., 2001; Vitousek et al., 1997b).

All of these concerns apply to invasive, predatory, Indo-Pacific lionfish (*Pterois volitans* and *Pterois miles* or *Pterois* spp.). Since 1985, lionfish have spread up the Atlantic seaboard from Dania Beach, Florida, expanded throughout the Caribbean, colonized the northern Gulf

of Mexico, and reached densities of 400–650 fish ha^{-1} in multiple locations (Frazer et al., 2012; Green and Côté, 2009; Morris and Whitfield, 2009; Schofield, 2010). As voracious predators that consume up to 4% of their body weight per day in fish and invertebrates, lionfish potentially reduce numbers of native species and increase competition for food (Albins, 2013; Albins and Hixon, 2008, 2013; Côté and Maljković, 2010; Côté et al., 2013; Green et al., 2012; Morris and Akins, 2009; Morris and Whitfield, 2009). For example, lionfish on experimental patch reefs in the Bahamas reduced recruitment of native, reef fishes that serve as prey for important fishery species by ~80% (Albins and Hixon, 2008). Furthermore, lionfish occupy and feed in mangroves (Barbour et al., 2010) and seagrass beds (Claydon et al., 2012), which serve as important nurseries for juvenile reef fish (Nagelkerken et al., 2002). Through predation and competition, lionfish can reduce recruitment of species that support fisheries and further lower yields that are predicted to decrease 30–45% by 2015 due to degradation of Caribbean reefs (Burke and Maidens, 2004). In addition, predation on parrotfishes, surgeonfishes and damselfishes reduces grazing on algae that can overgrow corals (Lesser and Slattery, 2011). In combination, reduced biodiversity, increased overgrowth of corals by algae, and the possibility of envenomation from lionfish spines can compromise the attractiveness of popular dive destinations, which

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presently generate US$2.1 billion per year (Burke and Maidens, 2004; Morris and Whitfield, 2009). In many places, these deleterious effects will exacerbate detrimental changes from other stressors, including anthropogenic nutrient loads, overfishing, pollution, coral bleaching and disease, and climate change (Albins and Hixon, 2013; Côté et al., 2013; Frazer et al., 2012).

Lionfish possess a suite of characteristics that promote a successful invasion. They grow quickly; mature early; potentially reproduce often; release their eggs in a protective, gelatinous mass that may enhance fertilization and provide protection; feed voraciously on diverse prey using novel techniques that include blowing jets of water; and appear to have been released from mortality caused by disease, parasites or predators (Albins and Hixon, 2013; Albins and Lyons, 2012; Côté et al., 2013; Morris and Whitfield, 2009). The potential release from predation comprises the focus of our work.

Reduced predation would explain why lionfish are substantially more abundant in the invaded range (Cure et al., 2012; Darling et al., 2011; Kulbicki et al., 2012). For example, naïve predators approaching lionfish likely are deterred when their potential prey do not flee but rather display their dorsal and pectoral fins equipped with venomous spines (Côté et al., 2013; Morris and Whitfield, 2008). In fact, there have been no direct observations of predation on uninjured lionfish in either their native or invaded ranges, with such events being inferred from the presence of lionfish in the stomachs of potential predators (Bernadsky and Goulet, 1991; Maljković et al., 2008). Two peer-reviewed reports (Jud et al., 2011; Pimiento et al., 2013) and numerous anecdotal reports indicated that predators consumed dead or injured lionfish from organized culls, including culls conducted off Little Cayman Island (Frazer et al., 2012). The dearth of direct observations has not deterred scientists from inferring either the presence or absence of significant predation based on spatial patterns in abundance or biomass documented during field surveys comprising mensurative experiments (Bruno, 2013; Bruno et al., 2013; Hackerott et al., 2013; Mumby et al., 2011, 2013).

In combination, the absence of direct observations of predation on uninjured lionfish, the debate surrounding interpretation of field surveys, records of native predators eating dead or injured lionfish generated during culls, and evidence that fish learn to feed on novel prey (Warburton, 2003) led us to design and implement a manipulative, tethering experiment at Little Cayman Island. This experiment tested the hypotheses that i) native predators will consume healthy, tethered lionfish and ii) experience with consuming dead or injured lionfish will enhance the potential for predation, i.e., naïve predators will learn to feed on lionfish.

2. Materials and methods

Lionfish were hand-collected off Little Cayman Island in January–August 2013. On the day of deployment, each fish was anesthetized, measured (mm total length; TL), and fitted with 20 cm of monofilament line secured to its lower jaw. Fish were held for ≥2 h to ensure tethers were secure, transported to field sites, and attached to lead weights (13:00–15:00 h). The following morning (07:30–09:00 h), fish missing from cleanly broken tethers were recorded as predation events, and the remaining lionfish were euthanized. Controls for tethering effects comprised three fish tethered in tanks for 24 h and video surveillance of fish in the field.

From 9 to 15 lionfish were tethered at intensely culled fore reef sites where spearfishers had removed lionfish approximately monthly for 3 years (Frazer et al., 2012; n = 3), rarely culled fore reef sites (n = 3), and back reef seagrass sites with no record of culling (n = 4). At sites with *Thalassia testudinum*, lionfish were tethered at 3-m intervals along transects at ~1 m depth. At reef sites, lionfish were tethered 3–5 m apart on sand or hard bottom at depths of 4.5–9.0 m. Tethered fish could not access a refuge, and fish were not deployed when large piscivores were visible.

Data were analyzed with a one-way analysis of variance and three binary logistic regressions. The analysis of variance assessed differences in fish size among habitats. An initial binary logistic regression assessed total length as a covariate and temporal differences in potential for predation between trials at rarely culled reefs. Additional regressions tested for differences with total lengths and among habitats using either data from seagrass or rarely culled reefs as reference values. Pearson's, deviance and Hosmer–Lemeshow tests assessed goodness of fit for these regressions.

3. Results

In total, 132 lionfish were tethered to lead weights in the three habitats, and these fish were similar in size ($F_{2,129} = 0.80$, p = 0.451), with mean TLs $\pm$ standard deviations (SD) of 115.3 $\pm$ 34.9 mm in seagrass, 119.7 $\pm$ 34.8 mm on rarely culled reefs, and 126.6 $\pm$ 44.1 mm on intensely culled reefs. Tethering was not considered a potential cause of mortality because tethered lionfish survived for 24 h after being attached to weights in tanks. In addition, a total of 21 videos showed that lionfish did not exhibit signs of stress, with fish resting just above the substrate or swimming slowly within 5 min of being deployed. Videos also revealed that tethered lionfish assumed a typical head-down, fins displayed position (Côté et al., 2013) as their initial response to Nassau grouper (*Epinephelus striatus*) and nurse sharks (*Ginglymostoma cirratum*), with multiple encounters culminating in predation.

Logistics associated with capturing live specimens meant that trials were conducted in January, March, May, July and August 2013. An initial binary logistic regression indicated that the potential for predation varied significantly with the TL of lionfish (range = 52–220 mm), but the potential for predation was not significantly different between the January–May and July–August 2013 trials conducted at rarely culled reefs (Table 1, Fig. 1A). As the TLs of lionfish increased by 1 mm, they became 1.02× more likely to be consumed. The lack of a significant difference between the two trials at the rarely culled reefs led us to pool all data to examine variation in predation among the three habitats.

The remaining logistic regressions indicated significant variation with TLs and between the intensely culled reefs and the other two habitats (Table 1; Fig. 1B). Again, as the TLs of lionfish increased by 1 mm, they were 1.02× more likely to be consumed. The potential for predation was significantly higher on intensely culled reefs, with lionfish tethered at these reefs being 13.56× more likely to be consumed than fish tethered on a rarely culled reef and 29.88× more likely to be consumed than fish tethered in seagrass. The potential for predation differed less between rarely culled reefs and seagrass (p = 0.089, Table 1), but lionfish tethered on rarely culled reefs were 2.20× more likely to be taken. In combination, the relationships with lionfish size and frequency of culling led to a potential for predation ≥90% for lionfish ≥116 mm TL when tethered on intensely culled reefs (Fig. 1).

4. Discussion

Successful invasions by medium-sized predators, such as lionfish, are facilitated by naïve prey (prey naïveté), naïve top predators (enemy release hypothesis), and diversion of time and energy from avoiding predators into feeding and reproducing (evolution of increased competitive ability; Sih et al., 2010). In fact, lionfish appear to be successful competitors in their invaded range because their feeding and antipredator behaviors are unlike those of similar predators in the Caribbean (Albins, 2013; Albins and Hixon, 2013; Albins and Lyons, 2012; Côté et al., 2013; Green et al., 2012).

With respect to the enemy release hypothesis, estimates of potential for predation in the three habitats suggested that predation on lionfish by native piscivores can be increased by taking advantage of the behavioral plasticity displayed by native predators (Carlsson et al., 2009). The potential for predation documented at our intensely culled reefs