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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.

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 ± standard deviations (SD) of 115.3 ± 34.9 mm in seagrass, 119.7 ± 34.8 mm on rarely culled reefs, and 126.6 ± 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

Table 1
Results of logistic regressions predicting potential for predation on *Pterois* spp. Pred = predictor; Coef = coefficient; SE = standard error for coefficient; OR = odds ratio; 95% CL = 95% confidence limits for coefficient; L = lower confidence limit; U = upper confidence limit; G-o-F = goodness of fit tests; Con = constant; TL = total length (mm); T1 = January–May 2013; T2 = July–August 2013; In = intensely culled; Sg = seagrass; Ra = rarely culled; P = Pearson's test; D = deviance test; H–L = Hosmer–Lemeshow test.

Pred	Coef	SE	Z	p	OR	95% CL		G-o-F	χ^2	df	p
						L	U				
Con	−2.605	1.064	−2.45	0.014				P	56.00	54	0.400
TL	0.020	0.009	2.27	0.023	1.02	1.00	1.04	D	70.17	54	0.069
T1 v T2	−0.198	0.557	−0.36	0.722	0.82	0.28	2.44	H–L	9.97	8	0.267
Con	−3.350	0.864	−3.87	<0.001				P	117.49	114	0.392
TL	0.018	0.006	2.96	0.003	1.02	1.01	1.03	D	125.58	114	0.216
In v Sg	3.397	0.740	4.59	<0.001	29.88	7.01	127.32	H–L	4.88	8	0.770
Ra v Sg	0.790	0.465	1.70	0.089	2.20	0.89	5.48				
Con	−2.560	0.809	−3.16	0.002				P	117.49	114	0.392
TL	0.018	0.006	2.96	0.003	1.02	1.01	1.03	D	125.58	114	0.216
In v Ra	2.607	0.687	3.79	<0.001	13.56	3.52	52.17	H–L	4.88	8	0.770
Sg v Ra	−0.790	0.465	−1.70	0.089	0.45	0.18	1.13				

indicated that native predators conditioned to eat lionfish killed or injured during culls learned to hunt, capture and consume this novel prey without human intervention. Similar learning has been observed in other predator–prey systems, including laboratory training of small-spotted catsharks (*Scyliorhinus canicula*) that was retained without reinforcement for up to 3 weeks (Carlsson et al., 2009; Kimber et al., 2014; Santos et al., 2009; Warburton, 2003). Thus, results indicated that biological control exerted by native predators could augment culling as a tool to manage the lionfish invasion.

In our study, video surveillance documented nurse sharks (*G. cirratum*) and Nassau grouper (*E. striatus*) consuming healthy, tethered lionfish. Data on the distribution and abundance of these predators from Little Cayman Island helped explain the observed differences in potential for predation among seagrass beds, rarely culled reefs and intensely culled reefs.

The abundance and diversity of sharks in the waters surrounding the Cayman Islands were equal to or greater than records for other locations in the Caribbean region according to a recent study of sharks and cetaceans (Department of Environment Cayman Islands, 2012). Nurse sharks were common, and they were observed, tracked and caught in multiple habitats, including seagrass and reefs. Nurse sharks tended to spend less time in shallow seagrass than in deeper habitats, with similar results reported within Glover's Reef Marine Reserve in Belize (Chapman et al., 2005; Pikitch et al., 2005), the Florida Keys (Heithaus et al., 2007), and the United States Virgin Islands (DeAngelis et al., 2008). Thus, the distribution of nurse sharks helped explain a higher potential for predation at reef sites.

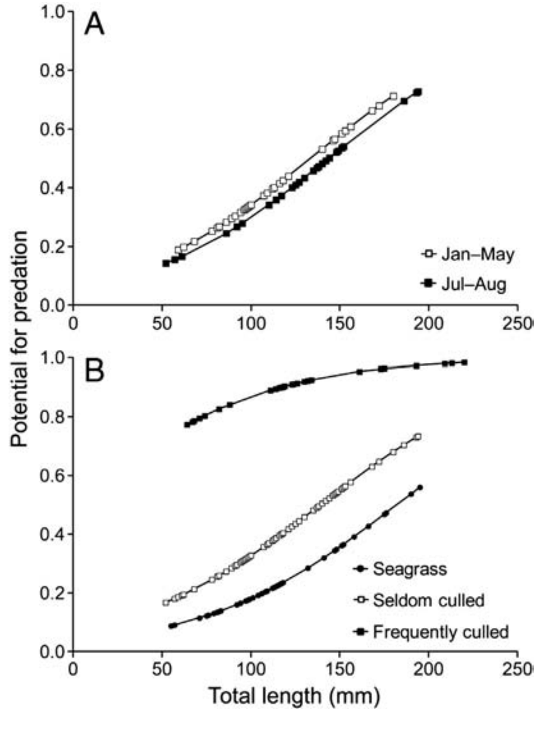

Fig. 1. Potential for predation versus total length for Pteropis spp. tethered A) on rarely culled reefs at two different times (Jan–May = January to May 2013; Jul–Aug = July to August 2013) and B) on intensely culled reefs, on rarely culled reefs and in seagrass.

Similarly, Nassau grouper occupied both seagrass and reef habitats off Little Cayman Island (Camp et al., 2013). Small Nassau grouper (mean TL ± SD = 184 ± 34 mm) predominately occupied off-reef seagrass habitats (Camp et al., 2013), with similar results reported for the Bahamas, Florida Keys, Puerto Rico, and Turks and Caicos Islands (Aguilar-Perera et al., 2006; Claydon and Kroetz, 2008; Claydon et al., 2009, 2011; Colin et al., 1997; Dahlgren and Eggleston, 2001; Eggleston, 1995; Eggleston et al., 1998, 2004; Grover et al., 1998; Sluka et al., 1999). Larger grouper (110 mm to >400 mm TL) were evenly distributed on reefs around the island ($F_{1,279} = 0.61$, $p = 0.437$; mean density ± standard error for leeward and windward reefs = 6.1 ± 2.1 grouper ha^{-1} and 6.4 ± 2.2 grouper ha^{-1}, respectively) according to data collected during Atlantic and Gulf Rapid Reef Assessments in 1999, 2006, 2007 and 2009. Given the tendency for Nassau grouper to eat prey that averaged 15% of their body size (Sadovy and Eklund, 1999), grouper in seagrass habitats would have been limited to preying on the smallest lionfish, which also helped explain a lower potential for predation in this habitat. The relatively consistent spatial distribution of larger grouper across all reefs suggested that variation in numbers of this predator did not cause a difference in potential for predation between intensely and rarely culled reefs.

Overall, available information suggested that the potential for predation should be greater on reefs than in seagrass, which it was. In addition, the abundances of nurse sharks and Nassau grouper on all reefs at Little Cayman Island pointed to conditioning as the cause of variation in potential for predation between intensely and rarely culled reefs.

The significant increase in potential for predation with increasing total length was relatively small. Nevertheless, the results indicated that native predators consumed lionfish spanning 168 mm TL. In fact, predation on smaller lionfish will complement repeated culls that tend to remove larger lionfish (de Leon et al., 2013; Frazer et al., 2012) and help overcome the resilience to culling predicted by models based on the best available estimates of key life history parameters (Barbour et al., 2011; Morris et al., 2011). A tethering experiment targeting larger lionfish may identify a size refuge from native predators.

We recognize the caveats associated with tethering experiments (Aronson and Heck, 1995; Aronson et al., 2001; Peterson and Black, 1994), but several lines of evidence suggest that our results yield value. Tethering generated minimal injury and did not release body fluids that would attract predators. As reported elsewhere (Aronson and Heck, 1995), the fact that fewer tethered lionfish were consumed at seagrass sites, where vertical structure was denser, indicated that entanglement was not a substantial bias. Videos showed that tethered fish behaved similarly to untethered lionfish by hovering near the substrate within minutes of deployment and employing a typical response to predators (Côté et al., 2013). Despite this latter behavior, videos documented predation by two different piscivores, nurse sharks and Nassau grouper, with predators not deterred by contact with the venomous spines. In addition, independent trials at rarely culled reefs yielded consistent and statistically equivalent results, which suggest that the potential for predation was stable through time.

5. Conclusion

Ecological aspects of the lionfish invasion continue to be elucidated by identifying patterns and discerning key processes likely to generate those patterns, which is typical of ecological investigations. This study provided an improved understanding of the process of predation by demonstrating that conditioning of native predators should be considered in efforts to characterize spatial patterns in the distributions of lionfish and likely predators. In fact, the results of tethering experiments indicated that conditioning of native piscivores will augment spatially restricted culling and potentially overcome the resilience to culling predicted for lionfish (Barbour et al., 2011; Morris et al., 2011). Even if the current geographic range and rapid population growth of lionfish make complete eradication untenable, increased predation would extend the effects of culling in space and through time, which would alleviate predation pressure on species that are vulnerable to extinction or critical to the health of coral reefs (Albins and Hixon, 2013; Côté et al., 2013; Frazer et al., 2012). Any attempt to condition native piscivores must be done in a way that minimizes threats to humans who share the environment with the predators being trained and invasive lionfish.

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References

Aguilar-Perera, A., Schärer, M., Nemeth, M., 2006. Occurrence of juvenile Nassau grouper, *Epinephelus striatus* (Teleostei: Serranidae), off Mona Island, Puerto Rico: considerations of recruitment potential. Caribb. J. Sci. 42, 264–267.

Albins, M.A., 2013. Effects of invasive red lionfish *Pterois volitans* versus a native predator on Bahamian coral-reef fish communities. Biol. Invasions 15, 29–43.

Albins, M.A., Hixon, M.A., 2008. Invasive Indo-Pacific lionfish *Pterois volitans* reduce recruitment of Atlantic coral-reef fishes. Mar. Ecol. Prog. Ser. 367, 233–238.

Albins, M.A., Hixon, M.A., 2013. Worst case scenario: potential long-term effects of invasive predatory lionfish (*Pterois volitans*) on Atlantic and Caribbean coral-reef communities. Environ. Biol. Fish 96, 1151–1157.

Albins, M.A., Lyons, P.J., 2012. Invasive red lionfish *Pterois volitans* blow directed jets of water at prey fish. Mar. Ecol. Prog. Ser. 448, 1–5.

Aronson, R.B., Heck Jr., K.L., 1995. Tethering experiments and hypothesis testing in ecology. Mar. Ecol. Prog. Ser. 121, 307–309.

Aronson, R.B., Heck Jr., K.L., Valentine, J.F., 2001. Measuring predation with tethering experiments. Mar. Ecol. Prog. Ser. 214, 311–312.

Barbour, A.B., Montgomery, M.L., Adamson, A.A., Díaz-Ferguson, E., Silliman, B.R., 2010. Mangrove use by the invasive lionfish *Pterois volitans*. Mar. Ecol. Prog. Ser. 401, 291–294.

Barbour, A.B., Allen, M.S., Frazer, T.K., Sherman, K.D., 2011. Evaluating the potential efficacy of invasive lionfish (*Pterois volitans*) removals. PLoS ONE 6, e19666.

Bernadsky, G., Goulet, D., 1991. A natural predator of the lionfish, *Pterois miles*. Copeia 1991, 230–231.

Bruno, J.F., 2013. A critique of Mumby et al. 2011 "Grouper as a natural biocontrol of invasive lionfish". PeerJ Preprints 1, e141v2.

Bruno, J.F., Valdivia, A., Hackerott, S., Cox, C.E., Green, S., Côté, I.M., 2013. Testing the grouper biocontrol hypothesis: a response to Mumby et al. 2013. PeerJ Preprints 1, e139v1.

Burke, L., Maidens, J., 2004. Reefs at risk in the Caribbean. World Resources Institute, Washington, D.C.

Camp, E.F., Lohr, K.E., Barry, S.C., Bush, P.G., Jacoby, C.A., Manfrino, C., 2013. Microhabitat associations of late juvenile Nassau grouper (*Epinephelus striatus*) off Little Cayman, BWI. Bull. Mar. Sci. 89, 571–581.

Carlsson, N.O.L., Sarnelle, O., Strayer, D.L., 2009. Native predators and exotic prey—an acquired taste? Front. Ecol. Environ. 7, 525–532.

Chapman, D.D., Pikitch, E.K., Babcock, E., Shivji, M.S., 2005. Marine reserve design and evaluation using automated acoustic telemetry: a case-study involving coral reef-associated sharks in the Mesoamerican Caribbean. Mar. Technol. Soc. J. 39, 42–55.

Claydon, J.A.B., Kroetz, A.M., 2008. The distribution of early juvenile groupers around South Caicos, Turks and Caicos Islands. Proc. Gulf Caribb. Fish. Inst. 60, 345–350.

Claydon, J.A.B., Calosso, M.C., Jacob, S.E., Wagner, C.W., Ryan, S.K., 2009. Juvenile habitat for Nassau grouper and spiny lobster is enhanced by discarded queen conch shells. Proc. Gulf Caribb. Fish. Inst. 63, 173–176.

Claydon, J.A.B., Calosso, M.C., Jacob, S.E., 2011. Large-scale deployment of discarded conch shells enhances juvenile habitat for spiny lobster, Nassau grouper and red hind. Proc. Gulf Caribb. Fish. Inst. 63, 457–461.

Claydon, J.A.B., Calosso, M.C., Traiger, S.B., 2012. Progression of invasive lionfish in seagrass, mangrove and reef habitats. Mar. Ecol. Prog. Ser. 448, 119–129.

Colin, P.L., Laroche, W.A., Brothers, E.B., 1997. Ingress and settlement in the Nassau grouper, *Epinephelus striatus* (Pisces: Serranidae), with relationship to spawning occurrence. Bull. Mar. Sci. 60, 656–667.

Côté, I.M., Maljković, A., 2010. Predation rates of Indo-Pacific lionfish on Bahamian coral reefs. Mar. Ecol. Prog. Ser. 404, 219–225.

Côté, I.M., Green, S.J., Hixon, M.A., 2013. Predatory fish invaders: insights from Indo-Pacific lionfish in the western Atlantic and Caribbean. Biol. Conserv. 164, 50–61.

Cure, K., Benkwitt, C.E., Kindinger, T.L., Pickering, E.A., Pusack, T.J., McIlwain, J.L., Hixon, M.A., 2012. Comparative behavior of red lionfish *Pterois volitans* on native Pacific versus invaded Atlantic coral reefs. Mar. Ecol. Prog. Ser. 467, 181–192.

Dahlgren, C.P., Eggleston, D.B., 2001. Spatio-temporal variability in abundance, size and microhabitat associations of early juvenile Nassau grouper *Epinephelus striatus* in an off-reef nursery system. Mar. Ecol. Prog. Ser. 217, 145–156.

Darling, E.S., Green, S.J., O'Leary, J.K., Côté, I.M., 2011. Indo-Pacific lionfish are larger and more abundant on invaded reefs: a comparison of Kenyan and Bahamian lionfish populations. Biol. Invasions 13, 2045–2051.

de Leon, R., Vane, K., Bertuol, P., Chamberland, V.C., Simal, F., Imms, E., Vermeij, M.J.A., 2013. Effectiveness of lionfish removal efforts in the southern Caribbean. Endanger. Species Res. 22, 175–182.

DeAngelis, B.M., McCandless, C.T., Kohler, N.E., Recksiek, C.W., Skomal, G.B., 2008. First characterization of shark nursery habitat in the United States Virgin Islands: evidence of habitat partitioning by two shark species. Mar. Ecol. Prog. Ser. 358, 257–271.

Department of Environment Cayman Islands, 2012. Public consultation. http://www.doe.ky/wp-content/uploads/2012/08/Shark_Research_Report_as_of_14_August_2012.pdf (accessed 22 February 2014).

Eggleston, D.B., 1995. Recruitment in Nassau grouper *Epinephelus striatus*: post-settlement abundance, microhabitat features, and ontogenetic habitat shifts. Mar. Ecol. Prog. Ser. 124, 9–22.

Eggleston, D.B., Grover, J.J., Lipcius, R.N., 1998. Ontogenetic diet shifts in Nassau grouper: trophic linkages and predatory impact. Bull. Mar. Sci. 63, 111–126.

Eggleston, D.B., Dahlgren, C.P., Johnson, E.G., 2004. Fish density, diversity, and size-structure within multiple back reef habitats of Key West National Wildlife Refuge. Bull. Mar. Sci. 75, 175–204.

Frazer, T.K., Jacoby, C.A., Edwards, M.A., Barry, S.C., Manfrino, C.M., 2012. Coping with the lionfish invasion: can targeted removals yield beneficial effects? Rev. Fish. Sci. 20, 185–191.

Green, S.J., Côté, I.M., 2009. Record densities of Indo-Pacific lionfish on Bahamian coral reefs. Coral Reefs 28, 107.

Green, S.J., Akins, J.L., Maljković, A., Côté, I.M., 2012. Invasive lionfish drive Atlantic coral reef fish declines. PLoS ONE 7, e32596.

Grover, J.J., Eggleston, D.B., Shenker, J.M., 1998. Transition from pelagic to demersal phase in early-juvenile Nassau grouper, *Epinephelus striatus*: pigmentation, squamation, and ontogeny of diet. Bull. Mar. Sci. 62, 97–113.

Hackerott, S., Valdivia, A., Green, S.J., Côté, I.M., Cox, C.E., Akins, L., Layman, C.A., Precht, W.F., Bruno, J.F., 2013. Native predators do not influence invasion success of Pacific lionfish on Caribbean reefs. PLoS ONE 8, e68259.

Heithaus, M.R., Burkholder, D., Hueter, R.E., Heithaus, L.I., Pratt, H.L., Carrier, J.C., 2007. Spatial and temporal variation in shark communities of the lower Florida Keys and evidence for historical population declines. Can. J. Fish. Aquat. Sci. 64, 1302–1313.

Jud, Z.R., Layman, C.A., Lee, J.A., Arrington, D.A., 2011. Recent invasion of a Florida (USA) estuarine system by lionfish *Pterois volitans/P. miles*. Aquat. Biol. 13, 21–26.

Kimber, J.A., Sims, D.W., Bellamy, P.H., Gill, A.B., 2014. Elasmobranch cognitive ability: using electroreceptive foraging behavior to demonstrate learning, habituation and memory in a benthic shark. Anim. Cogn. 17, 55–65.

Kulbicki, M., Beets, J., Chabanet, P., Cure, K., Darling, E., Floeter, S.R., Galzin, R., Green, A., Harmelin-Vivien, M., Hixon, M., Letourneur, Y., de Loma, T.L., McClanahan, T., McIlwain, J., MouTham, G., Myers, R., O'Leary, J.K., Planes, S., Vigliola, L., Wantiez, L., 2012. Distributions of Indo-Pacific lionfishes *Pterois* spp. in their native ranges: implications for the Atlantic invasion. Mar. Ecol. Prog. Ser. 446, 189–205.

Lesser, M.P., Slattery, M., 2011. Phase shift to algal dominated communities at mesophotic depths associated with lionfish (*Pterois volitans*) invasion on a Bahamian coral reef. Biol. Invasions 13, 1855–1868.

Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M., Bazzaz, F.A., 2000. Biotic invasions: causes, epidemiology, global consequences, and control. Ecol. Appl. 10, 689–710.

Maljković, A., Van Leeuwen, T.E., Cove, S.N., 2008. Predation on the invasive red lionfish, *Pterois volitans* (Pisces: Scorpaenidae), by native groupers in the Bahamas. Coral Reefs 27, 501.

Morris Jr., J.A., Akins, J.L., 2009. Feeding ecology of invasive lionfish (*Pterois volitans*) in the Bahamian archipelago. Environ. Biol. Fish 86, 389–398.

Morris Jr., J.A., Whitfield, P.E., 2009. Biology, ecology, control and management of the invasive Indo-Pacific lionfish: an updated integrated assessment. NOAA Tech. Memo. NOS NCCOS, p. 99.

Morris Jr., J.A., Shertzer, K.W., Rice, J.A., 2011. A stage-based matrix population model of invasive lionfish with implications for control. Biol. Invasions 13, 7–12.

Mumby, P.J., Harborne, A.R., Brumbaugh, D.R., 2011. Grouper as a natural biocontrol of invasive lionfish. PLoS ONE 6, e21510.

Mumby, P.J., Brumbaugh, D.R., Harborne, A.R., Roff, G., 2013. On the relationship between native grouper and invasive lionfish in the Caribbean. PeerJ Prepr. 1, e45v1.

Nagelkerken, I., Roberts, C.M., van der Velde, G., Dorenbosch, M., van Riel, M.C., Cocheret de la Morinière, E., Nienhuis, P.H., 2002. How important are mangroves and seagrass beds for coral-reef fish? The nursery hypothesis tested on an island scale. Mar. Ecol. Prog. Ser. 244, 299–305.

Peterson, C.H., Black, R., 1994. An experimentalist's challenge: when artifacts of intervention interact with treatments. Mar. Ecol. Prog. Ser. 111, 289–297.

Pikitch, E.K., Chapman, D.D., Babcock, E.A., Shivji, M.S., 2005. Habitat use and demographic population structure of elasmobranchs at a Caribbean atoll (Glover's Reef, Belize). Mar. Ecol. Prog. Ser. 302, 187–197.

Pimental, D., McNair, S., Janecka, J., Wrightman, J., Simmonds, C., O'Connell, C., Wong, E., Russell, L., Zern, J., Aquino, T., Tsomondo, T., 2001. Economic and environmental threats of alien plant, animal, and microbe invasions. Agric. Ecosyst. Environ. 84, 1–20.

Pimiento, C., Monaco, E., Barbour, A.B., Silliman, B.R., 2013. Predation on speared red lionfish, *Pterois volitans*, by spotted moray, *Gymnothorax moringa*. Fla. Sci. 76, 391–394.

Sadovy, Y., Eklund, A.-M., 1999. Synopsis of biological data on the Nassau grouper, *Epinephelus striatus* (Bloch, 1792), and the jewfish, *E. itajara* (Lichtenstein, 1822). NOAA Tech. Rept. NMFS, p. 146.

Santos, A.F.G.N., Santos, L.N., García-Berthou, E., Hayashi, C., 2009. Could native predators help to control invasive fishes? Microcosm experiments with the Neotropial characid, *Brycon orbignyanus*. Ecol. Freshw. Fish 18, 491–499.

Schofield, P., 2010. Update on geographic spread of invasive lionfishes (*Pterois volitans* [Linnaeus, 1758] and *P. miles* [Bennett, 1828]) in the Western North Atlantic Ocean, Caribbean Sea and Gulf of Mexico. Aquat. Invasions 5, S117–S122.

Sih, A., Bolnick, D.I., Luttbeg, B., Orrock, J.L., Peacor, S.D., Pintor, L.M., Preisser, E., Rehage, J. S., Vones, J.R., 2010. Predator–prey naïveté, antipredator behavior, and the ecology of predator invasions. Oikos 119, 610–621.

Sluka, R., Chiappone, M., Sullivan, K.M., De Garine-Wichatitsky, M., 1999. Benthic habitat characterization and space utilization by juvenile epinepheline groupers in the Exuma Cays Land and Sea Park, central Bahamas. Proc. Gulf Caribb. Fish. Inst. 45, 23–36.

Vitousek, P.M., D'Antonio, C.M., Loope, L.L., Rejmánek, M., Westbrooks, R., 1997a. Introduced species: a significant component of human-caused global change. N. Z. J. Ecol. 21, 1–16.

Vitousek, P.M., Mooney, H.A., Lubchenco, J., Milello, J.M., 1997b. Human domination of the Earth's ecosystems. Science 277, 494–499.

Warburton, K., 2003. Learning of foraging skills by fish. Fish Fish. 4, 203–215.