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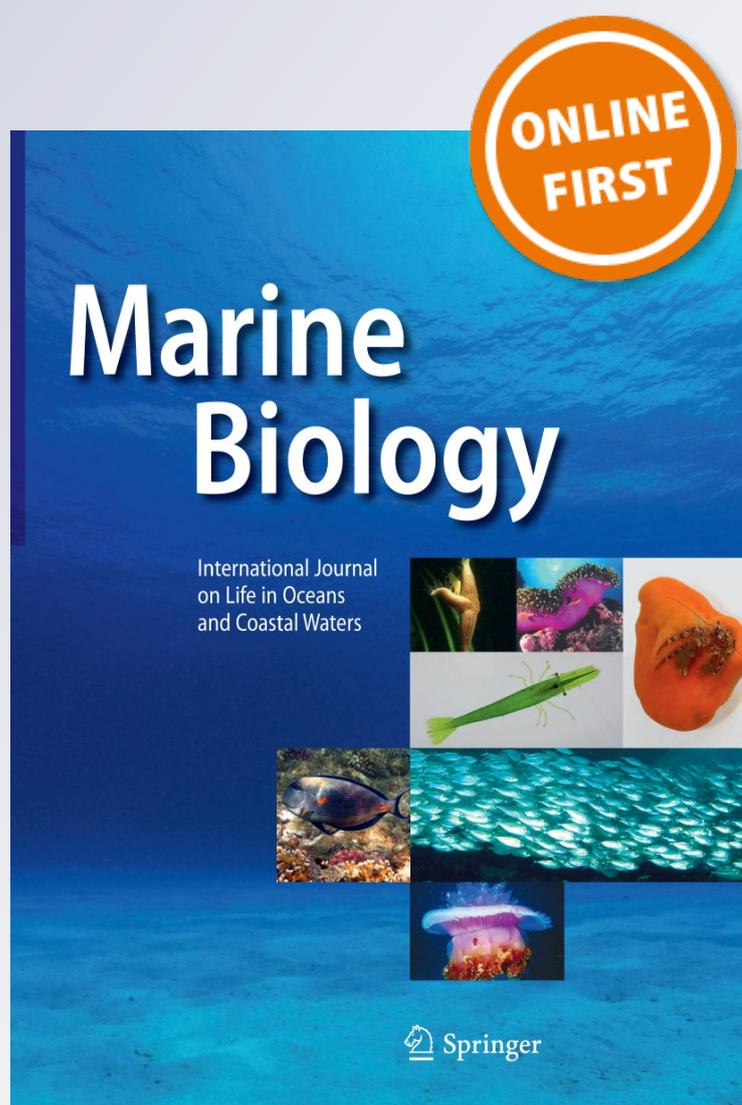
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# Lionfish alter benthic invertebrate assemblages in patch habitats of a subtropical estuary

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**Abstract** Invasive lionfish (primarily *Pterois volitans*) have spread throughout the Caribbean region, Gulf of Mexico, and the Southeast US coast, and resulting impacts on reef fish populations have been well documented. We examined whether lionfish can likewise affect benthic invertebrate communities, using an in situ caging experiment, in the Loxahatchee Estuary, Florida, USA. We found that lionfish caused significant declines in the three most abundant benthic invertebrate species, driving an overall shift in assemblage composition. For example, grass shrimp (Palaemonidae) abundance was reduced by nearly 90 % in the presence of lionfish. Species richness of benthic organisms was significantly higher when lionfish were present, suggesting potentially complex emergent effects of lionfish predation on benthic assemblages. Despite the fact that this experiment was conducted in just a single location using relatively small experimental units, we show altered benthic invertebrate communities could well be an additional outcome of the lionfish invasion.

## Introduction

The rapid invasion of the Western Atlantic and Caribbean by the Indo-Pacific lionfish *Pterois volitans* and *P. miles* (morphologically indistinguishable species, hereafter referred to as lionfish) is now widely documented (Albins and Hixon 2013; Côté et al. 2013), with some suggesting it may be one of the globe's most pressing environmental problems (Sutherland et al. 2010). The central concern revolves around potential lionfish impacts (through competitive or predatory interactions) on native fish communities. Average consumption rates of individual lionfish have been estimated as 1–2 prey fish per hour (Côté and Maljkovic 2010), with much higher rates sometimes observed (Albins and Hixon 2008), suggesting potentially strong functional control by lionfish on local prey fish populations. Field experiments provide evidence that declines in local prey fish abundance are indeed manifest (Albins and Hixon 2008), and that effects of lionfish on prey fishes may substantially exceed those of native predators (Albins 2013).

Additionally, lionfish, especially relatively small individuals, consume many small, mobile, invertebrates (Morris and Akins 2009). DNA barcoding will be a key tool to document the likely wide diversity of invertebrate prey consumed by lionfish, as partially digested invertebrate prey can be difficult to identify to genus or species using traditional stomach content analysis; for example, Valdez-Moreno et al. (2012) obtained 45 distinct crustacean prey DNA sequences in just 157 lionfish specimens from a coral reef site in Mexico. In a Florida estuary, 88 % of lionfish individuals sampled contained shrimp and 23 % crabs, as based on direct stomach content analysis (Jud et al. 2011). Predation on invertebrates may be especially common in areas where relatively small lionfish individuals

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predominate, such as estuaries (Jud and Layman 2012) or in shallow back reef habitats (Layman and Allgeier 2012).

No studies have examined whether lionfish predation can affect local abundance or composition of invertebrates. We conducted a field experiment to this end, demonstrating the potential for lionfish to influence benthic invertebrate communities in a subtropical estuarine ecosystem. These data provide another step toward understanding the pervasive impacts that lionfish may have in different ecosystems within the invaded range.

## Materials and methods

The Loxahatchee Estuary (26°57'N, 80°06'W) is located on the Southeast Atlantic coast of Florida, USA, draining a 620 km<sup>2</sup> watershed and connecting to the ocean through Jupiter Inlet. Upstream portions of the estuary are undeveloped, with extensive cypress (*Taxodium distichum*) swamps and mangrove (*Rhizophora mangle*)-lined shorelines. The lower 6.5 km of the estuary are highly urbanized with almost no natural shoreline remaining. Historical fringing mangroves have been replaced by residential lands, and contemporary shorelines are largely dominated by docks and bulkheads. Lionfish are now found throughout this lower 6.5 km section of the estuary, primarily associated with human-made structures such as docks and seawalls (Jud et al. 2011). Because lionfish under docks move very little (Jud and Layman 2012), our experiment was intended to examine potential impacts of lionfish on benthic communities in these habitat patches. We selected three docks along the estuary shoreline as experimental sites, located 2.4, 6.2, and 7.0 km up the estuary from the ocean. A prolonged rain event soon after initiation of the experiments resulted in lionfish mortality at the two upstream sites (Jud et al. In press), as such, we discuss only the downstream site hereafter.

Cylindrical cages (55 cm diameter, 45 cm tall; Fig. 1) were constructed out of plastic mesh (13 mm openings). The bottom and lower ~15 cm of the sides of each cage were lined with polyethylene mesh shade cloth. We added 20 l of limestone gravel (~20 mm diameter) to each cage, as well as one small brick, to provide habitat for small invertebrates and fishes. Fine rock and coral rubble are common substrates in inshore coastal areas of Florida, including under docks in the Loxahatchee Estuary; as such, our cages simulated a natural substrate that occurs in locations where lionfish are found in this estuarine system. Eight cage pairs were deployed under the dock, with each placed directly onto the estuary bottom. Individual cages were ~10–30 cm apart. Lionfish were collected from docks and other human-made structures along shorelines within 1.5 km of the experimental site (using hand nets), and then transported in a cooler filled with aerated estuarine water.



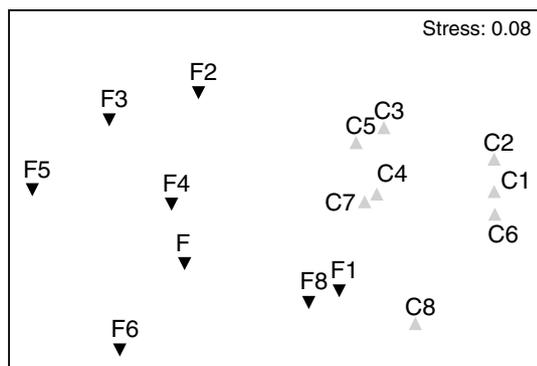
**Fig. 1** Cages were removed from the water at the end of the experiment using a plastic tray and benthic organisms immediately removed by hand

Mean standard length of the eight lionfish was 113 mm (SD  $\pm$  12; range 87–125). Lionfish were added to one cage in each of the eight pairs (through a small seam at the cage top, which was subsequently secured with cable ties); the other cage in each pair served as a control (i.e., no lionfish added). Because lionfish were added at the time of cage deployment, the experiment quantified effects that lionfish may have on colonization of newly created habitat patches, potentially leading to emergent differences in benthic community structure. Detailed salinity data over the experimental period (May 28–July 16, 2013) is provided in Jud et al. (in press), which ranged 7–37 ppt.

To collect benthic organisms contained in the cages at the culmination of the study, a plastic tray (64  $\times$  52  $\times$  10 cm; Fig. 1) was slid under the cage to provide support while lifting it into a boat. In the process, water drained through the polyethylene mesh shade cloth, trapping benthic invertebrates and demersal fishes within the cage. All organisms were removed by hand, placed on ice, and transported to the laboratory for identification and wet mass measurement. Lionfish (all eight survived the duration of the experiment) were euthanized using MS-222 in aerated estuarine water (400 mg/l), stomachs dissected, and stomach contents identified and enumerated.

## Results and discussion

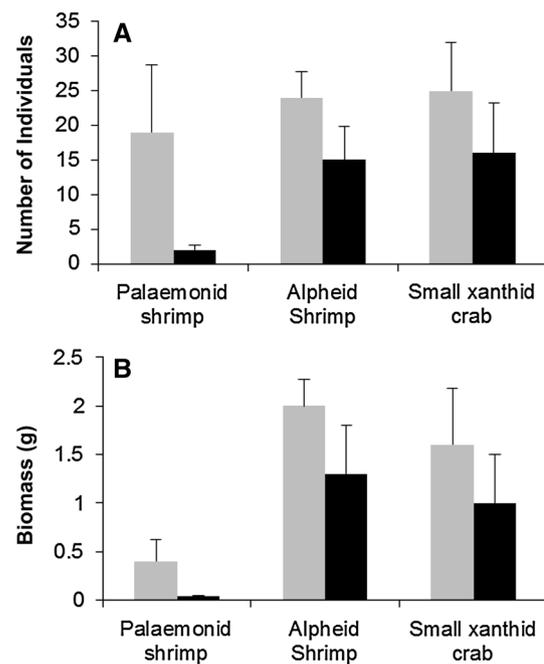
Twenty-three benthic taxa were identified in experimental cages, with numerical abundance dominated by three



**Fig. 2** Non-metric multidimensional scaling plot depicting relative similarity of benthic faunal communities in control (C) and lionfish (L) cages. Numbers associated with symbols depict cage pairs. Symbols closer in bi-plot space represent communities that have similar relative abundance of organisms

taxa (87 % of total numerical abundance): grass shrimp (Palaemonidae), snapping shrimp (Alpheidae), and small mud crabs (Xanthidae; xanthid crabs <9 mm carapace width were not identified to genus or species). Other species collected in cages included (in decreasing order of abundance): mud crabs (*Panopeus* spp.), mud shrimp (*Upogebia* spp.), snails (*Neritina* spp.), spider crabs (*Libinia* sp.), and green porcelain crabs (*Petrolisthes armatus*). Just 5 fish individuals were collected, including crested goby (*Lophogobius cyprinoides*), frillfin goby (*Bathygobius soporator*), and snake eel (Ophichthidae). There was a significant difference in benthic community composition between cages that contained lionfish and those that did not (ANOSIM Global R 0.69,  $p = 0.001$ ; Fig. 2). The difference was driven primarily by the three most common taxa, with abundance and biomass significantly higher in control cages (i.e., cages without lionfish) for each taxa ( $t$  test, all  $p < 0.001$ ; Fig. 3). Species richness was slightly higher in lionfish (mean  $\pm$  SD,  $7.9 \pm 1.5$ ) than control ( $6.6 \pm 1.4$ ) cages ( $t = 2.8$ ,  $p = 0.03$ ). Relatively rare prey that were found more frequently in lionfish cages included clinging crabs (*Mithrax* spp.), green porcelain crabs, spider crabs, mud shrimp, and snake eel.

At the end of the experiment, 7 of the 8 lionfish had identifiable prey items in their stomachs. In these lionfish, we identified 3 small mud crabs (carapace width:  $7.3 \pm 4.9$  mm) and 11 grass shrimp (length:  $8.1 \pm 2.1$  mm). In a previous study of lionfish diets in this estuarine system (Jud et al. 2011), 88 % of lionfish individuals sampled contained shrimp and 23 % crabs, suggesting that caged lionfish in the present study had similar diets to fish at liberty in the estuary. This is consistent with other studies that have shown lionfish have very plastic diets, and often feed on particular prey that are abundant in local habitat patches (Muñoz et al. 2011; Layman and Allgeier 2012).



**Fig. 3** Mean (error bars are SD) abundance and biomass of the three most common taxa in control (gray bars) and lionfish (black bars) cages at the end of the experiment. Abundance (a) and biomass (b) were significantly higher in the control (cages with no lionfish) for each taxa ( $t$  test, all  $p < 0.001$ )

These data are the first to suggest that lionfish may reduce local abundance of invertebrates, as has been previously documented for prey fishes (Albins and Hixon 2008; Green et al. 2012; Albins 2013). This finding is important for several reasons. First, in areas where small lionfish are abundant, impacts of lionfish may be greater on invertebrates than fishes because smaller lionfish tend to consume more invertebrate prey (Morris and Akins 2009). This may result in a high degree of competition with common native predators, such as snapper in the Loxahatchee River system, that also rely on crustaceans as prey (Yeager and Layman 2011; Yeager et al., in press). Also these data suggest that as prey fish populations become depleted in areas where larger lionfish are abundant (Green et al. 2012), subsequent impacts on invertebrates may occur as lionfish are forced to shift away from preferred fish prey. The slight increase in invertebrate species richness in lionfish cages suggest that impacts on benthic communities may be indirect and complex; for instance, the pattern of increased richness is consistent with the idea of a keystone predator controlling the abundance of a dominant competitor (Paine 1966).

At least four caveats are apparent in this study. Most importantly, individual lionfish were confined to a relatively small area, which may have resulted in disproportionate effects on fauna within cages (although lionfish do have relatively small activity ranges in this system, Jud and

Layman 2012). As such, we do not suggest using these data to infer actual per capita interaction strengths between lionfish and prey. Second, the small mesh (13 mm) may have precluded movement of some fishes into cages, prey that may have been preferred to the small invertebrates. But we note that frillfin goby and crested goby were abundant (typically >15 individuals) in cages at the other two experimental sites, suggesting that small fishes were simply not as common in the specific location that this experiment was carried out. Third, because of lionfish mortality at 2 of 3 sites due to heavy rainfall, we are just presenting data from a single location. Fourth, we were not able to quantify the proportion of the experimental effect that was due to direct predation pressure by lionfish versus potential behavioral avoidance of lionfish by prey (i.e., prey moving out of cages containing lionfish). Despite these limitations, our data suggest that lionfish impacts on other aspects of native communities (i.e., in addition to prey fishes) warrants more attention.

Particularly relative to their diversity and abundance, we know far less about the ecology of invertebrates than vertebrates in coastal ecosystems (Plaisance et al. 2011). Likewise, with the lionfish invasion, attention has been focused primarily on interactions between the invader and fish prey. But as lionfish establish themselves as permanent constituents of Western Atlantic food webs, we are likely to see more effects on communities and ecosystems than are currently acknowledged.

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