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Short communication

Patterns of predation of native reef fish by invasive Indo-Pacific lionfish in the western Atlantic: Evidence of selectivity by a generalist predator



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HIGHLIGHTS

- Null simulations can identify patterns of selective predation by invasive predators.
- Lionfish feed broadly but some prey are eaten more or less than expected by chance.
- The taxon eaten most frequently by lionfish was very abundant in the environment.
- Some rare taxa were prey more often than expected and may be selected by lionfish.

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ABSTRACT

Among invasive species, introduced predators have some of the most dramatic impacts on native biodiversity, causing declines and extinctions. Selective predation by invasive predators may contribute to their effects on native taxa and taxa that are preyed upon out of proportion to their abundance may be at greatest risk of decline. In this study we aimed to document patterns of selective predation by a spreading invasive species, the Indo-Pacific lionfish (Pterois volitans/miles), with the goal of the identification of native taxa that may be subject to future decline. We took advantage of published data on invasive lionfish stomach contents and native reef fish abundances from a single region (hardbottom reef habitats of North Carolina) and applied a null simulation model to identify native fish taxa that were occurred as lionfish prey more or less frequently than would be expected based on their abundances. Using this method, we found that six of 28 native fish families were significantly under-represented in lionfish stomachs, suggesting that these taxa are avoided by lionfish or occur in different microhabitats. Twelve taxa appeared as prey items only as frequently as would be expected, given their abundance. We identified ten fish families that occurred as lionfish prey drastically and significantly more frequently than would be expected based on their abundance alone. These families include ecologically important species that play important functional roles and help maintain reefs (some parrotfish; Scaridae) and popular food and sport fish and some of the few native species to have been observed eating lionfish in the wild (some groupers; Serranidae). Preferred families were consumed at rates up to 90 times greater than would be expected based on natural abundance, suggesting the potential for local population declines as a result of lionfish predation. © 2016 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (http://creativecommons.org/licenses/by-nc-nd/4.0/).

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1. Introduction

Some of the most significant negative effects of invasive nonindigenous species on native biodiversity are the result of direct predation. Invasive predators have caused or are associated with significant extinction events on islands (Blackburn et al., 2004; Savidge, 1987), in freshwater aquatic systems (Witte and Goldschmidt, 1990), and on mainland habitats (Dorcas et al., 2012). Once invasive predators become established in new locations, the identification and understanding of their potential effects on native biodiversity is critical to the effective management of biodiversity (Byers et al., 2002).

For these reasons, significant effort has been applied to understanding the potential negative effects of the invasive Indo-Pacific lionfish (*Pterois volitans/miles*) within its introduced range. Indo-Pacific lionfish (hereafter, "lionfish") are generalist, broadly piscivorous fish that are established throughout the tropical and temperate western Atlantic Ocean, with areas of high density along the southeastern coast of the United States and in the Bahamas and Caribbean Sea (Whitfield et al., 2002). Despite the lionfish's relatively recent establishment in this region, declines of reef fish have been reported in the Bahamas (Green et al., 2012) and experimental evidence suggests that lionfish can cause severe and rapid local declines of reef fish (Albins and Hixon, 2008).

Lionfish are most often characterized as generalist predators that consume a broad range of native Atlantic fish species (Albins, 2012; Albins and Hixon, 2008; Green et al., 2012; Layman and Allgeier, 2012; Morris Jr and Akins, 2009; Muñoz et al., 2011). These assessments are largely based on the richness of taxonomic groups that have been identified as lionfish prey, which number in the dozens of species (Green et al., 2012; Muñoz et al., 2011). More detailed analyses have added important nuance to this characterization, however, providing evidence for some degree of specialization even within the broad diets of invasive lionfish. These studies suggest that despite their apparently opportunistic diet, lionfish may specialize on small prey fishes that are solitary, nocturnal, and bottom-dwelling (Green and Côté, 2014; Layman and Allgeier, 2012). The results of these studies indicate that more refined analyses of dietary breadth, specialization, and prey selectivity of lionfish may provide useful information for the management and conservation of native taxa within the invasive range of the lionfish. Such analyses could help predict the taxa most likely to suffer future declines owing to lionfish predation, a critical goal given the continued spread and probable permanence of lionfish populations in the western Atlantic.

We aim to further refine the understanding of dietary composition and selectivity of lionfish in the western Atlantic by applying a simple null model approach (Gotelli and Graves, 1996). In this approach we develop specific null hypotheses for how frequently lionfish would be expected to consume particular prey taxa, given the known abundance of those prey taxa in the natural environment. Our null hypotheses are based on the expectation that a true generalist (i.e., nonselective) predator would consume prey items in proportion to their abundance in the environment. This approach goes beyond quantifying the dietary breadth of lionfish, instead aiming to identify particular taxa that are consumed by lionfish more frequently than would be expected if lionfish were true generalists. Thus, by combining information on dietary breadth of lionfish with data on the diversity and abundance of potential prey in the environment, we focus on defining the degree to which lionfish are selective predators. Of particular importance is the identification of relatively rare native taxa that appear frequently as lionfish prey, which may provide early warning of potential impact to susceptible native taxa. Further, by identifying native taxa that are over-represented and under-represented in lionfish stomach contents, this approach can provide additional insight regarding traits that may be predictive of susceptibility to lionfish predation (Green and Côté, 2014).

2. Materials and methods

We used two recent published datasets from the continental shelf of Onslow Bay, North Carolina, USA to assess patterns of lionfish predation in this region. The first dataset documented native reef fish abundances. Trained observers (Whitfield et al., 2014) documented native fish community structure via visual SCUBA surveys conducted from 2006–2010. Surveys were conducted at depths up to 46 m and all visible reef fish were identified to species or lowest possible taxonomic unit. Fish in these surveys were divided into two categories based on size, \leq 10 cm total length (TL) (i.e., cryptic fish) and > 10 cm TL (i.e., conspicuous fish). Although individual lionfish can consume prey as large as 48% of their TL (Morris Jr and Akins, 2009) and therefore potentially as large as > 15, 10 cm is the approximate maximum length of lionfish prey items collected from lionfish in this region (Muñoz et al., 2011). For this reason we focus on reef fish diversity and abundance from the benthic cryptic fish (\leq 10 cm TL) surveys of Whitfield et al. (2014). Seventy-two cryptic fish surveys were conducted at 38 sites using underwater visual census band transect methods, with transect dimensions of 50 m \times 2 m. Based on these methods, the focus of the surveys on benthic habitat where lionfish occurred, and the fact that most lionfish prey are \leq 10 cm TL, we consider the large number of fish counted during these surveys (ca. 122,023 individuals) to be representative of the abundance distribution of potential prey items for lionfish in this region.

Our second dataset comes from a stomach contents analysis of 226 lionfish collected from 18 sites in 2004 and 2006 by Muñoz et al. (2011), also from Onslow Bay, North Carolina. Lionfish were captured via spearfishing and were placed in bags until they could be dissected for stomach contents at the surface. Lionfish stomachs were immediately removed from speared fish at the surface and preserved for later identification to the family level through microscopic examination and comparison to published taxonomic keys (Muñoz et al., 2011). From the 226 lionfish, 359 fish prey items were collected and identified, which we assume comprise a representative sample of lionfish diet breadth and prey choice in the study region. This assumption is validated by the nearly asymptotic species accumulation curve of Muñoz et al. (2011), suggesting that most prey consumed by lionfish were observed in the sample of 226 speared fish. Because stomach items could be reliably

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