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Worst case scenario: Potential long-term effects of invasive predatory lionfish (*Pterois volitans*) on Atlantic and Caribbean coral-reef communities

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Abstract

The Pacific red lionfish has recently invaded Western Atlantic and Caribbean coral reefs, and may become one of the most ecologically harmful marine fish introductions to date. Lionfish possess a broad suite of traits that makes them particularly successful invaders and strong negative interactors with native fauna, including defensive venomous spines, cryptic form, color and behavior, habitat generality, high competitive ability, low parasite load, efficient predation, rapid growth, and high reproductive rates. With an eye on the future, we describe a possible "worst case scenario" in which the direct and indirect effects of lionfish could combine with the impacts of preexisting stressors -- especially overfishing -- and cause substantial deleterious changes in coral-reef communities. We also discuss management actions that could be taken to minimize these potential effects by, first, developing targeted lionfish fisheries and local removals, and second, enhancing native biotic resistance, particularly via marine reserves that could conserve and foster potential natural enemies of this invader. Ultimately, the lionfish invasion will be limited either by starvation -- the worst end to the worst case scenario -- or by some combination of native pathogens, parasites, predators, and competitors.

Keywords

Biological invasions, biotic resistance, coral-reef fishes, ecological release, invasive species

Introduction

Biological invasions are a major cause of ecosystem disruption and biodiversity loss, and are a major source of human-caused global change (Elton 1958; Vitousek et al. 1997; Mack et al. 2000). Invasive species are estimated to result in environmental and economic costs exceeding 120 billion dollars annually in the United States alone (Pimentel et al. 2005). While the majority of invasions have occurred in terrestrial and freshwater systems, marine invasions are increasing at an alarming rate and may have substantial impacts on the stability of ocean ecosystems and the multitude of goods and services they provide (Ruiz et al. 1997). However, until recently there have been no documented cases in which an introduced marine fish has become a major invasive threat. This situation has now changed with the invasion of Atlantic and Caribbean coral reefs by the Indo-Pacific red lionfish (*Pterois volitans*), an event that has recently been recognized as one of the world's top conservation issues (Sutherland et al. 2010).

Two species of Indo-Pacific lionfish (*Pterois volitans* and *P. miles*) were apparently introduced to Florida coastal waters during the mid 1980s (Morris and Whitfield 2009), and have become the first truly invasive marine fishes in the Atlantic. The most likely vectors for the introduction were releases or escapes from marine aquaria (Hare and Whitfield 2003; Semmens et al. 2004; Ruiz-Carus et al. 2006). Over the past two decades and especially since 2005, the range of *P. volitans* has expanded rapidly across a substantial portion of the tropical and sub-tropical Western Atlantic and Caribbean (Schofield 2009), with the highest densities currently reported from coral reefs in the Bahamas (Green and Côté 2009). *P. volitans* occurs throughout the invaded range, whereas sibling species *P. miles* appears to be restricted to the U.S. mainland (Freshwater et al. 2009). A recent detailed review of the lionfish invasion is provided by Morris and Whitfield (2009).

Here, we briefly examine the potential for lionfish to cause one of the most devastating marine invasions to date. We summarize possible long-term direct and indirect effects of the invasion based on current knowledge of coral-reef ecology, and discuss potential mitigation measures.

Consummate invader and strong negative interactor

Invasive lionfish exhibit high individual growth and reproductive rates, apparently spawning throughout the year and several times per month, with an estimated annual fecundity of over two-million eggs per female (Morris and Whitfield 2009). Consequently, population growth rates have been phenomenal in some invaded regions (Fig. 1). Lionfish at certain locations in the Bahamas have reached densities greater than 390 fish per hectare (Green and Côté 2009), far exceeding the highest densities reported from their native Pacific range of about 80 fish per ha (Schiel et al. 1986; Fishelson 1997; Kulbicki et al., submitted). Lionfish densities at sites along the eastern seaboard of the United States exceed those of all but one species of native grouper (Whitfield et al. 2007). Though mostly found on coral reefs, invasive lionfish are also somewhat generalized among warm shallow marine habitats, including seagrass beds (authors personal observation) and mangroves (Barbour et al. 2010), as well as artificial structures, such as shipwrecks (authors personal observation). In the Bahamas, they have been observed from submersibles at a depth of 300 m R. G. Gilmore, personal communication).

Growing rapidly (M. A. Albins, submitted) and measuring up to nearly 50 cm in total length (L. Akins, personal communication), invasive lionfish are both unique and effective predators of small fishes and crustaceans. They are unique predators in two ways. First, their slow movements, cryptic coloration, and elongated fin rays give them the appearance of a tuft of seaweed, a crinoid, or a tube-worm, perhaps a case of masquerade mimicry as well as camouflage (general reviews by Endler 1981; Skelhorn et al. 2010). Second, while stalking prey, lionfish flare their large, fan-like pectoral fins and slowly herd small fish, which are typically cornered then rapidly consumed. Atlantic prey fishes have not encountered such a predator in their evolutionary history, and native prey seem to take no evasive action. These patterns help to explain why invasive lionfish exhibit higher consumption rates than similarly sized native predators occupying the same habitats (M. A. Albins, submitted). Divers in the Bahamas have observed a single lionfish consume over 20 juvenile reef fish in just 30 minutes (Albins and Hixon 2008), and average consumption rates throughout the day are on the order of 1-2 prey per hour (Côté and Maljković 2010). Prey include a broad diversity of small reef fishes, as well as shrimps and other small mobile invertebrates (Morris and Akins 2009). Prey reef fishes include over 40 species from over 20 families, making lionfish a highly generalized predator of both small species and juveniles of large species.

As well as being efficient predators, invasive lionfish themselves appear to be largely impervious to predation, although available data are sparse and contradictory. Perhaps due to the slow movements and crypsis/mimicry of the invader, native predators seldom appear to recognize lionfish as potential prey (Morris 2009; authors personal observation). Lionfish are also defended by long venomous fin spines, such that, even when sharks or large grouper do attack, they almost always immediately retreat without obvious injury to the lionfish (authors personal observation). Nonetheless, there is a published report of fishermen in the Bahamas capturing one tiger grouper (*Mycteroperca tigris*) and two Nassau grouper (*Epinephelus striatus*), each with a lionfish in its stomach (Maljković et al. 2008). Additionally, divers in the Cayman Islands have trained wild Nassau grouper to consume lionfish, without the grouper showing ill effects (authors personal observation). However, one large Nassau grouper that ate a large lionfish tail first appeared to be literally stunned (authors personal observation). Additionally, large and clearly hungry Nassau grouper held in tanks will not eat small lionfish (M. Cook and W. Raymond, unpublished data). In controlled field experiments, Nassau grouper have no effect on the growth and survival of small lionfish (T. J. Pusack, unpublished data). Thus, it is presently uncertain whether or not large Atlantic grouper are effective predators of invasive lionfish.

Additionally, invasive lionfish appear to be effective competitors and resistant to parasitism. A field experiment in the Bahamas demonstrated that lionfish have 2.4 times the negative effect on native reef-fish populations as do ecologically similar native coney grouper (*Cephalopholis fulva*), and grow about 4 times as rapidly (M. A. Albins, submitted). Lionfish in the Bahamas are also infected by very low levels of endo- and ecto-parasites that commonly infect native fishes inhabiting the same reefs (Morris et al. 2009, Sikkel et al. in preparation), and parasite loads appear to be greater in their native Pacific habitats (Sikkel et al. in preparation). Lower parasite loads in invaded Atlantic habitats could translate to higher growth rates and greater fecundity.

Overall, it appears that a broad combination of traits make lionfish consummate invaders and particularly strong negative interactors with native fishes (review by Morris and Whitfield 2009). In contrast, lionfish are relatively rare throughout most of their native Pacific range (Kulbicki et al., submitted). While rarity alone does not necessarily indicate low ecological importance, and while conclusive data comparing the ecological impact of lionfish in their native range to that in the invaded range are not yet available, lionfish tentatively appear to play a relatively minor ecological role on Pacific coral reefs. This contrast indicates that, upon invading the relatively species-poor Atlantic from the relatively diverse Pacific, lionfish have undergone substantial "ecological release" from natural controls (sensu Elton 1958). In other words, Atlantic coral reefs thus far exhibit little "biotic resistance" to the lionfish invasion.

Worst case scenario: depauperate reef-fish communities and degraded coral reefs

To date there have been few studies of the ecological impacts of the lionfish invasion. Albins and Hixon (2008) compared the net recruitment of fishes to 10 coral patch reefs with lionfish vs. 10 reefs without lionfish in the Bahamas. Over 5 weeks during the height of the summer recruitment season, single lionfish reduced recruitment significantly, by an average of 79% relative to controls, including 23 of 38 species (14 families) that settled on both sets of reefs. A subsequent field experiment in the same location and season showed that, after two months, native coney grouper alone had reduced the abundance of small fish on the reefs by an average of 35%, whereas invasive lionfish alone had reduced prey fish by 90% (M. A. Albins, submitted). Such rates of reduction in fish abundances cannot be sustained (S. Green et al., submitted). Clearly, lionfish pose a potential threat to native reef fishes as both a predator and a competitor. Yet, given the scarcity of data, we can only speculate on the future.

Sampling over 1,000 lionfish stomachs from the Bahamas, Morris and Akins (2009) documented that the invaders consumed a broad variety of small reef fishes, especially gobies (Gobiidae), wrasses (Labridae), and basslets (Grammatidae). Other reef fishes affected by lionfish predation include important food species, such as groupers, snappers, and goatfishes (Albins and Hixon 2008; Morris and Akins 2009). If populations of preferred prey are depleted through time, then it is possible that lionfish will eventually concentrate on juveniles of these economically important fisheries species. In any case, the possibility that lionfish could substantially divert the biomass of small fishes otherwise destined to grow and feed higher trophic levels, including humans, is certainly conceivable. The Caribbean coral-reef aquarium fish trade would also likely suffer. Of the top 20 ornamental species collected from the Western Atlantic (Bruckner 2005), seven are members of the top ten families that comprise lionfish diets in the Bahamas (Morris and Akins 2009).

Indirect effects of lionfish predation may be even more severe, given that their prey include parrotfishes (Albins and Hixon 2008; Morris and Akins 2009). It is well-documented that overfishing parrotfishes and other herbivores contributes to the demise of reef corals by reducing the herbivory that normally helps to prevent seaweeds from outcompeting corals and/or interfering with coral recruitment (Mumby et al. 2006; Mumby and Steneck 2008). Lionfish can thus be viewed as potentially effective at "overfishing" juvenile parrotfishes and other small herbivorous fishes, with possibly devastating indirect effects on reef-building corals. This impact could be exacerbated in food webs that exhibit trophic cascades where top predators are already overfished (Stallings 2009). In such circumstances, top predators (such as large groupers) no longer reduce the abundance of native mesopredators (such as small groupers), thereby freeing the smaller predators to reduce the abundance of small herbivorous fishes (Stallings 2008). This phenomenon has been called “mesopredator release,” and in general is capable of destabilizing communities and causing local extinctions (Prugh et al. 2009). Given that lionfish may be naturally "released" mesopredators simply because they may be impervious to predation, they may also have free reign to reduce the abundance of herbivores, thereby indirectly negatively affecting reef corals by fostering seaweed growth. In this case, a combination of ecological release of an invasive mesopredator and release of native mesopredators due to overfishing could conspire to deal a substantial double blow to already threatened reef-building corals. More extreme fishing that targets all trophic levels yet ignores lionfish because of their venomous spines could eliminate release of native mesopredators, yet still trap native reef fishes between "the devil" of lionfish eating juveniles and "the deep blue sea" of humans overfishing adults.

These potential direct and indirect effects are illustrated in Figure 2, which shows greatly simplified interaction webs on undisturbed reefs vs. reefs with both human and lionfish impacts, typical of the Caribbean region. The left-hand web shows the normal trophic cascade that indirectly benefits corals. The right-hand web -- the worst case scenario -- shows how fishing can reduce the abundance of all larger fishes of all trophic levels. Such overfishing is now exacerbated by over-consumption of the juveniles of many of these same species by lionfish, further worsening the phase shift toward seaweeds replacing corals as the dominant benthos.

Besides possible indirect effects of invasive lionfish on corals and other benthos, the decline of other mid-sized predators via predation by or competition with lionfish, could destabilize populations of still other reef fishes. Such native predators, including mid-sized grouper, have been documented to be important sources of density-dependent mortality that may regulate local populations of reef fishes (review by Hixon and Jones 2005, see Hixon and Carr 1997 and Carr et al. 2002 for examples from the Bahamas).

Overall, one can imagine a worst case scenario in which most reef-fish biomass is converted to lionfish biomass, leaving invaded reefs depauperate of native fishes, except for those species that are not susceptible to (or perhaps indirectly benefit from) lionfish predation. Such survivors could include sharks and rays (whose new-born pups are too large to be eaten by lionfish), tunas and other transient predators (which do not visit reefs until reaching invulnerable sizes), puffers and relatives (which are morphologically and chemically defended), and scattered survivors of species that live and spawn in areas inaccessible to lionfish (perhaps reefs with strong prevailing currents). Unfortunately, sharks and other large predators are already overfished by humans in many regions (Stallings 2009), which produces a double jeopardy for reefs: (1) human-caused decline of species that may be naturally resistant to lionfish predation, and (2) human-caused decline of species that could possibly learn to consume and thereby control lionfish abundance. In the worst case scenario, the geographic range of invasive lionfish would eventually be limited only by water temperature and associated physiological constraints, with gradual expansion due to ocean warming. Their abundance would be controlled only by within-species competition as living space and/or food became limited, perhaps resulting in extensive cannibalism. Based on sea surface temperature constraints, Morris and Whitfield (2009) predicted the potential invasive range of adult lionfish as extending from Cape Hatteras, North Carolina, in the Northern Hemisphere, to the southern border of Brazil in the Southern Hemisphere. Combined with the accelerated demise of corals due to overfishing herbivores, coral bleaching, and local environmental degradation, the resulting reef ecosystems could become vastly different from even the present despoiled state of Atlantic reefs (Jackson 2010).

Avoiding the worst case scenario

Efforts to stem the lionfish invasion have thus far focused on local control via periodic collections by divers on specific reefs. Fortunately, slow swimming lionfish are usually easy to locate and capture by divers using hand nets (authors personal observation). Successful "lionfish derbies" have been held in the Bahamas and Florida that result in hundreds to thousands of fish being removed in a single day, typically followed by a lionfish cookout. Such efforts are promoted by the Reef Environmental Education Foundation (REEF, www.reef.org), the Bahamas Reef Environment Educational Foundation (BREEF, www.breef.org), and similar volunteer organizations. The Bahamas and other nations are encouraging lionfish fisheries, given that the venom of the fish spines denatures when cooked and that lionfish flesh is tasty, much like other scorpionfishes, although the fillets are small. Bounties would foster such fisheries. Some restaurants in the United States are offering invasive lionfish as a conservation dish, which could further encourage lionfish fisheries. If such fisheries are successful, it will be important to ensure that they are restricted to the Atlantic Ocean, given that lionfish are relatively rare in their native Pacific range (Kulbicki et al., submitted).

Unfortunately, there are far more reefs to patrol than there are divers in most areas, and in any case, invasive lionfish have been reported to several hundred meters depth, providing an effective deepwater refuge unless effective traps can be developed. Therefore, the ultimate hope is regional control via natural agents of biotic resistance. These agents are presently unknown, but may eventually include some combination of native pathogens, parasites, predators, and competitors. Although there is presently no evidence for Atlantic diseases or parasites attacking lionfish in any substantial way, it is certainly conceivable that native sharks, groupers, and other top predators will eventually learn to target lionfish (review by Csányi and Dóka 1993). Besides anecdotal information that Atlantic grouper occasionally eat lionfish (Maljković et al. 2008), there are scattered reports from the Pacific that cornetfish (Bernadsky and Goulet 1991) and other predatory fishes also attack lionfish. Such predation could be fostered by divers training such piscivores to consume lionfish at particular reefs.

Ultimately, fishing restrictions and marine reserves that protect species capable of controlling lionfish abundance may be the most effective management action to address the invasion. Marine reserves on coral reefs are well-documented to effectively protect predatory fishes and otherwise foster larger body sizes (Halpern 2003). While it is unknown whether native piscivores, even under the best circumstances, will be capable of reducing lionfish numbers sufficiently or quickly enough to mitigate their negative effects, preserving the integrity of native apex predator populations via fishing restrictions and marine reserves remains a precautionary and foresighted management approach to the lionfish invasion. In any case, the ongoing spread of invasive lionfish throughout the greater Caribbean region will eventually be controlled either by starvation of lionfish, which would be the most extreme ending of the worst case scenario, or by native species (competitors, predators, parasites, and/or pathogens) finally providing biotic resistance to the invasion. Only time will tell whether local and regional control efforts, or simply nature running its course, will limit the potentially disastrous invasion of Atlantic and Caribbean coral reefs by Pacific lionfish.

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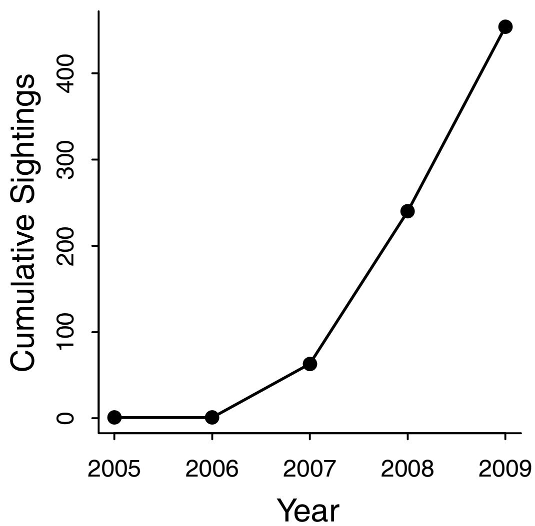
Figure Captions

Fig. 1. Cumulative number of lionfish sightings at 7 coral reefs annually surveyed by the authors and their colleagues in the vicinity of Lee Stocking Island, Bahamas, from 2005, when the first juvenile was observed, through 2009 (observations began in the early 1990s). New sightings were calculated as the number of fish observed at a site during a given survey year minus the number observed at that site during the previous survey year.

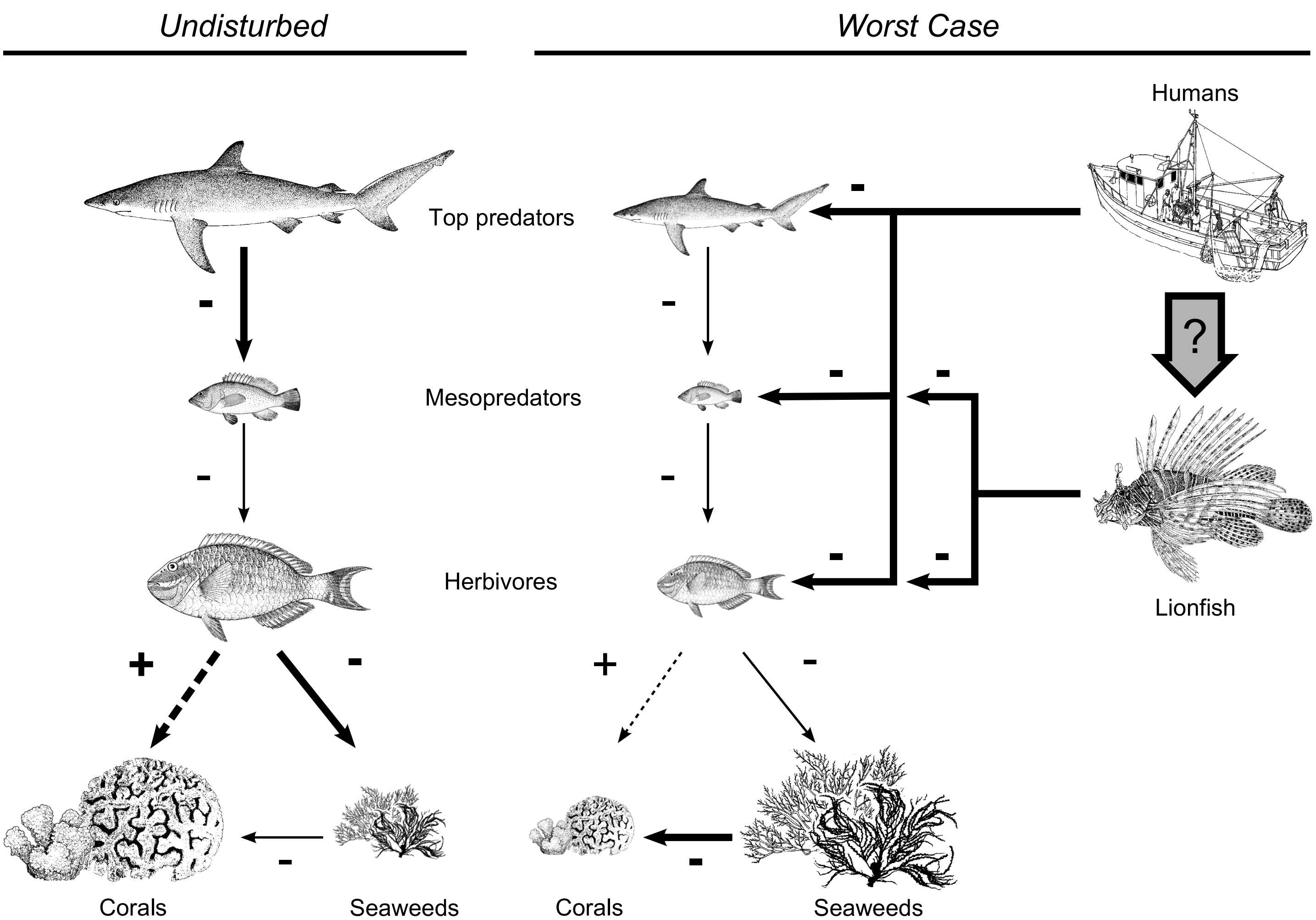
Fig. 2. Worst case scenario for future Atlantic and Caribbean coral-reef ecosystems caused by a combination of human overfishing of larger fishes of all trophic levels and invasive lionfish consuming small fishes and competing with other mesopredators (right), compared to an undisturbed system (left). The size of each kind of organism represents its relative abundance comparing the two interaction webs, and the thickness of each arrow represents the relative interaction strength between organisms. Solid arrows are direct effects representing predation (including fishing), except in two cases: competitive effects of (1) seaweeds on corals and (2) lionfish on other mesopredators and juveniles of some top predators (such as juveniles of large grouper species). The dashed arrow is the indirect positive effect of herbivores on reef-building corals. The unknown future effect of humans on lionfish is indicated by a question mark, and will be the focus of control efforts. Images courtesy of FAO.

FIGURE 1



Cumulative Sightings
0
100
200
300
400
2005
2006
2007
2008
2009
Year

FIGURE 2



Undisturbed
Worst Case
Humans
Top predators
Mesopredators
Herbivores
Lionfish
?
Corals
Seaweeds
Corals
Seaweeds