Invasive Lionfish Increase Density-independent Mortality and Cause Local Extinctions of Native Prey on Atlantic Coral Reefs

Invasiva Pez León Aumento Independiente de la Densidad Causa de la Mortalidad y la Unidad Extinciones Locales de Presa Nativa en Atlantic Arrecifes de Coral

Lionfish Envahissantes Augmenter la Mortalité, Indépendamment de la Densité et de Provoquer des Extinctions Locales de Proies Indigènes sur les Récifs Coralliens de l'Atlantique

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EXTENDED ABSTRACT

Invasive predators have caused some of the most severe impacts of species introductions (Salo et al. 2007, Jones et al. 2008) and have precipitated numerous extinctions via strong, direct, consumptive effects (Blackburn et al. 2004, Kumschick et al. 2015). These invasive predator-mediated extinctions necessarily imply a disruption of the mechanisms that had previously regulated native populations. One condition of regulation is a compensatory response in one or more demographic rates to changes in prey density, causing populations to increase when rare and to decrease when abundant (Murdoch 1994, Hixon et al. 2002). Therefore, predicting the impact of a novel predator requires an understanding of whether and how the invader alters existing compensatory mechanisms that underlie native population regulation; in particular how the invader affects a prey species' demographic response to changes in its own density.

The Indo-Pacific lionfish (*Pterois volitans*) is an invasive mesopredator that voraciously consumes native coral-reef fishes of the tropical Western Atlantic and Caribbean. The fairy basslet (*Gramma loreto*) is a common prey of lionfish, and pre-invasion research has demonstrated that basslet populations undergo regulating density-dependent mortality due to predation. To rigorously test the effects of an invasive predator on the density-dependent dynamics of prey, we conducted a controlled field experiment wherein both *G. loreto* settlement density and *P. volitans* presence were manipulated by divers on natural coral-reefs. Because the home ranges of adult *P. volitans* span multiple local populations of *G. loreto* prey, predator treatments where maintained at a larger scale (reef) than basslet density treatments (ledges within reef). One reef in each pair was assigned by randomization to receive periodic *P. volitans* removals. Within each reef, two *G. loreto* populations were chosen based on similarity in initial population size, ledge area, proximity to reef margin, and orientation to prevailing currents. One *G. loreto* population from each reef was then randomly chosen to receive artificially enhanced recruitment. Thus, natural variation in the densities of unmanipulated populations created a continuous density-gradient that was extended by diver-enhanced artificial recruitment. We repeatedly censused *G. loreto* populations over the 28-day experimental period and quantified lionfish-induced changes to the prey density-mortality relationship. To quantify the effect of *P. volitans* on both the magnitude of density-independent prey loss and the intensity and direction of density dependence in the response per capita loss, we employed linear mixed effects models (LMMs) with 'ledge' as a random effect; 'lionfish presence' and 'time-step' as categorical fixed effects; and 'prey density' as a continuous fixed effect.

Per capita loss was density-dependent on reefs with and without introduced *P. volitans*. That is, recruitment-enhanced populations experienced greater per capita loss compared to unmanipulated basslet populations on both native-only reefs (24.8% versus 6.5% loss) and on *P. volitans* reefs (60.0% versus 33.8% loss). However, the magnitude of this loss was significantly higher on reefs with the invader present, owing to a density-independent increase compared to native-only controls. High mortality rates at low prey density resulted in local extinction of approximately 15% of *G. loreto* populations, a phenomenon observed only on lionfish reefs. Further, nine out 14 prey populations exposed to the invader showed loss rates of greater than 50% compared with just three prey populations with such rates on native-only reefs.

Modeling cumulative per capita loss as a linear function of *G. loreto* density using LMMs, there was a significant effect of 'prey density' (LRT, $p = 0.039$), indicating the presence of density-dependence in per capita rates of prey loss (positive slope in Figure 1). However, we found no evidence to suggest that *P. volitans* altered either the direction or intensity of density dependence (LRT for the 'lionfish x prey density' interaction $p = 0.975$). By the final censuses *P. volitans* had significantly increased the magnitude of mortality but caused no change in the intensity of density dependence, indicating a density-independent increase in prey mortality on *P. volitans* reefs (Figure 1).

As *G. loreto* have previously been shown to undergo population regulation via density-dependent predation by native piscivores, this experiment provides strong evidence that this invasive predator destabilizes the compensatory dynamics that previously bounded prey populations above zero by increasing the magnitude of density-independent mortality without altering the intensity of density dependence. There are several possibilities that may underlie the observation that *P. volitans* remain effective predators at low prey density. First, while native piscivores have shown to cause density-

dependent mortality through an aggregative effect, spatially congregating and increasing attack rates in the vicinity of high prey densities (reviewed by White et al. 2010), there is thus far no evidence that *P. volitans* do the same, continuing to hunt even as prey densities decline and native predators move on to richer patches where foraging is more efficient. Alternatively, *P. volitans* may be less likely than other generalist native piscivores to employ prey switching at low densities of the target species. In either case, per capita predation rates caused by natives would fall with decreasing prey density but *P. volitans* predation rates would remain high. These mechanisms assume that *P. volitans* have a lower threshold of prey density below which foraging becomes inefficient compared with native piscivores, a distinct possibility for a novel predator with no behavioral or morphological analogue in the Western Atlantic (Albins and Lyons 2012).

While we observed increased mortality rates and the local extinction of native prey populations, it is unlikely that *G. loreto* is at high risk of global extinction as a result of this predator introduction; this common species is buffered from the risk of global extinction by high-fecundity, large range size and fairly broad habitat tolerances (Böhlke and Chaplin 1994). Of greater conservation concern are rare species, those with demographically isolated populations, and species whose range is complete encompassed by the *P. volitans* invaded range. As this study demonstrates, such native populations are no longer protected from high predator consumption rates by low local prey densities, a result that mangers should consider when designing and evaluating conservation and mitigation efforts throughout the invaded range.
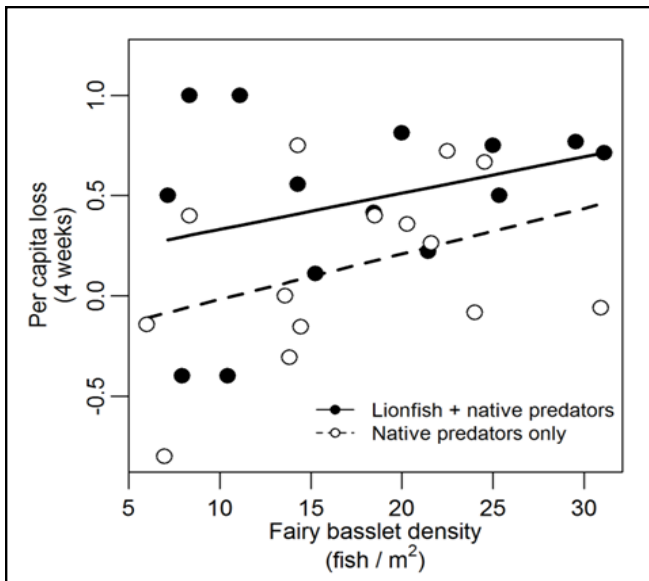
Figure 1. Per capita loss of fairy basslet on native predator only reefs and reefs with *P. volitans*. After accounting for the effect of prey densities, per capita loss was higher in the presence of *P. volitans* yet the slopes of the pre-invasion and post-invasion curves were not statistically different, suggesting that *P. volitans* presence not altered the intensity of density-dependence but has increased density-independent mortality.

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