

PREDATION ON INVASIVE LIONFISH VARIES WITH THEIR SIZE, AMONG  
HABITATS, AND WITH CONDITIONING OF NATIVE PREDATORS

By

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To my dad, who inspired my love of the ocean and science

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Abstract of Thesis Presented to the Graduate School  
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Invasive species often exacerbate global and local stresses on ecosystems, with invaders commonly experiencing a release from enemies, including diseases and predators. Release from predation helps explain the lionfish (*Pterois volitans/miles*) invasion of the western Atlantic, Caribbean and Gulf of Mexico. However, the extent of biological control exerted by native predators is a topic of debate centered on interpretation of spatial distributions of lionfish and predators. In many places, control of lionfish relies on people acting as predators via 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 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 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.

## CHAPTER 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 (Vitousek et al. 1997a; Mack et al. 2000). Each year, invasive species ultimately generate hundreds of billions of dollars in global environmental and economic costs (Pimental et al. 2001). 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 (Vitousek et al. 1997b; Mack et al. 2000; Pimental et al. 2001).

All of these concerns apply to invasive, predatory, Indo-Pacific lionfish (*Pterois volitans* and *P. 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<sup>-1</sup> in multiple locations (Morris and Whitfield 2009; Schofield 2010; Green and Côté 2009; Frazer et al. 2012). 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 and Hixon 2008; Morris and Akins 2009; Morris and Whitfield 2009; Côté and Maljković 2010; Green et al. 2012; Albins 2013; Albins and Hixon 2013; Côté et al. 2013). 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 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 (Frazer et al. 2012; Albins and Hixon 2013; Côté et al. 2013).

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 (Morris and Whitfield 2009; Albins and Lyons 2012; Albins and Hixon 2013; Côté et al. 2013). The potential release from predation comprises the focus of this work.

Reduced predation would explain why lionfish are substantially more abundant in the invaded range (Darling et al. 2011; Cure et al. 2012; 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 (Morris and Whitfield 2009; Côté et al. 2013). In fact, there have been no reported 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 manuscripts (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 (Mumby et al. 2011; Hackerott et al. 2013; Mumby et al. 2013; Bruno 2013; Bruno et al. 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 likelihood of predation, i.e., naïve predators will learn to feed on lionfish.

## CHAPTER 2 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  $\geq 2$  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), missing fish and 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  $\sim 1$  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 independent 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.

## CHAPTER 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 a controlled laboratory environment. In addition, a total of 21 videos showed that lionfish in the field 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 spread 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 two, temporally independent trials at the rarely culled reefs (January–May and July–August 2013, Table 3-1, Figure 3-1A). As the TLs of lionfish increased by 1 mm, they became 1.02 $\times$  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 3-1; Figure 3-1B).

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 3-1), 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  $\geq 90\%$  for lionfish  $\geq 116$  mm TL when tethered on intensely culled reefs (Figure 3-1).

Table 3-1. Results of logistic regressions predicting potential for predation on *Pterois* spp.

Pred	Coef	SE	Z	p	OR	95% CL		G-o-F	$\chi^2$	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				

Note: 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.

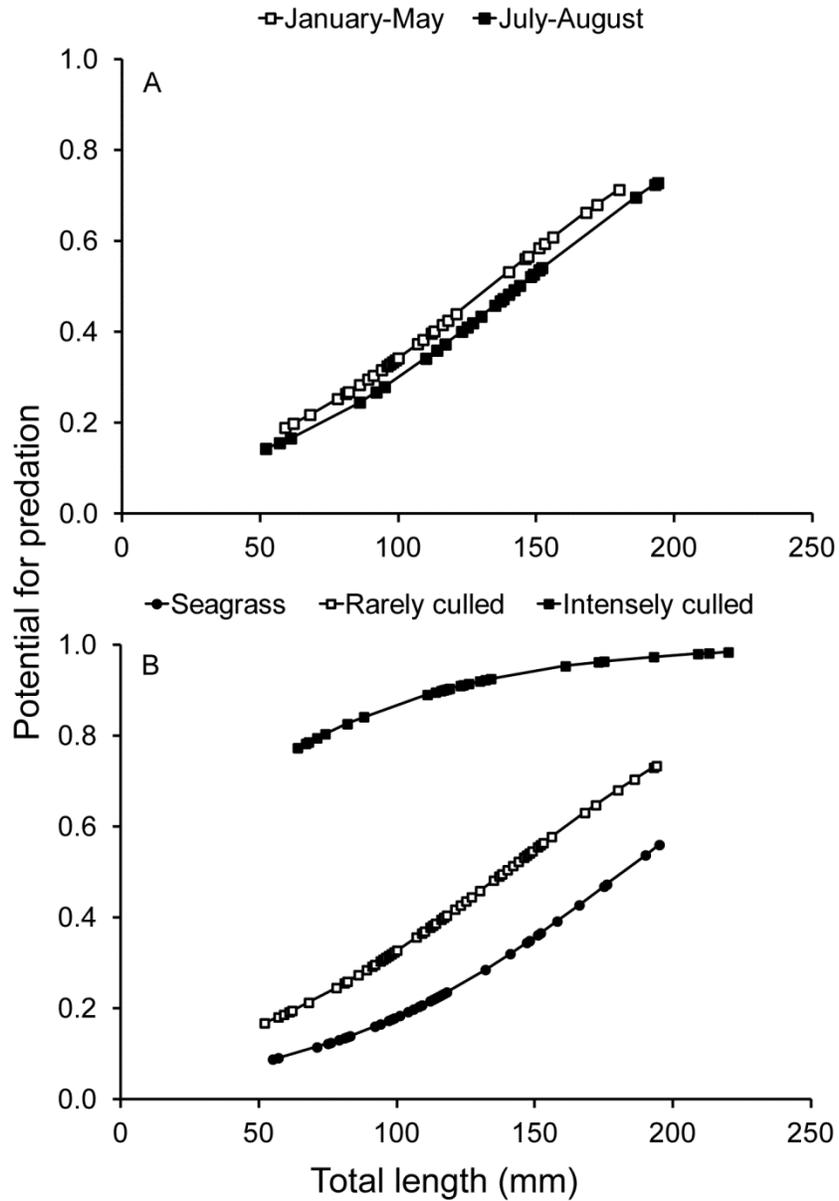


Figure 3-1. Potential for predation versus total length for *Pterois* spp. tethered A) on rarely culled reefs at two different times and B) on intensely culled reefs, on rarely culled reefs and in seagrass.

## CHAPTER 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 and Lyons 2012; Green et al. 2012; Albins 2013; Albins and Hixon 2013; Côté et al. 2013).

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 the intensely culled reefs 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 (Warburton 2003; Carlsson et al. 2009; Santos et al. 2009; Kimber et al. 2014). Thus, results indicated that biological control exerted by native predators could augment culling as a tool to manage the lionfish invasion.

The observed increase in potential for predation with lionfish body size could be explained, in part, by lionfish crypticity. Juvenile lionfish are light colored, and the smallest individuals are nearly transparent. They become darker and more conspicuous

as they age and grow (Allen and Eschmeyer 1973). If juvenile lionfish are indeed more cryptic, increasing predators' abilities to recognize this potential prey would be an important management intervention because culling tends to target larger lionfish (Frazer et al. 2012) and models have identified removal of juvenile lionfish as a way to increase the efficacy of this management technique (Barbour et al. 2011; Morris et al. 2011). Previous studies have shown that repeated exposure to novel prey items increases predator recognition efficiency (Ware, 1972; Colgan et al. 1986); therefore, conditioning native predators with juvenile lionfish could be a crucial addition to controlling lionfish populations. Furthermore, a tethering experiment targeting larger lionfish may identify a size refuge from native predators.

In this study, nurse sharks (*G. cirratum*) and Nassau grouper (*E. striatus*) definitely consumed healthy, tethered lionfish. Data on the abundance and distribution of these predators from Little Cayman Island provided explanations for increases in potential for predation from seagrass to rarely culled reefs to 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.

Similarly, Nassau grouper occupied both seagrass and reef habitats off Little Cayman Island (Camp et al. 2013). Small Nassau grouper (mean TL  $\pm$  SD = 184  $\pm$  34 mm) predominately occupied seagrass habitats (Camp et al. 2013), and data collected during Atlantic and Gulf Rapid Reef Assessments in 1999, 2006, 2007 and 2009 indicated that 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  $\pm$  standard error for leeward and windward reefs = 6.1  $\pm$  2.1 grouper ha<sup>-1</sup> and 6.4  $\pm$  2.2 grouper ha<sup>-1</sup>, respectively). Given the tendency for Nassau grouper to eat prey that average 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.

There are caveats associated with tethering experiments (Peterson and Black 1994; Aronson and Heck 1995; Aronson et al. 2001), but several lines of evidence suggest the results reported here 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 neither predator deterred by contact with the venomous spines. In addition, independent trials at rarely culled reefs yielded consistent and statistically equivalent results, which suggest the potential for predation was stable through time.

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 (Frazer et al. 2012; Albins and Hixon 2013; Côté et al. 2013; de Leon et al. 2013). 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.

## LIST OF REFERENCES

- 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.
- Allen G.R., Eschmeyer, W.N., 1973. Turkeyfishes at Eniwetok. *Pac. Discov.* 26, 3–11.
- Aronson, R.B., Heck, K.L. Jr., 1995. Tethering experiments and hypothesis testing in ecology. *Mar. Ecol. Prog. Ser.* 121, 307–309.
- Aronson, R.B., Heck, K.L. Jr., Valentine, J.F., 2001. Measuring predation with tethering experiments. *Mar. Ecol. Prog. Ser.* 214, 311–312.
- 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.
- 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.
- 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., Calosso, M.C., Traiger, S.B., 2012. Progression of invasive lionfish in seagrass, mangrove and reef habitats. *Mar. Ecol. Prog. Ser.* 448, 119–129.
- Colgan, P.W., Brown, J.A., Orsatti, S.D., 1986. Role of diet and experience in the development of feeding behavior in largemouth bass, *Micropterus salmoides*. *J. Fish Biol.* 28, 161-170.
- 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.
- Côté, I.M., Maljković A., 2010. Predation rates of Indo-Pacific lionfish on Bahamian coral reefs. *Mar. Ecol. Prog. Ser.* 404, 219–225.
- 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.
- 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.
- 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.
- 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. *Endang. Species Res.* 22, 175–182.
- 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](http://www.doe.ky/wp-content/uploads/2012/08/Shark_Research_Report_as_of_14_August_2012.pdf); accessed 22 February 2014.
- 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., Akins, J.L., Maljković, A., Côté, I.M., 2012. Invasive lionfish drive Atlantic coral reef fish declines. *PLoS ONE* 7, e32596.
- Green, S.J., Côté, I.M., 2009. Record densities of Indo-Pacific lionfish on Bahamian coral reefs. *Coral Reefs* 28, 107.
- 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., 2009. Predation on the invasive red lionfish, *Pterois volitans* (Pisces: Scorpaenidae), by native groupers in the Bahamas. *Coral Reefs* 27, 501.
- Morris, J.A. Jr., Akins, J.L., 2009. Feeding ecology of invasive lionfish (*Pterois volitans*) in the Bahamian archipelago. *Environ. Biol. Fish.* 86, 389–398.
- Morris, J.A. Jr., 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.

- Morris, J.A. Jr., Whitfield, P.E., 2009. Biology, ecology, control and management of the invasive Indo-Pacific lionfish: an updated integrated assessment. NOAA Tech. Memo. NOS NCCOS 99.
- 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 Preprints 1, e45v1.
- Mumby, P.J., Harborne, A.R., Brumbaugh, D.R., 2011. Grouper as a natural biocontrol of invasive lionfish. PLoS ONE 6, e21510.
- 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. Agr. 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 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 Neotropical 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.

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. *New Zeal. 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.

Ware, D.M., 1972. Predation by rainbow trout (*Salmo gairdner*) – Influence of hunger, prey density and prey size. *J. Fish. Res. Board Can.* 29, 1193-1201.

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Jessica received a Bachelor of Science in Biology from the University of Texas in 2008. She became interested in integrating human dimensions into natural sciences while working on the Deepwater Horizon Oil Spill in 2010, and was accepted into the University of Florida's School of Natural Resources and the Environment in the fall of 2011. While taking diverse coursework focusing on marine ecology, tropical conservation and development, communication skills, environmental education, and science education, she earned a graduate certificate in Environmental Education and Communication. In May of 2014 she received her Master of Science degree in Interdisciplinary Ecology.