Lionfish cause increased mortality rates and drive local extirpation of native prey

Kurt E. Ingeman*

Department of Integrative Biology, Oregon State University, 3029 Cordley Hall, Corvallis, OR 97331, USA

ABSTRACT: As predators play a central role in prey population regulation, predicting the impact of a novel predator requires determining how the invader affects the compensatory dynamics that underlie native prey persistence. The Indo-Pacific lionfish *Pterois volitans* is an invasive meso-predator 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 unequivocally measure lionfish effects on prey mortality and to test whether prey survival remained density-dependent when exposed to predation by the invader, a controlled field experiment was conducted wherein both fairy basslet settlement density and lionfish presence were manipulated by divers on natural coral reefs. On reefs with and without lionfish, fairy basslet populations were repeatedly censused over the 28 d experimental period and mortality rates across a gradient of prey densities were quantified. Per capita loss of fairy basslet was density-dependent on reefs with and without introduced lionfish; however, the magnitude of this loss was significantly higher on reefs with the invader present. High mortality rates at low prey density resulted in local extinction of 2 of 14 fairy basslet populations exposed to the invader, a phenomenon observed only on lionfish reefs. Further, 9 out of 14 lionfish-exposed prey populations showed loss rates of >50% compared with just 3 prey populations with such rates on native-only reefs.

KEY WORDS: Coral reefs · Density dependence · Invasive species · Marine fishes · Population regulation · Predator recognition · Predator–prey

INTRODUCTION

Anthropogenic species introductions have been identified as a top conservation priority (Wilcove et al. 1998), as invasions can lead to altered community structure and ecosystem function, and to native species loss (Gurevitch & Padilla 2004, Pimentel et al. 2005, Vilà et al. 2011). Invasive predators have caused some of the most severe impacts of introductions (Salo et al. 2007, Jones et al. 2008) and have precipitated numerous extinctions via strong, direct, and consumptive effects (Blackburn et al. 2004, Kumschick et al. 2015). These invasive, predator-mediated extinctions necessarily imply a change in the processes that have previously ensured persistence of regulated prey 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 the existing compensatory dynamics that underlie native population regulation.

Demersal marine fishes have been instrumental in the detection and quantification of such demographic

*Corresponding author: ingemank@science.oregonstate.edu

density dependence, as these populations are often amenable to the local-scale manipulations that can provide insight into the mechanisms behind density-mediated effects (Hixon & Webster 2002). Consensus has emerged that post-settlement mortality of demersal marine fishes often displays direct density dependence — a positive relationship between prey density and per capita mortality (Hixon 1998, Hixon & Webster 2002, White et al. 2010). Numerous studies have demonstrated that predation is often the proximate cause of density-dependent (hereafter DD) mortality (Hixon & Carr 1997, Anderson 2001, Carr et al. 2002, Holbrook & Schmitt 2002, Hixon 2015) and that this mechanism can lead to temporal population regulation (Steele 1997, Carr et al. 2002, Webster 2003, Hixon et al. 2012).

Of vital importance for understanding the implications of a predator introduction is characterizing the effects of multiple predators on patterns of prey mortality. Previous work on patch reefs has demonstrated emergent, synergistic effects of resident and transient predators on prey mortality patterns. Hixon & Carr (1997) showed that the effects of predators with differing hunting modes and scales of foraging (resident ambush piscivores versus transient pelagic hunters) — which separately caused density-independent (DI) mortality — interacted to produce DD mortality only when both predator types were present. Thus, the addition of a predator to an existing community has the potential to qualitatively alter the relationship between prey density and predation risk.

As the role of native predators in causing DD mortality is well understood in demersal fish communities, the introduction of a novel piscivore provides the opportunity to test how mortality patterns are altered by an invader. Theory predicts that density dependence (at some life stage and at some spatial scale) is a necessary condition for regulation (Murdoch 1994, Hixon et al. 2002), and simulations suggest that the effects of introduced predators on prey consumption rates may be particularly pronounced at low prey densities (Saul & Jeschke 2015), so the potential for a novel predator to weaken or even reverse DD demands study. Previously, Ingeman & Webster (2015) used manipulative field experiments — replicated before and after the introduction of the Indo-Pacific lionfish *Pterois volitans* to western Atlantic marine habitats — to measure changes in the density–mortality patterns of a common reef fish, the fairy basslet *Gramma loreto*. Per capita loss in fairy basslet remained DD after the invasion despite an increase in overall loss rates since the introduction of

the novel predator (Ingeman & Webster 2015). However, the authors could not unequivocally attribute the altered mortality patterns to lionfish since the presence of the invader was confounded by possible environmental or biotic changes (e.g. increased native predator abundance and/or consumption rates) in the interval between experiments.

Therefore, in order to detect the effects of an invasive predator on the relationship between density and predation risk in native prey, I conducted a controlled field experiment on natural coral reefs in the Bahamas, manipulating both prey density and invasive predator presence, such that differences in loss rates are attributable to predation by the invader alone. On reefs with and without invasive lionfish, I compared (1) the immediate post-settlement and longer-term changes in density over the 28 d experimental period, (2) the magnitude of per capita loss due to predation between repeated censuses, and (3) the presence or absence of density dependence in populations of fairy basslet.

MATERIALS AND METHODS

Study species

The fairy basslet *Gramma loreto*, family Grammatidae, is a common aquarium fish inhabiting coral-reefs throughout the tropical western Atlantic (Böhlke & Randall 1963). Like most reef fishes, the fairy basslet has a bipartite life-cycle with pelagic larvae and demersal juveniles and adults (Böhlke & Chaplin 1994). Fairy basslet are typically found on the ceilings of caves, outcrops, and open reef ledges (hereafter 'ledges' collectively), where they feed opportunistically on passing plankton (Randall 1967). Individuals form dense aggregations, with the largest individuals occupying prime feeding positions nearest the outer edge of the ledge (Freeman & Alevizon 1983). Population size at the local level is tightly regulated by high and DD mortality caused by aggregating mesopredators (Webster 2003). Tagging studies have confirmed static membership of local aggregations and demonstrated that juveniles and adults rarely move farther than 3 m from their home ledge, such that post-settlement immigration is negligible and where each ledge supports a distinct local population (Webster 2003).

The Indo-Pacific lionfish *Pterois volitans/miles*, family Scorpaenidae, is an invasive mesopredator introduced in the mid-1980s that has rapidly spread throughout the region from an invasion locus near

Southeast Florida (Whitfield et al. 2002) and now inhabits most of the western Atlantic and Caribbean, including the Gulf of Mexico (Schofield 2010). These voracious, generalist predators have strong direct effects on native prey fishes via consumption of newly settled recruits and adults of small species (Albins & Hixon 2008, Albins 2013, 2015, Côté et al. 2013, Benkwitt 2015, Ingeman & Webster 2015) and have the potential to alter invaded reef ecosystems directly through consumption of ecologically important native fishes and via the indirect effects of predation (Albins & Hixon 2013). To date, few biotic controls have been identified in the invaded range: Atlantic lionfish are relatively free of parasites (Sikkel et al. 2014) and do not experience increased mortality or emigration even at extreme densities (Benkwitt 2013). Lionfish possess an impressive array of traits that may render them difficult to detect and/or may confuse prey (Lönnstedt & McCormick 2013, Marsh-Hunkin et al. 2013, Black et al. 2014) and are themselves well-defended from predation by venomous dorsal spines (Halstead et al. 1955). As such, predation on lionfish in the invaded range, although reported, is irregular and thus far insufficient to control their densities (Hackerott et al. 2013), which have been reported as high as 393 ind. ha^{-1} (Green & Côté 2009). Fairy basslet are common prey of the invader, which actively stalks juveniles and adults with large pectoral fins extended, herding individuals before striking rapidly (Albins & Lyons 2012). Anecdotally, fairy basslet individuals do not employ as robust an anti-predator response (fleeing into small refugia in the reef) to lionfish as toward native mesopredators, and experiments with other native Atlantic prey species have demonstrated a suboptimal response to the threat of predation by this novel predator (Black et al. 2014).

Study area

This study was conducted on coral patch reefs near the Cape Eleuthera Institute, Eleuthera, Bahamas. Patch reefs of highly variable structure occur on a 2–30 m deep shelf lining the 1500 m deep Exuma Sound to the southwest of Cape Eleuthera. Prior to initiation of the experiment, teams of divers on SCUBA identified 14 patch reefs ranging in surface area from 137 to 1290 m^2 at depths of 4–20 m, surrounded by sand and seagrass, and separated from all other hard substrate by at least 80 m. Experimental patch reefs were roughly cylindrical in shape and of variable diameter (10–30 m) and height (2–18 m).

The benthos was dominated by small coral heads, algae, sponges, and soft corals of various species scattered over highly convoluted dead coral surfaces.

Experimental design

To determine the effects of invasive lionfish predation on prey density–mortality patterns, local fairy basslet populations were manipulated to create a range of prey densities on reefs with and without the introduced predator. Because the home ranges of adult lionfish span multiple local populations of fairy basslet prey, which restrict their movements to individual reef ledges, this study employed a split-plot design, whereby predator treatments where maintained at a larger scale (reef) than basslet density treatments (ledges within a reef). Reefs were paired by proximity, as well as similarity in size, depth, vertical relief, and relative coral cover, to form 7 experimental reef pairs. One reef in each pair was assigned by randomization to receive periodic lionfish removals (with randomization constrained to avoid excessive clustering of this treatment; 'native-only reef'); the other reef received variable levels of lionfish addition with the goal of achieving a standardized lionfish density ('lionfish reef'; see subsection 'Density manipulations'). Within each reef, 2 fairy basslet populations were chosen based on similarity in initial population size, ledge area, proximity to reef margin, and orientation to prevailing currents. In order to maximize the demographic isolation of experimental fairy basslet populations, only discrete ledges that were >3 m from other occupied ledges were chosen. Divers then performed an initial baseline census of all fairy basslet individuals on each experimental ledge and measured ledge surface area (0.4–1.5 m^2) to determine unmanipulated densities (6.3–18.9 fish m^{-2}). One fairy basslet population from each reef was then randomly chosen to receive artificially enhanced recruitment sufficient to increase density to levels commonly observed after a recruitment event (Webster 2003, Ingeman & Webster 2015). Fairy basslet additions rather than removals were employed to avoid artificially inflating extirpation rates by lowering prey density below ambient levels. Natural variation in the densities of unmanipulated populations created a continuous density-gradient that was thus extended by diver-enhanced artificial recruitment (manipulated population densities: 13.6–31.1 fish m^{-2}, see subsection 'Density manipulations').

Density manipulations

To maintain native-only reefs, divers conducted removals as needed, capturing lionfish using hand-nets where possible and employing pole spears where conditions made live-capture impossible. While the target for native-only reefs was complete removal of lionfish, the cryptic nature of this species, highly protected reef refugia, and occasional immigration resulted in low but non-zero densities on removal reefs. To maintain treatment densities on lionfish reefs, divers periodically captured juvenile and adult lionfish (8–38 cm total length [TL]) from native-only reefs and non-experimental habitats then translocated them to distant (>500 m) lionfish reefs. A target density of 300 lionfish ha^{-1} was chosen to represent a realistic average lionfish density based on observations of unmanipulated reefs in the region and other parts of the invaded range (Green & Côté 2009, Albins 2015). Transplant effects and variable emigration throughout the study duration necessitated repeated 'stocking' of lionfish reefs. However, targeted censuses indicated a strong density gradient between predator treatment levels, with lionfish reefs maintaining approximately 6 times higher densities (240.4 ± 35.7 lionfish ha^{-1}) compared to native-only reefs (40.1 ± 18.3 lionfish ha^{-1}).

To enhance the natural range in fairy basslet density, recruits (approximately 1–2 wk post-settlement and <2.0 cm TL) were captured using dip nets and anesthetic clove oil, transferred into seawater-filled plastic bags, and translocated to target populations. Recruits were captured from distant locations to minimize emigration from study ledges. Small numbers of recruits (<10) were added to a population during any single dive, and additions were conducted over several days in order to simulate a natural recruitment pulse and to minimize immediate (pre-census) loss of basslet transplants to aggregating predators. Censuses for the experiment commenced 24 h after recruit manipulations, thereby allowing a day for transplanted fish to recover from any handling effects and ensure that transplanted individuals did not suffer disproportionate mortality compared to resident fish.

Following the establishment of treatments and baseline censuses, a minimum of 2 divers re-censused each population after 2 d, 4 d, and weekly thereafter, with a final census after 4 wk. During each census, divers recorded the size of each fairy basslet individual, the total population size, and any predators within 2 m of the target basslet ledge. Observations of fairy basslet populations and individual sizes were highly congruent between divers, indicating that observation error was negligible.

Statistical analysis

All fairy basslet populations were censused prior to artificial recruitment enhancement, and initial densities were checked for systematic bias by both predator treatment and assignment to recruitment enhancement. Mean densities among treatment groups were compared using Welch's 2-sample t-tests, with no assumption of equal variance. These comparisons were repeated for fairy basslet observations at the first post-manipulation census to ensure that (1) mean fairy basslet density differed significantly among recruitment-enhanced versus unmanipulated populations and that (2) differences in fairy basslet density were not biased among reefs with and without lionfish. Additionally, cumulative population-level effects of fairy basslet on prey density were assessed by comparing the 4 resulting categorical treatment levels created by cross-factoring predator treatment (lionfish versus native-only reefs, 7 reefs each) and fairy basslet recruitment regimes (enhanced versus unmanipulated, 14 ledges each, 28 ledges total).

Prey per capita loss was defined as the proportional change in abundance accumulated between intervals.

$$(1 - N_{t+1}/N_t) \qquad (1)$$

Thus, positive values for per capita loss at a given time-step indicate that the total number of individuals decreased since the previous census, and this value is scaled to the previously observed abundance. Natural recruitment of fairy basslet was observed in between the 3rd and 4th censuses, indicated by reduced net loss and even population increases on some ledges. Uncontrolled recruitment means that net loss (as an aggregate measure of population change) likely underestimates mortality but is not likely to systematically bias results, since fairy basslet recruitment has been shown to be density-independent. I did not explicitly account for the difference in length of time intervals, which is likely to increase variability around estimates of per capita loss. However, time intervals were identical among treatment groups so this would not bias comparisons among groups or introduce a spurious effect of lionfish on patterns of mortality. To detect lionfish-induced changes in the magnitude of mortality and the presence of density dependence in fairy basslet per capita loss, I employed linear mixed effects models (LMMs) with 'ledge' nested within

'reef' as random effects, 'lionfish presence' and 'time-step' as categorical fixed effects, and 'prey density' (Note: this term represents the density at the beginning of each sampling interval and not the initial prey density.) as a continuous fixed effect. In order to test the significance of lionfish presence on per capita loss at each census, I included a 'lionfish × time-step' (fixed) interaction term. A significant interaction between lionfish and time-step would indicate a lionfish-induced change in the magnitude of mortality in interval since the previous census. Further, to measure an effect of lionfish on density dependence, I incorporated a 'lionfish × basslet density' (fixed) term. This inclusion allows separately fitted slopes of the response of fairy basslet loss to prey density on lionfish and native-only reefs. A slope coefficient for lionfish reefs that does not differ from zero would be consistent with the hypothesis that lionfish predation eliminates regulating density dependence.

I fitted full models (including all fixed effects and interactions) with and without random effects using restricted maximum likelihood estimation (REML)
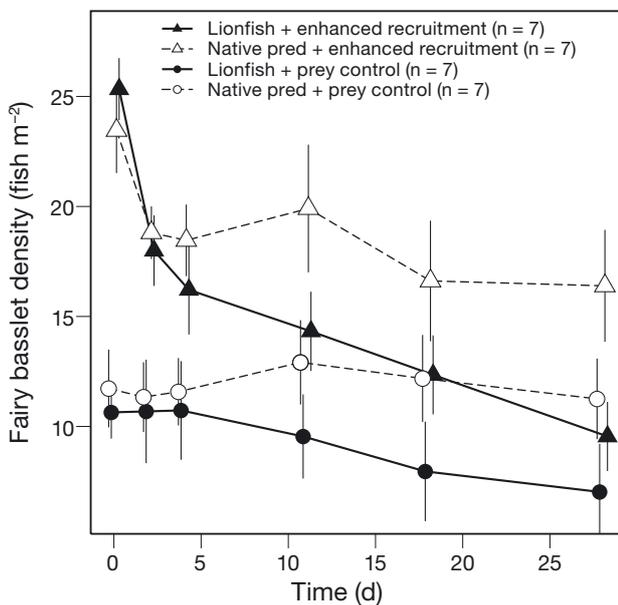
and compared them using likelihood ratio test (LRTs) with an adjustment for testing on the boundary (Zuur et al. 2009). The inclusion of a random intercept at the 'ledge' level resulted in a better fit than a fixed effects only model (L-ratio = 9.43, p = 0.001). Visual inspection of the residuals of the resulting models showed no departures from the assumptions of homogenous variance and normality among populations. However, there was evidence of temporal autocorrelation in the residuals, and inclusion of an AR1 structure substantially improved the model (ΔAIC $\gg$ 2). Re-examination of the residuals indicated that all assumptions had been met. After selecting the optimum random effects and correlation structure (see Appendix), I refit the competing models using maximum likelihood (ML) and tested the significance of fixed effects using LRTs. Where LRTs indicated that interaction terms were not significant, they were dropped from the model and the main effects were tested using LRTs. Finally, I estimated parameters and effect sizes from the final model using REML (Zuur et al. 2009). All statistical analyses were conducted in the R language and software environment, v. 3.2 (R Development Core Team 2015) using add-on packages nlme v. 3.1-128 (Pinheiro et al. 2014).

RESULTS

Prior to diver manipulation, fairy basslet densities showed no systematic bias by lionfish treatment ($t = -0.26$, p = 0.79) nor by assignment to enhanced recruitment treatment ($t = -0.73$, p = 0.47). In contrast, during the initial census (24 h post-manipulation) the fairy basslet population that received enhanced recruitment showed significantly higher densities of 24.1 fish m^{-2} compared to 11.2 fish m^{-2} in unmanipulated populations ($t = 25.0$, p < 0.0001; Fig. 1: circles versus triangles at initial census). Within each prey recruitment level, initial post-manipulation densities did not vary significantly by predator treatment ($t = -0.51$, p = 0.62 and $t = 0.80$, p = 0.44 for unmanipulated and recruitment-enhanced fairy basslet populations, respectively; Fig. 1: open versus filled symbols at initial census). Over 4 wk and across all reefs, net change in fairy basslet population density ranged from −22.7 fish m^{-2} (negative values indicating a decrease in density) to 5.5 fish m^{-2}, with far greater average decreases observed on lionfish reefs compared to native predator only reefs. This pattern was true of both recruitment-enhanced fairy basslet populations — where a decrease in density was approximately 140% greater on reefs with lionfish present

Fig. 1. Time series of fairy basslet *Gramma loreto* density (mean ± SE) over the 28 d experimental period on reefs with lionfish *Pterois volitans* (filled symbols and solid lines) and with native predators only (open symbols and dashed lines). Fairy basslet populations with artificially enhanced recruitment (triangles) were at significantly higher densities at the beginning of the experiment compared to unmanipulated populations (circles). However, high and directly density-dependent mortality reduced the difference in final densities within each predator treatment. Further, prey populations on lionfish reefs (filled symbols, far right) achieved lower final densities than native-only reefs (open symbols, far right), regardless of initial density

(mean change in density −15.8 versus −6.6 fish m^{-2}) — and at unmanipulated populations, with lionfish reefs experiencing 97% greater decreases compared to native-only reefs (mean change in density −3.62 with lionfish present versus −1.83 fish m^{-2} on native-only reefs). Over the course of 4 wk and despite initial differences in prey density, fairy basslet populations on reefs with the invader were lower than those subject to predation by natives only (Fig. 1: filled symbols versus open at $t = 28$).

Cumulative per capita loss of fairy basslet over 28 d was DD for both native-only reefs and those with lionfish present (Fig. 2; circles versus triangles). 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 lionfish reefs (60.0% versus 33.8% loss). However, the magnitude of this loss was substantially greater on lionfish reefs regardless of prey density (Fig. 2; filled versus open symbols). Notably, unmanipulated (low-density) fairy basslet experienced slightly higher mean loss rates on lionfish reefs even compared to recruitment-enhanced (high-density) populations at native predator-only reefs (Fig. 2; filled circle versus open triangle)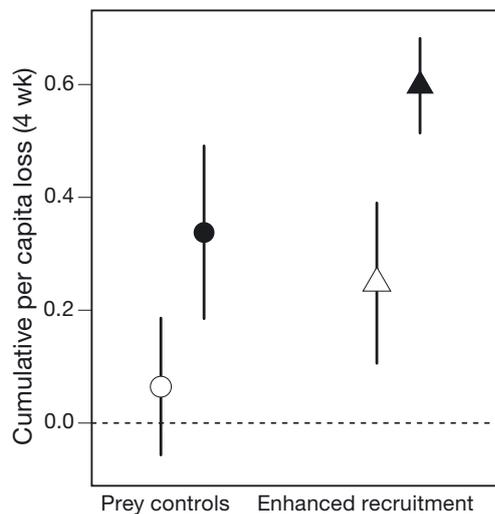. High mortality rates on lionfish reefs resulted in extirpation of 2 out of 14 fairy basslet populations; no fairy basslet populations on native-only reefs reached zero abundance. Further, 9 out 14 prey populations exposed to the invader showed loss rates of >50% over 4 wk. In contrast, only 3 prey populations demonstrated such high mortality rates on native-only reefs.

Modeling interval per capita loss as a function of fairy basslet density using LMMs, there was a significant effect of 'prey density' (LRT, p < 0.001, see Table 1 for fixed effects selection criteria), indicating the presence of density dependence in per capita rates of prey loss (see Table 2 for parameter coefficients and variance). Further, I found no evidence to suggest that lionfish eliminated the presence of density dependence (LRT for the 'lionfish × prey density'

Table 1. Selection criteria for fixed effects. Likelihood ratio and associated p-values comparing models with each potential explanatory variable (with all other fixed effects and optimal random structure in place) to a reduced model without the focal parameter. ΔAIC indicates the change in model fit associated with retaining the variable in the model; p-values <0.05 (and negative ΔAIC values) provide evidence for retaining the variable. Fixed effects retained in final model are indicated in **bold**

Explanatory variable	Likelihood ratio	p	ΔAIC
Lionfish (presence)	**8.330**	**0.004**	**−6.330**
Prey density	**11.124**	**<0.001**	**−9.124**
Lionfish × Prey density	0.018	0.975	1.982
Native predator biomass	0.867	0.352	4.017
Time step	**13.274**	**0.021**	**−3.274**
Lionfish × Time step	**11.197**	**0.003**	**−1.197**

Table 2. Summary of fixed effects for final model. Model coefficients and variance estimated using restricted maximum likelihood for all variables retained in final linear mixed effects model

Effect	Value	SE	df	t	p
Intercept	−0.351	0.165	128	−2.12	0.035
Prey density	0.021	0.008	128	2.48	0.014
Lionfish	0.123	0.227	26	0.54	0.590
Prey density:Lionfish	−0.008	0.011	128	−0.711	0.478
Time Step 2	0.076	0.097	128	0.788	0.432
Time Step 3	0.069	0.097	128	0.716	0.475
Time Step 4	−0.05	0.097	128	−0.525	0.601
Time Step 5	0.057	0.097	128	0.588	0.557
Time Step 6	0.143	0.097	128	1.481	0.141
Lionfish:Time Step 2	0.083	0.137	128	0.605	0.546
Lionfish:Time Step 3	0.124	0.137	128	0.906	0.366
Lionfish:Time Step 4	0.297	0.137	128	2.174	0.032
Lionfish:Time Step 5	0.323	0.137	128	2.380	0.020
Lionfish:Time Step 6	0.330	0.137	128	2.262	0.018

Fig. 2. Cumulative per capita loss (proportional change in abundance) for cross-factored treatment groups over 28 d (group means ± SE). At both unmanipulated and recruitment-enhanced fairy basslet *Gramma loreto* populations (circles and triangles, respectively), per capita loss was higher on reefs with lionfish *Pterois volitans* compared to native-only reefs (closed versus open symbols). Per capita loss at unmanipulated prey populations subject to lionfish predation were similar to recruitment-enhanced populations on native-only reefs (comparing filled circle to open triangle), suggesting that lionfish cause high mortality even at low prey density

interaction, p = 0.98; Table 1). The coefficient for the effect of lionfish on the density–mortality relationship was small relative to the slope coefficient itself (0.008 and 0.021, respectively), and the confidence interval for this effect includes zero (Table 2). Together, these results indicate that prey loss was DD regardless of predator treatment. The effect of lionfish was mediated by time-step as indicated by a significant 'lionfish × time-step' interaction (LRT, p = 0.003), precluding the interpretation of the main effect of lionfish presence singularly across the duration of the experiment. However, in the final model, after accounting for prey density, during Time-Steps 4, 5, and 6 (11, 18, and 28 d post manipulation) per capita loss was higher on reefs with lionfish than on those without (Table 2).

DISCUSSION

Density dependence in vital rates represents a crucial component of population regulation, and the detection of density dependence and the identification of the mechanisms that lead to density dependence remain relevant areas of study in population ecology (reviews by Hixon et al. 2002, Lande et al. 2002, Osenberg et al. 2002, Brook & Bradshaw 2006, White et al. 2010, Lebreton & Gimenez 2013, Thorson et al. 2015). As predation is often the proximate cause for this compensatory pattern in reef fishes (Hixon 2015), understanding how an introduced marine piscivore may alter patterns of density-mediated mortality in native prey is an important step in predicting the ultimate effects of invasion, including the risk of local or global extinction of native species. In this experiment, I found evidence that fairy basslet mortality remains DD in the presence of invasive lionfish. However, lionfish predation caused an overall increase in prey mortality and contributed to the local extinctions of 2 of 14 of prey populations; in contrast, no fairy basslet populations were extirpated on native-only reefs. Both extirpated populations began the experiment at low initial density, suggesting that, unlike native piscivores alone, the invader can cause high per capita loss rates at low prey density. Further, 9 out 14 fairy basslet populations that were exposed to the invader — across a range of initial densities — had a per individual predation risk of >50% across the experimental period compared with 3 prey populations showing such mortality rates on native-only reefs. Thus, while patterns of fairy basslet mortality were qualitatively DD (per capita loss increasing with higher prey densities) regardless of predator

treatment, lionfish nevertheless reduced the likelihood of local persistence of fairy basslet populations by increasing the magnitude of mortality across a broad range of prey densities.

The observation that lionfish lower the probability of local prey persistence corroborates previous experimental research from the invaded range. Albins (2013) demonstrated that, over 8 wk, a single lionfish on a small patch reef can reduce prey richness by nearly 5 species compared to predator-free controls, an effect nearly twice as large as that caused by native piscivores. Similarly, Benkwitt (2015) observed increases in native species richness over the summer recruitment period only on lionfish-free control reefs; in the presence of the invader species richness remained unchanged. Additionally, on large patch reefs and over multiple recruitment periods, Albins (2015) showed that lionfish significantly reduced species richness and that the invader caused the greatest per capita effects on the rarest species. While the increased mortality rate of native prey driven by lionfish is not itself a novel result, this study demonstrates how an introduced generalist predator can cause extirpation of rare species (or a low-density population of a single species). By increasing loss rates even at the lowest prey densities — when prey populations are at their most vulnerable — predation by the invader heightens the likelihood that demographic stochasticity in local prey populations will result in local extinction.

The observation that lionfish remain effective predators at low prey density corroborates recent theory on the differential effects of a novel predator. Saul & Jeschke (2015) used mechanistic steady-state satiation equations (based on the predator functional response) to demonstrate that a novel predator with higher attack efficiency than natives and whose prey have low experience with the new predator will have higher consumption rates than natives across all prey densities. In such a scenario, the difference in consumption rate experienced by the prey will be most pronounced at low to intermediate prey densities (Saul & Jeschke 2015). Indeed, lionfish may 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 & Lyons 2012). While native piscivores often cause strongly DD 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 lionfish 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, lionfish 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 lionfish predation rates would remain high.

Another mechanism that could drive high predation rates at low prey density is naïveté, when prey fail to recognize and/or respond suboptimally to the threat of predation by a non-native predator (Banks & Dickman 2007, Sih et al. 2010, Anson & Dickman 2013). DD mortality caused by native predators often relies on intense competition for predator-free shelter at high prey densities. In contrast, when prey are rare, shelter is plentiful and predation risk low (Forrester & Steele 2004). However, if native prey are naïve to the risk of predation by this cryptic hunter with novel foraging behavior (Albins & Lyons 2012), lionfish would continue to consume prey at high rates even when shelter is abundant. Evidence of naïveté toward lionfish has been mixed in the invaded range. Recently, Anton et al. (2016) demonstrated that the Atlantic grunt, *Haemulon plumierii*, maintains a greater approach distance from native predators than from lionfish. Similarly, Kindinger (2015) showed that territorial 3-spot damselfish, *Stegastes planifrons*, that responded aggressively to all native fishes had reactions to captive lionfish that did not differ from the response toward empty controls. In contrast, Black et al. (2014) demonstrated, using another native Atlantic pomacentrid, *S. leucostictus*, that native prey can recognize and respond with anti-predator behavior in the presence of lionfish. However, this prey species did not modify their high-risk courtship behavior in the presence of the invader (Black et al. 2014), a result that suggests that other prey may similarly increase their risk predation when managing tradeoffs with foraging and/or reproductive demands.

Finally, differences in feeding behavior between lionfish and native predators could explain the observed mortality patterns in prey. Fairy basslet often occupy reef ledges where highest mortality rates occur toward the back of the ledges, the location at which native ambush hunters have the shortest pursuit distance (Webster & Hixon 2000). Larger, competitively dominant individuals that occupy the outer reaches of the ledge have access to passing plankton while remaining relatively near shelter, leading to lower predation risk. Thus, these individuals may represent a partial prey population refuge, such that native predators alone rarely cause complete extirpa-

tion of a population. Anecdotally, lionfish often hunt in the open along the outer margins of reef ledges and do not rely on a high-velocity pursuit from a hidden location. They may therefore have access to prey individuals unavailable to native predators. While both native predators and lionfish employ variants of a hybrid 'ram-suction' feeding behavior — combining a rapid burst of acceleration of the body (ram) with jaw protrusion and expansion of the buccal cavity to cause rapid flow of water into the mouth (suction) (Wainwright & Bellwood 2002) — common native predators of fairy basslet, such as serranids and aulostomids, employ considerably more ram movement than lionfish, which may approach prey quite closely before initiating a strike (Muller & Osse 1984). Speculatively, lionfish may therefore employ a more effective capture method for prey that are very near shelter or those that occupy primary feeding positions near the outer margin of a reef ledge.

While the pre- and post-invasion experimental design employed in previous work could not unequivocally attribute the altered patterns of prey mortality to lionfish (Ingeman & Webster 2015), here I provide evidence that the increase in prey mortality observed between predator treatments is caused by the invader. However, while the cumulative effect of lionfish and native predators (the invasion scenario) represents an increase in prey mortality rates compared to native predators alone, it is possible that interactions with lionfish alter consumption patterns by native predators. The experimental design employed here cannot distinguish the singular and interactive effects of native and invasive predators, and other studies of lionfish predatory effects have suggested non-additive effects of lionfish and native predators (Albins 2013). In all cases examined, the magnitude of the lionfish effect has been greater than that of native predators and the cumulative mortality rates have been higher than those caused by either predator alone. Yet, the marginal difference in loss rates observed between predator treatments may represent an underestimate of the lionfish effect if native predators' consumption rates are reduced in the presence of the invader (compensatory mortality).

Another limitation of the study is the use of per capita loss (or its converse, survival) in quantifying density dependence. First, as an aggregate demographic measure, survival does not distinguish between the presence of a prior resident individual and a new recruit that has replaced a prior resident that was consumed in the interval between studies. In the latter case, both the effective prey density over the

interval and the true mortality rate would be underestimated in calculating per capita loss. It is possible that natural recruitment rates in this study were not systematically biased by predator treatment, especially as native post-larval settlers have been shown to selectively avoid reefs with caged native predators but not reefs with lionfish (C. Benkwitt unpubl. data). Alternatively, in this study, higher consumption of fairy basslet may have increased the level of conspecific, olfactory distress cues in the proximity of fairy basslet ledges on lionfish reefs, leading to reduced settlement and unreliable comparisons of basslet mortality. Notably, I observed that a natural recruitment pulse drove an increase in average fairy basslet population size (associated with a new moon soon after the third census) on native predator-only reefs. The absence of such an uptick in density on lionfish reefs is consistent with either reduced settlement or high post-settlement lionfish predation on uncensused fairy basslet recruits. In either case, measuring per capita loss as a function of previous population density may not capture the total effect of lionfish on DD dynamics.

In addition, if the underlying population dynamics follow a Beverton-Holt function, as is commonly observed in reef fishes (Osenberg et al. 2002, Shima & Osenberg 2003), fitting per capita loss as a linear function of prey density may not be appropriate for identifying changes in the intensity of density dependence caused by the invader (C. Osenberg pers. comm.). The mixed-effect model I employ here provides no evidence for lionfish-induced alteration of the intensity of density dependence (suggesting that lionfish could alter only the DI component of fairy basslet mortality). In contrast, an alternative analytical method assuming Beverton-Holt dynamics and using maximum likelihood parameter estimation for both recruitment and predator-specific mortality rates (K. Ingeman unpubl. data) suggests that lionfish in fact increase the DD component of mortality, albeit with wide confidence intervals around estimates of both DI and DD parameters. In the face of mixed evidence for changes in the intensity of density dependence and high variability in the data, I therefore refrain from making inference about lionfish changes to the DI or DD components of mortality based on these results. Future efforts should unambiguously measure demographic rates through tagging of prior resident fishes, and should adopt the appropriate dynamic model to infer effects of introduced predators on DD and DI mortality.

While I observed increased mortality rates and the local extinction of native prey populations, I do not conclude that fairy basslet is at high risk of global extinction as a result of this predator introduction; for this species, post-settlement demographics are largely disconnected from recruitment due to a pelagic larval phase, and local populations are regularly replenished by DI larval settlement (Webster 2003). Further, this common species is buffered from the risk of global extinction by high fecundity, large range size, and fairly broad habitat tolerances (Böhlke & Chaplin 1994). Of greater conservation concern are rare species, those with demographically isolated populations, and species whose range is completely encompassed by the lionfish invaded range, such as the fairy basslet congener, *G. dejongi* (Victor & Randall 2010). This recently described basslet has been observed only in Cuba and the nearby Cayman Islands (Lohr et al. 2014), and its entire geographic and habitat range (reef walls at 20–30 m depth) are inhabited by lionfish. Another endemic coral-reef fish with a restricted range, the critically endangered social wrasse, *Halichoeres socialis*, has recently been documented as a primary prey item in lionfish diet contents in Belize (Rocha et al. 2015). 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 rage.

LITERATURE CITED

Albins MA (2013) Effects of invasive Pacific red lionfish *Pterois volitans* versus a native predator on Bahamian coral-reef fish communities. Biol Invasions 15:29–43

Albins MA (2015) Invasive Pacific lionfish *Pterois volitans* reduce abundance and species richness of native Baha-

mian coral-reef fishes. Mar Ecol Prog Ser 522:231–243

Albins MA, Hixon MA (2008) Invasive Indo-Pacific lionfish *Pterois volitans* reduce recruitment of Atlantic coral-reef fishes. Mar Ecol Prog Ser 367:233–238

Albins MA, Hixon MA (2013) Worst case scenario: potential long-term effects of invasive predatory lionfish (*Pterois volitans*) on Atlantic and Caribbean coral-reef communities. Environ Biol Fishes 96:1151–1157

Albins MA, Lyons PJ (2012) Invasive red lionfish *Pterois volitans* blow directed jets of water at prey fish. Mar Ecol Prog Ser 448:1–5

Anderson TW (2001) Predator responses, prey refuges, and density-dependent mortality of a marine fish. Ecology 82: 245–257

Anson JR, Dickman CR (2013) Behavioral responses of native prey to disparate predators: naiveté and predator recognition. Oecologia 171:367–377

Anton A, Cure K, Layman CA, Puntila R, Simpson MS, Bruno JF (2016) Prey naiveté to invasive lionfish *Pterois volitans* on Caribbean coral reefs. Mar Ecol Prog Ser 544: 257–269

Banks PB, Dickman CR (2007) Alien predation and the effects of multiple levels of prey naiveté. Trends Ecol Evol 22:229–230

Benkwitt CE (2013) Density-dependent growth in invasive lionfish (*Pterois volitans*). PLOS ONE 8:e66995

Benkwitt CE (2015) Non-linear effects of invasive lionfish density on native coral-reef fish communities. Biol Invasions 17:1383–1395

Black AN, Weimann SR, Imhoff VE, Richter ML, Itzkowitz M (2014) A differential prey response to invasive lionfish, *Pterois volitans*: prey naiveté and risk-sensitive courtship. J Exp Mar Biol Ecol 460:1–7

Blackburn TM, Cassey P, Duncan RP, Evans KL, Gaston KJ (2004) Avian extinction and mammalian introductions on oceanic islands. Science 305:1955–1958

Böhlke JE, Chaplin CC (1994) Fishes of the Bahamas and adjacent tropical waters, second edition. Rev Fish Biol Fish 4:136–138

Böhlke JE, Randall JE (1963) The fishes of the western Atlantic serranoid genus *Gramma*. Proc Acad Nat Sci Philadelphia 115:33–52

Brook BW, Bradshaw CJ (2006) Strength of evidence for density dependence in abundance time series of 1198 species. Ecology 87:1445–1451

Carr MH, Anderson TW, Hixon MA (2002) Biodiversity, population regulation, and the stability of coral-reef fish communities. Proc Natl Acad Sci USA 99:11241–11245

Côté IM, Green SJ, Hixon MA (2013) Predatory fish invaders: insights from Indo-Pacific lionfish in the western Atlantic and Caribbean. Biol Conserv 164:50–61

Forrester GE, Steele MA (2004) Predators, prey refuges, and the spatial scaling of density-dependent prey mortality. Ecology 85:1332–1342

Freeman S, Alevizon W (1983) Aspects of territorial behavior and habitat distribution of the fairy basslet *Gramma loreto*. Copeia 1983:829–832

Green SJ, Côté IM (2009) Record densities of Indo-Pacific lionfish on Bahamian coral reefs. Coral Reefs 28:107

Gurevitch J, Padilla DK (2004) Are invasive species a major cause of extinctions? Trends Ecol Evol 19:470–474

Hackerott S, Valdivia A, Green SJ, Côté IM and others (2013) Native predators do not influence invasion success of Pacific lionfish on Caribbean reefs. PLOS ONE 8: e68259

Halstead BW, Chitwood MJ, Modglin FR (1955) The anatomy of the venom apparatus of the zebrafish, *Pterois volitans* (Linnaeus). Anat Rec 122:317–333

Hixon MA (1998) Population dynamics of coral-reef fishes: controversial concepts and hypotheses. Aust J Ecol 23: 192–201

Hixon MA (2015) Predation: piscivory and the ecology of coral-reef fishes. In: Mora C (ed) Ecology and conservation of fishes on coral reefs. Cambridge University Press, Cambridge, p 41–52

Hixon MA, Carr MH (1997) Synergistic predation, density dependence, and population regulation in marine fish. Science 277:946–949

Hixon MA, Webster MS (2002) Density dependence in reef fishes: coral-reef populations as model systems. In: Sale PF (ed) Coral reef fishes: dynamics and diversity in a complex ecosystem. Academic Press, San Diego, CA, p 303–325

Hixon MA, Pacala SW, Sandin SA (2002) Population regulation: historical context and contemporary challenges of open vs. closed systems. Ecology 83:1490–1508

Hixon MA, Anderson TW, Buch KL, Johnson DW, McLeod JB, Stallings CD (2012) Density dependence and population regulation in marine fish: a large-scale, long-term field manipulation. Ecol Monogr 82:467–489

Holbrook SJ, Schmitt RJ (2002) Competition for shelter space causes density-dependent predation mortality in damselfishes. Ecology 83:2855–2868

Ingeman KE, Webster MS (2015) Native prey mortality increases but remains density-dependent following lionfish invasion. Mar Ecol Prog Ser 531:241–252

Jones HP, Tershy BR, Zavaleta ES, Croll DA, Keitt BS, Finkelstein ME, Howald GR (2008) Severity of the effects of invasive rats on seabirds: a global review. Conserv Biol 22:16–26

Kindinger TL (2015) Behavioral response of native Atlantic territorial three spot damselfish (*Stegastes planifrons*) toward invasive Pacific red lionfish (*Pterois volitans*). Environ Biol Fishes 98:487–498

Kumschick S, Gaertner M, Vilà M, Essl F and others (2015) Ecological impacts of alien species: quantification, scope, caveats, and recommendations. Bioscience 65:55–63

Lande R, Engen S, Saether BE, Filli F, Matthysen E, Weimerskirch H (2002) Estimating density dependence from population time series using demographic theory and life-history data. Am Nat 159:321–337

Lebreton JD, Gimenez O (2013) Detecting and estimating density dependence in wildlife populations. J Wildl Manag 77:12–23

Lohr KE, Camp EF, Manfrino C (2014) First record of the basslet *Gramma dejongi* outside of Cuba. Coral Reefs 33: 221

Lönnstedt OM, McCormick MI (2013) Ultimate predators: lionfish have evolved to circumvent prey risk assessment abilities. PLOS ONE 8:e75781

Marsh-Hunkin KE, Gochfeld DJ, Slattery M (2013) Antipredator responses to invasive lionfish, *Pterois volitans*: interspecific differences in cue utilization by two coral reef gobies. Mar Biol 160:1029–1040

Muller M, Osse JWM (1984) Hydrodynamics of suction feeding in fish. Trans Zool Soc Lond 37:51–135

Murdoch WW (1994) Population regulation in theory and practice. Ecology 75:271–287

Osenberg CW, St Mary CM, Schmitt RJ, Holbrook SJ, Chesson P, Byrne B (2002) Rethinking ecological inference: density dependence in reef fishes. Ecol Lett 5:715–721

Pimentel D, Zuniga R, Morrison D (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecol Econ 52: 273–288

Pinheiro J, Bates D, DebRoy S, Sarkar D (2014) R Core Team (2014). nlme: linear and nonlinear mixed effects models. R package version 3.1–128. http://cran.r-project.org/web/packages/nlme/index.html

Randall JE (1967) Food habits of reef fishes of the West Indies. Institute of Marine Sciences, University of Miami, FL

R Development Core Team (2015) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. www.r-project.org

Rocha LA, Rocha CR, Baldwin CC, Weigt LA, McField M (2015) Invasive lionfish preying on critically endangered reef fish. Coral Reefs 34:803–806

Salo P, Korpimäki E, Banks PB, Nordström M, Dickman CR (2007) Alien predators are more dangerous than native predators to prey populations. Proc R Soc B 274:1237–1243

Saul WC, Jeschke JM (2015) Eco-evolutionary experience in novel species interactions. Ecol Lett 18:236–245

Schofield PJ (2010) Update on geographic spread of invasive lionfishes (*Pterois volitans* [Linnaeus, 1758] and *P. miles* [Bennett, 1828]) in the western North Atlantic Ocean, Caribbean Sea and Gulf of Mexico. Aquat Invasions 5(Suppl 1):117–122

Shima JS, Osenberg CW (2003) Cryptic density dependence: effects of covariation between density and site quality in reef fish. Ecology 84:46–52

Sih A, Bolnick DI, Luttbeg B, Orrock JL and others (2010) Predator–prey naïveté, antipredator behavior, and the ecology of predator invasions. Oikos 119:610–621

Sikkel PC, Tuttle LJ, Cure K, Coile AM, Hixon MA (2014) Low susceptibility of invasive red lionfish (*Pterois volitans*) to a generalist ectoparasite in both its introduced and native ranges. PLOS ONE 9:e95854

Steele MA (1997) Population regulation by post-settlement mortality in two temperate reef fishes. Oecologia 112: 64–74

Thorson JT, Skaug HJ, Kristensen K, Shelton AO, Ward EJ, Harms JH, Benante JA (2015) The importance of spatial models for estimating the strength of density dependence. Ecology 96:1202–1212

Victor BC, Randall JE (2010) *Gramma dejongi*, a new basslet (Perciformes: Grammatidae) from Cuba, a sympatric sibling species of *G. loreto*. Zool Stud 49:865–871

Vilà M, Espinar JL, Hejda M, Hulme PE and others (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. Ecol Lett 14:702–708

Wainwright PC, Bellwood DR (2002) Ecomorphology of feeding in coral reef fishes. In: Sale PF (ed) Coral reef fishes: dynamics and diversity in a complex ecosystem. Academic Press, San Diego, CA, p 33–56

Webster MS (2003) Temporal density dependence and population regulation in a marine fish. Ecology 84:623–628

Webster MS, Hixon MA (2000) Mechanisms and individual consequences of intraspecific competition in a coral-reef fish. Mar Ecol Prog Ser 196:187–194

White JW, Samhouri JF, Stier AC, Wormald CL, Hamilton SL, Sandin SA (2010) Synthesizing mechanisms of density dependence in reef fishes: behavior, habitat configuration, and observational scale. Ecology 91:1949–1961

Whitfield PE, Gardner T, Vives SP, Gilligan MR, Courtenay WR Jr, Ray GC, Hare JA (2002) Biological invasion of the Indo-Pacific lionfish *Pterois volitans* along the Atlantic coast of North America. Mar Ecol Prog Ser 235:289–297

Wilcove DS, Rothstein D, Dubow J, Phillips A, Losos E (1998) Quantifying threats to imperiled species in the United States. Bioscience 48:607–615

Zuur A, Ieno EN, Walker N, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer Science & Business Media, Heidelberg

Appendix. Selection criteria for random effects and auto-correlation structure. Random effects—None: no random effects; Reef: separate random intercepts at the reef level; Ledge: separate random intercepts at the ledge level. LRT (likelihood ratio test) results display the likelihood ratio and associated p-value (corrected for testing-on-the-boundary) comparing the model with optimal random structure to a fixed-effects-only model. Optimum structure was chosen by AIC (Aikake's information criterion); the best fit model is indicated in **bold**

LRT results		Random effect	Autocorrelation structure	AIC
Likelihood ratio	p			
		None	None	125.3
		Reef	None	120.1
		Ledge	None	118.1
		None	AR(1)	96.4
		Reef	AR(1)	126.9
9.28	**0.0010**	**Ledge**	**AR(1)**	**87.6**