



INTRODUCTION

Lionfish: a major marine invasion

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ABSTRACT: Indo-Pacific lionfish *Pterois volitans/miles* were likely introduced to Florida coastal waters via the aquarium trade and have spread rapidly along the southeastern coast of the United States and throughout the greater Caribbean region, including Bermuda and the Gulf of Mexico. This mesopredator has strong consumptive effects on native demersal fishes, especially on coral reefs but also including a variety of other nearshore habitats. The invader may also have substantial indirect effects on reef ecosystems by overconsuming ecologically important species. Given growing concern over what is likely the most damaging marine fish invasion to date globally, this Theme Section presents findings reported during a lionfish symposium at the Gulf and Caribbean Fisheries Institute annual conference convened in Panama City, Panama, in November 2015. New findings include mechanisms that enhance the success of the invader, the extremely broad and variable diet of invasive lionfish, the ecological effects of the invader on native fish populations in various environmental contexts, and non-consumptive interactions between invasive lionfish and native predators.

KEY WORDS: Lionfish · Invasion · Predation · Reef fishes

The invasion of tropical and subtropical Western Atlantic coastal ecosystems by Indo-Pacific lionfish *Pterois volitans/miles* (Fig. 1) first became apparent in the early 2000s when multiple individuals were documented off the coast of North Carolina (Whitfield et al. 2002). Lionfish were likely introduced through aquarium releases (Semmens et al. 2004), and not by Hurricane Andrew (www.sciencemag.org/news/2010/04/mystery-lionfish-dont-blame-hurricane-andrew). Their geographic spread has been rapid and broad: up the eastern seaboard of the United States as far north as Rhode Island (summer recruits dying back to Cape Hatteras during the winter), across to Bermuda, throughout the Bahamas and the greater Caribbean region to Brazil, and into the Gulf of Mexico (Schofield 2010). Invaded habitats

include coral reefs, other hard seafloors, seagrass beds, mangroves, river estuaries, and various artificial structures, and individuals have been sighted from manned submersibles as deep as 300 m (reviews by Morris 2012, Albins & Hixon 2013, Côté et al. 2013a). This unprecedented invasion has been facilitated by rapid growth rates of individual lionfish (Pusack et al. 2016), exponentially increasing local population sizes (Green et al. 2012, Albins & Hixon 2013), and resulting high densities (Green & Côté 2009, Kulbicki et al. 2012, Dahl & Patterson 2014), indicating that these largely piscivorous invaders are quickly converting native prey into lionfish biomass.

The success of lionfish has likely been enhanced by the lack of substantial biotic resistance by invaded communities. Native predators are apparently de-

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Fig. 1. Invasive red lionfish *Pterois volitans* in the Bahamas (photo by Rich Carey)

tered by the unusual shape, cryptic coloration, and venomous spines of lionfish, although there is debate regarding whether large native groupers are a major threat to the invader (Mumby et al. 2011, Hackerott et al. 2013, Valdivia et al. 2014, Bruno et al. doi: 10.7287/peerj.preprints.139v1, Mumby et al. doi: 10.7287/peerj.preprints.45v1). Few parasites attack invasive lionfish (Sikkel et al. 2014), native mesopredators appear to be ineffective competitors (Albins 2013), and even highly territorial damselfish do not chase them (Kindinger 2015). Additionally, lionfish use a variety of feeding behaviors, including ambushing and corralling prey (Morris & Akins 2009), as well as blowing jets of water at prey (Albins & Lyons 2012). Combined with cryptic coloration and unusual appearance, such flexible feeding behavior apparently allows high consumption rates of native prey (Albins & Hixon 2008, Côté & Maljković 2010, Green et al. 2011, Cure et al. 2012). To date, the only local controls of the invasion have been targeted fisheries and removals by divers, especially lionfish derbies (Barbour et al. 2011, Frazer et al. 2012, Morris 2012). In the absence of such local controls, lionfish eventually reach densities where they may become self-limiting (Benkwitt 2013).

Lionfish are rapidly depleting local abundances of native reef fishes, as shown by both controlled field experiments (Albins & Hixon 2008, Albins 2013, 2015, Green et al. 2014, Benkwitt 2015) and observational studies (Green et al. 2012, Benkwitt 2016a).

Lionfish diets comprise a broad variety of native fishes and invertebrates (Morris & Akins 2009, Muñoz et al. 2011, Valdez-Moreno et al. 2012, Côté et al. 2013b, Dahl & Patterson 2014), including not only small species but also the juveniles of larger species. Native prey consumed as juveniles include commercially and recreationally important groupers and snappers, as well as ecologically important grazers such as surgeonfishes and parrotfishes, which keep reef surfaces clean so that corals can flourish (review by Hixon 2015). Invasive lionfish also have non-consumptive effects, in that their mere presence inhibits grazing activity by these reef fishes (Kindinger & Albins 2016). The list of native species consumed by lionfish will undoubtedly continue to grow with additional diet studies from across the invaded region. However, studies of lionfish prey selection suggest that solitary, narrow-bodied fish that reside near the seafloor are most vulnerable (Green & Côté 2014). Importantly, extirpation of native fishes is evident (Albins 2015). Consequently, the lionfish invasion has been identified as one of the greatest emerging threats to global biodiversity (Sutherland et al. 2010).

Given this unprecedented invasion, a symposium on invasive lionfish (the 8th thus far) was hosted by the 68th Gulf and Caribbean Fisheries Institute annual conference in Panama City, Panama, on November 11, 2015, funded by the Florida Sea Grant Program, the Florida Fish and Wildlife Conservation

Commission, the National Oceanic and Atmospheric Administration, and the Reef Environmental Education Foundation. With over 80 submissions from across the invaded region, the symposium featured 24 talks and as many posters, presenting a broad range of information related to lionfish biology, the ecological and economic effects of the invasion, and efforts to manage the invasion. The 9 articles in this Theme Section reflect much of the diversity of topics covered during the symposium:

Several papers focus on the success of lionfish as invasive species. Stevens et al. (2016, this Theme Section [TS]) found that the skin bacteria of lionfish show antibacterial activity against known fish pathogens, indicating that resistance to disease may be added to the list of mechanisms that enhance the success of the invader. One established measure of success is that invasive lionfish are generalist mesopredators. Harms-Tuohy et al. (2016, this TS) used DNA metabarcoding to characterize the complete gut contents of lionfish in Puerto Rico, finding that the diets are even broader than detectable by traditional visual identification: 63 lionfish had consumed 39 native fish species representing 16 families. Eddy et al. (2016, this TS) further documented the broad diet of the invader. Lionfish in Bermuda, near the northern limit of the invasive range, consume more crustaceans and fewer fishes than further south.

Most papers examine the ecological effects of the invasion. Dahl et al. (2016, this TS) compared fish communities on artificial reefs in the northern Gulf of Mexico before and after the invasion, and conducted a field experiment comparing no versus single versus repeated removals of lionfish. Lionfish rapidly recolonized removal reefs. Although the experiment was confounded by possible effects of the Deepwater Horizon oil spill, there was a clear indication that smaller resident fishes were less abundant following the invasion. Working in Panama, Palmer et al. (2016, this TS) conducted a shorter-term lionfish removal experiment that also indicated a negative effect on the abundance of several native fishes, yet no effect on the genetic diversity of the bicolor damselfish *Stegastes partitus*.

A field experiment by Ingeman (2016, this TS) in the Bahamas demonstrated that invasive lionfish add substantial density-independent mortality of the native fairy basslet *Gramma loreto* to the density dependence caused by native predators, pushing some local populations toward extirpation. Aquarium experiments by Kindinger & Anderson (2016, this TS) showed that lionfish prefer fairy basslet over blackcap basslet *G. melacara*, whereas a native meso-

predator, graysby grouper *Cephalopholis cruentata*, prefers blackcaps. Thus, interactions among native prey, native predators, and invasive lionfish may have unforeseen indirect effects on community interactions. Benkwitt (2016b, this TS) documented movements and behaviors of lionfish on patch reefs in the Bahamas, showing that at higher densities, lionfish forage over surrounding seagrass meadows at night. These findings indicate that localized culling of lionfish may limit the area over which the invaders affect native fish populations.

The ecological effects of lionfish may be moderated by large native fishes having negative effects on the invader. Red grouper *Epinephelus morio* defend karst solution holes in Florida Bay. Ellis & Faletti (2016, this TS) experimentally demonstrated that, relative to holes where both predators were excluded, juvenile reef fish abundance was much higher where only grouper were present, much lower where only lionfish were present, and not different if both predators were present. This result indicates that grouper somehow inhibit piscivory by lionfish, which switch to invertebrate prey in the presence of the larger native predator.

In summary, the lionfish invasion is unprecedented and potentially catastrophic from multiple perspectives. Given that eradication is currently not possible with the tools and resources available, the possibility remains that this major marine fish invasion will permanently alter the ecology of coastal ecosystems of the greater Caribbean region and southeastern United States, especially coral-reef systems already degraded by various human activities (Albins & Hixon 2013).

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