

Invasive lionfish had no measurable effect on prey fish community structure across the Belizean Barrier Reef

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ABSTRACT

Invasive lionfish are assumed to significantly affect Caribbean reef fish communities. However, evidence of lionfish effects on native reef fishes is based on uncontrolled observational studies or small-scale, unrepresentative experiments, with findings ranging from no effect to large effects on prey density and richness. Moreover, whether lionfish affect populations and communities of native reef fishes at larger, management-relevant scales is unknown. The purpose of this study was to assess the effects of lionfish on coral reef prey fish communities in a natural complex reef system. We quantified lionfish and the density, richness, and composition of native prey fishes (0–10 cm total length) at sixteen reefs along ~250 km of the Belize Barrier Reef from 2009 to 2013. Lionfish invaded our study sites during this four-year longitudinal study, thus our sampling included fish community structure before and after our sites were invaded, i.e., we employed a modified BACI design. We found no evidence that lionfish measurably affected the density, richness, or composition of prey fishes. It is possible that higher lionfish densities are necessary to detect an effect of lionfish on prey populations at this relatively large spatial scale. Alternatively, negative effects of lionfish on prey could be small, essentially undetectable, and ecologically insignificant at our study sites. Other factors that influence the dynamics of reef fish populations including reef complexity, resource availability, recruitment, predation, and fishing could swamp any effects of lionfish on prey populations.

Subjects Biodiversity, Conservation Biology, Ecology, Marine Biology

Keywords Belize, Community composition, Invasive species, Coral reefs, Lionfish, Belize Barrier Reef, Predators, Species diversity, Predator-prey, *Pterois volitans*

INTRODUCTION

Exotic predators can have striking effects on native communities (*Simberloff, 1981; Bruno et al., 2005; Sax et al., 2007*). For example, the introduction of brown tree snakes to the island

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of Guam caused the local extinction of at least a dozen bird species (*Wiles et al., 2003*). Likewise, the addition of the Nile perch to Lake Victoria, and of bass and trout to thousands of lakes in North America, have had similar effects on native fishes and invertebrates (*Gido & Brown, 1999; Beisner, Ives & Carpenter, 2003; Eby et al., 2006*). Yet these and other well-known case studies of extreme impacts are typically from isolated communities with limited connectivity, e.g., lakes and islands. The general effects of exotic predators on open ecosystems, including in marine communities, is less clear.

Indo-Pacific lionfish (*Pterois volitans* and *Pterois miles*, hereafter called “lionfish”) were introduced to south Florida in the mid-1980’s and became established and common throughout the Greater Caribbean only ten years later (*Schofield, 2009*). Several characteristics such as cryptic coloration (*Kindinger, 2014*), undetectable chemical cues (*Lönnstedt & McCormick, 2013*), and novel predation tactics (*Albins & Lyons, 2012; Anton et al., 2016*), are believed to increase their predatory efficiency in the invaded range. These traits combined with high densities and their generalist diet—consuming over a hundred Caribbean fish and invertebrate species (*Morris & Akins, 2009; Green et al., 2012; Green & Côté, 2014*)—suggest that lionfish are capable of causing substantial changes in native fish communities (*Green et al., 2012*). Based on these characteristics, *Albins & Hixon (2011)* described a “worst case scenario in which most reef-fish biomass was converted to lionfish biomass, leaving invaded reefs depauperate of native fishes”. Similarly, a modeling study based on Ecopath-with-Ecosim suggested that the biomass of small and medium-size carnivorous–omnivorous fishes could decline after 15 years following the lionfish invasion (*Arias-González et al., 2011*). However, evidence for such extreme effects is largely based on small-scale experiments using artificial reefs and artificially high lionfish densities (*Albins & Hixon, 2008; Albins, 2013; Albins, 2015*). In fact, a relationship between reef fish communities and natural lionfish densities has not been detected on natural reef habitats (*Elise et al., 2014*). Additionally, whether the effects observed on small and isolated patch reefs occur on contiguous reefs or at larger management-relevant scales is unknown.

The effects of lionfish on native prey in small-scale experiments (e.g., cages or artificial reefs of $1\text{--}4\text{ m}^2$) may not necessarily reflect outcomes in nature. Small-scale experiments have shown predatory reef fishes can have strong effects on prey population and community dynamics. For example, natural levels of post-settlement mortality of recently settled fishes are high with over 50% of individuals eaten during the first 1–2 days after settlement (*Almany & Webster, 2004*). Small-scale studies of prey community response to predation suggest piscivores can alter community composition, either by increasing (*Webster & Almany, 2002*) or decreasing (*Almany & Webster, 2004*) prey diversity depending on the density and identity of predators. However, due to the high mobility of predatory fishes, it is difficult to document the degree to which small-scale and short-term fish dynamics apply to larger scales (i.e., kilometers) and longer time scales more relevant to management and conservation. Therefore, large-scale monitoring of prey population and community response before and after lionfish invasion will not only provide insight into the effects of lionfish, but also a unique “natural” experiment to understand the response of native fish communities to shifts in predation pressure.

The purpose of this study was to measure the realized effects of the lionfish invasion on reef fish communities and whether reported short-term effects from controlled settings and at small spatial scales (Albins & Hixon, 2008; Green et al., 2012; Albins, 2013) are evident at larger scale reef habitats. We quantified the relationship between lionfish density and the density, richness, and community composition of small native prey fishes at 16 sites along the Belizean Barrier Reef (BBR). Lionfish were first documented in Belize in 2008 (Schofield, 2009; Schofield, 2010). Our study began in 2009, with no lionfish present on our study sites, and continued until 2013. Due to the timing of our study, we were able to track changes in the community of small reef fish from before lionfish invaded our sites, during the onset of the invasion of our sites in 2010, and for two years after the invasion in 2012 and 2013. Based on previous studies we hypothesized that: (1) the density and species richness of small potential prey fish would be negatively related to lionfish density due to predation; and (2) that there would be a shift in small reef fish community composition because lionfish differentially reduce prey density (Green et al., 2012) by selectively feeding on species with certain morphological and behavioral traits (Green & Côté, 2014).

METHODS

Study sites and reef fish surveys

Our longitudinal study began during the onset of the lionfish invasion in Belize in 2009 (Schofield, 2009) and continued until 2013. We used a modified-BACI design (Before-After-Control-Impact) as we tracked changes in native fishes among sites as lionfish density varied over time. The “Before-After” aspect of the project was accomplished by surveying sites before and after they were invaded by lionfish. For this study, we considered a site to have been “invaded” when the measured density of lionfish was >0 . The modified aspect was that the “Control-Impact” categorization was continuous (i.e., based on lionfish density) rather than categorical as in a traditional BACI design (i.e., we did not base the analysis on lionfish presence/absence).

We monitored 16 fore-reef sites at 12–15 m depth, spanning ~ 250 km, across gradients of natural environmental conditions (Fig. 1, Table S1). To minimize habitat variability of study sites, we only surveyed spur-and-groove habitats formerly dominated by the reef building corals *Orbicella* spp. At each site, we performed underwater visual censuses of reef fish using six to eight belt transects placed along the spur-and-groove formations. We counted and identified reef fish to species and estimated total length (TL) in 5–10 cm intervals (McClanahan et al., 2007; McClanahan & Humphries, 2012; McClanahan, 2014). Divers counted fish less than 5 cm in TL in 15×1 m belt transects and fish between 6 and 40 cm TL in 30×2 m belt transects. Fish >40 cm TL as well as lionfish were counted in 50×10 m belt transects. Lionfish and large fish counts included a thorough search for cryptic individuals within the surveyed area. At each site, the longer and wider transect (50×10 m) encompassed the smaller transects (30×2 m). One diver surveyed fish <40 cm TL while laying the transect. After completing the 30×2 m survey, this diver continued to lay the same transect line for a total length of 50 m. A separate diver followed behind to survey lionfish and large predators, swimming in a zig-zag pattern, surveying the benthos as well as the

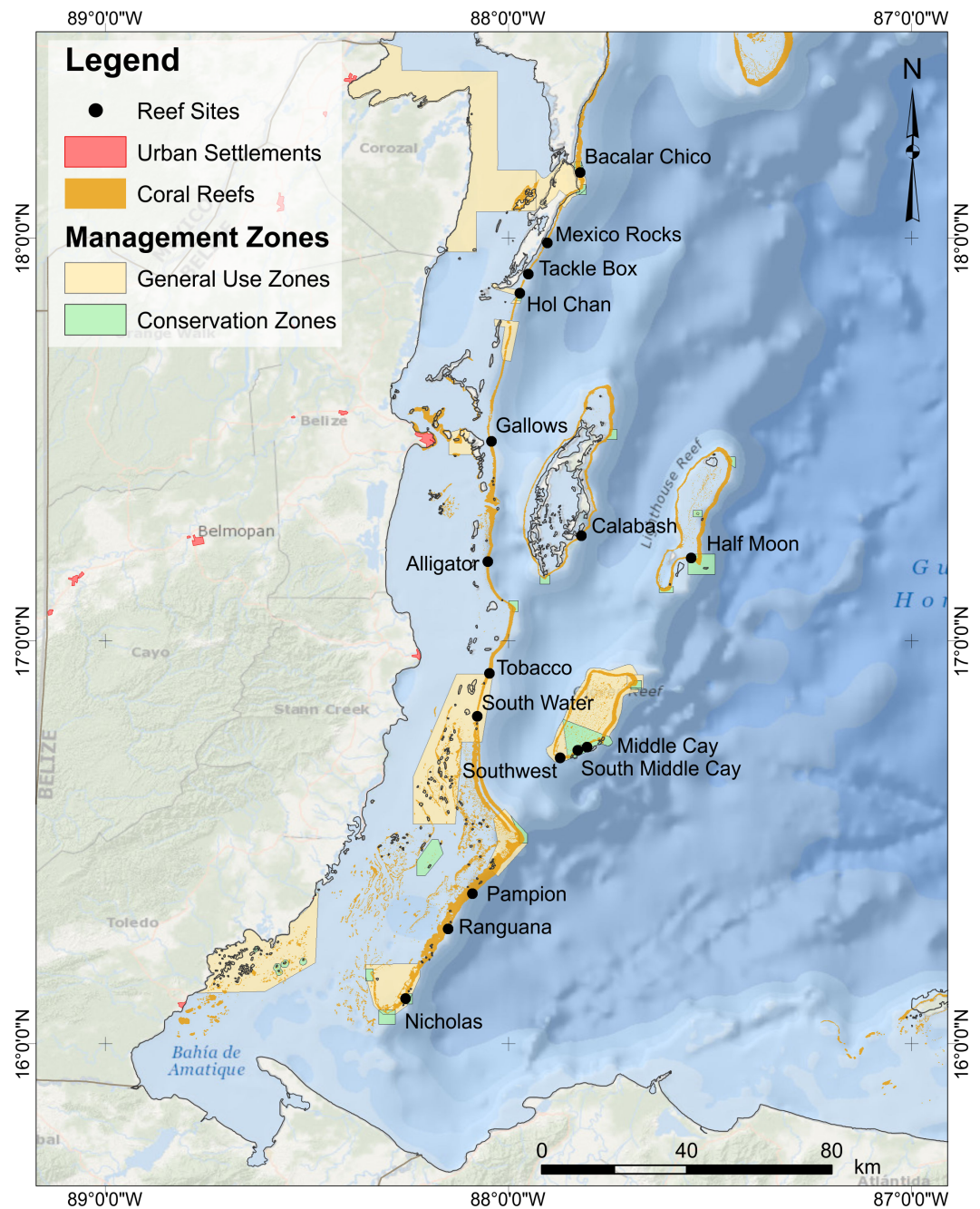


Figure 1 Location of survey sites. For sites abbreviations, coordinates, and other site info, refer to [Table S1](#).

water column for both benthic and pelagic species >40 cm TL as well as lionfish. Fish surveyors were consistent across years to avoid surveyor-bias. Sites were surveyed once per year in 2009, 2010, 2012, and 2013 from mid-May to early June. Due to logistical constraints, surveys were not conducted in 2011. Field work was approved by the Belize Fisheries Department (permit numbers 000028-11 and 000018-09).

Reef fish community structure

We quantified changes in reef fish density, richness, and community composition for all small individuals that are potential prey for lionfish. We defined potential prey based on the sizes of lionfish on our sites. Of the 143 lionfish recorded on our sites throughout the study, ~80% were >20 cm in TL (Fig. S1). As lionfish likely consume prey less than half their own body length (Albins & Hixon, 2008; Morris & Akins, 2009), we determined that potential prey were likely within the 6–10 cm TL size class, and therefore focused our analysis on this range. We further defined potential prey fish as species documented as lionfish prey on comparable Caribbean habitats (Albins & Hixon, 2008; Morris & Akins, 2009; Layman & Allgeier, 2011; Green et al., 2012; Valdez-Moreno et al., 2012; Albins, 2013; Côté et al., 2013; Green & Côté, 2014; Dahl & Patterson, 2014; Rocha et al., 2015) (Table S2). Although densities of fish <5 cm in TL are potentially too variable at the scale of our study for meaningful conclusions, we have included models of the abundance of this size class in the supplement (Text S1).

Reef complexity

We included reef complexity as a covariate in our analysis because highly complex reefs have been shown to support higher reef fish abundances or diversity compared with less complex reefs (Friedlander et al., 2003). Habitat complexity can also potentially influence predator–prey interactions (and per capita predation intensity) (Crowder & Cooper, 1982; Persson & Eklov, 1995; Beukers & Jones, 1998). However, based on previous studies, we did not expect reef complexity to influence lionfish abundance (Anton, Simpson & Vu, 2014; Valdivia et al., 2014). To estimate reef structural complexity, we used a semi-quantitative index from 0 to 5, where “0” was a reef with no vertical relief and “5” was an exceptionally complex reef with overhangs, crevices and deep cuts (Polunin & Roberts, 1993; Valdivia et al., 2014). Reef complexity was visually estimated along each transect and then averaged to obtain a single value for each site (Table S1).

Analysis of the effects of the lionfish invasion

Small reef fish density (individuals/m²) was calculated for each prey species, and summed to obtain the total density of small prey fish. Species richness for small prey fish was calculated as the total number of species present on each transect, excluding lionfish, at each site for each year.

We used generalized linear mixed effect models (GLMM) to evaluate the response of two reef fish community metrics (e.g., density and richness) of all potential prey species 6–10 cm TL, as well as the density of small prey fish within each of the most abundant families, to lionfish density (individuals/ha), with year and site-specific reef complexity as co-variates. Additional models were ran with the density of 0–5 cm TL and 0–10 cm TL prey fish as response variables (Text S1). Reef fish community responses (density and richness) were averaged over transect for each site and each year and all predictor variables were standardized (centered and divided by standard deviation) in all models. Transect-level data were highly zero-inflated and did not meet assumptions of a GLMM; however, we have included transect-level models in the supplement (Text S2). We used a Gamma distribution with a

log link function in the prey fish density model and a Gaussian distribution in the prey fish richness model, both using the *lme4* (v1.1-5) package in R (Bates et al., 2014, p. 4). Lionfish density, year, and reef complexity were included as fixed effects in each model. Site was included as a random effect in all models to account for variability across sites.

In addition to using lionfish as a continuous variable in our models (which assesses the relationship between lionfish density and prey density), we also ran similar models for prey fish density with lionfish as a discrete variable, splitting lionfish density into “low” or “high” levels. We identified sites in each year with “high” lionfish densities as those with average lionfish densities greater than the approximate maximum native density of 25 individuals/ha (Kulbicki et al., 2011; Darling et al., 2011; Cure, McIlwain & Hixon, 2014; McTee & Grubich, 2014). We also repeated this analysis using threshold values of 20 individuals/ha, 15 individuals/ha, and 10 individuals/ha to test the effect of lionfish on prey fish density at a range of thresholds.

To check for homogeneity of variance of the model residuals, we visually inspected plots of the residuals against the fitted values and each of the predictors. To test for collinearity in our explanatory variables, we used a Spearman’s correlation matrix and calculated the variance inflation factor (VIF) for each predictor; a threshold of $VIF < 2$ was used to determine if variables were significantly correlated (Graham, 2003). Quantile–quantile plots (*car* package v2.0-19) were used to check for normality of the model residuals (Fox & Weisberg, 2011). Spline-correlograms (*ncf* package v1.1-5) using the spatial coordinates of each site with 1,000 resamples revealed no evidence of spatial autocorrelation of the residuals of each final model (Bjornstad, 2013).

We quantified small prey fish community composition in terms of Bray–Curtis dissimilarity. Changes in prey fish community composition in response to year and lionfish density were assessed using permutational multivariate analysis of variance (PERMANOVA) of transect-level data with 10,000 permutations, stratified by site (*vegan* package v2.0-10) (Oksanen et al., 2013). Prey fish community composition was visualized with a nonmetric multidimensional scaling (NMDS) analysis, using both species density and species presence/absence data, at the site level. Both density and presence/absence were analyzed to determine if changes in community composition were driven by changes in species identity or abundance. For both analyses, we visualized changes in community composition over time by drawing ellipses of the standard deviation around the centroids for each year using the *ordiellipse* function (*vegan* package v2.0-10) (Oksanen et al., 2013).

RESULTS

No lionfish were recorded on any of our study sites in 2009. Lionfish were present on two sites (Calabash and South Middle Caye, Fig. S2) at relatively low densities (mean \pm SE, 6.7 ± 6.7 individuals/ha on both sites) in 2010. By 2012, lionfish were observed on 14 of 16 surveyed sites and on all sites by 2013. Across all sites, the average lionfish density (mean \pm SE) increased from 0.9 ± 0.7 individuals/ha in 2010 to 16.3 ± 5 individuals/ha in 2012, and dropped to 11.1 ± 4.2 individuals/ha in 2013. The highest lionfish density found during our study was 70 ± 29.2 individuals/ha at Pampion in 2012. Lionfish density varied among sites over time (Fig. S2).

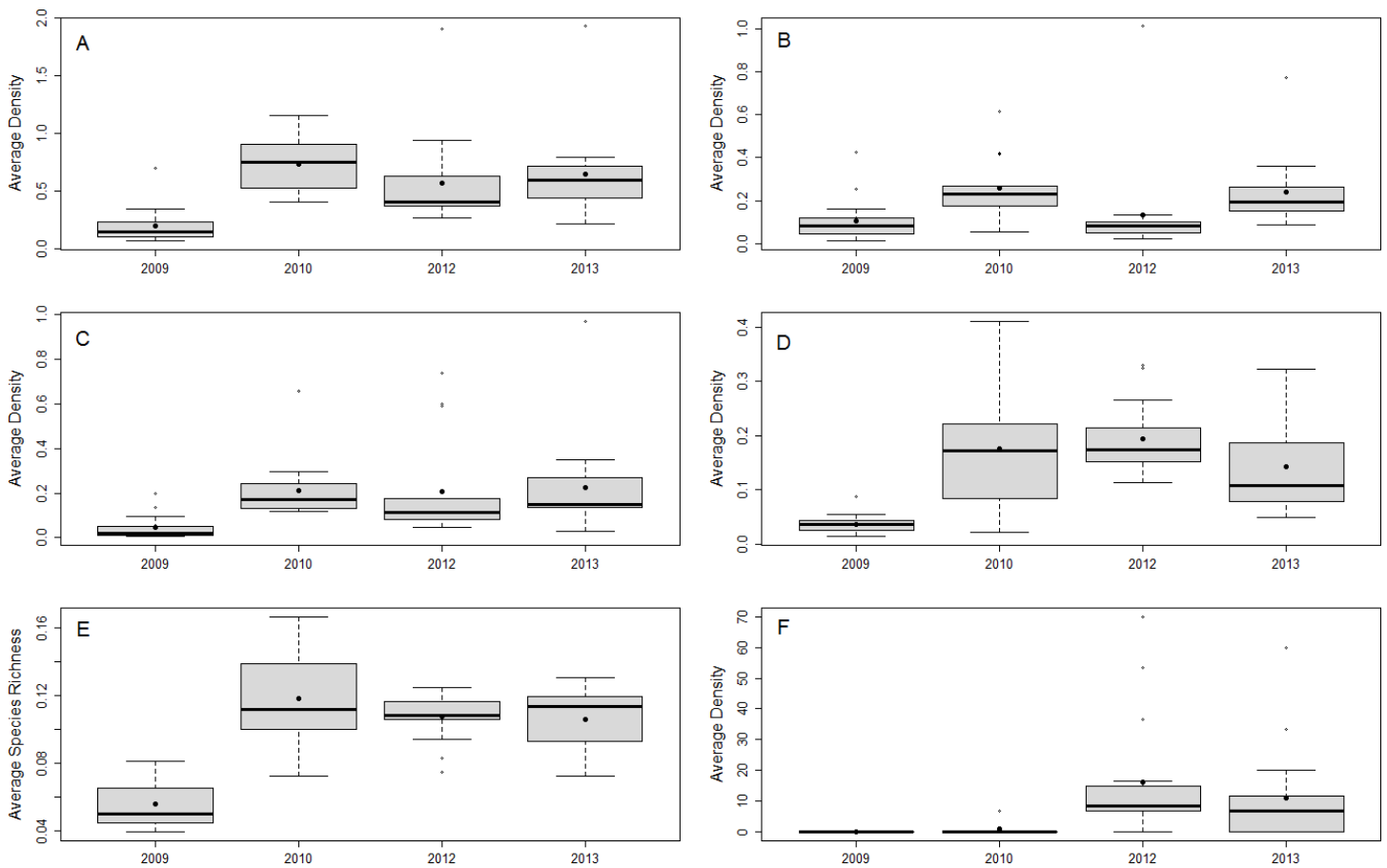


Figure 2 Small fish community responses and lionfish abundance over time. Boxplots of site-averaged total abundance (individuals/m²) (A), family-specific abundance (individuals/m²) (Pomacentridae, Labridae, and Scaridae B–D, respectively), and species richness (species/m²) (E) of prey small fish, as well as lionfish abundance (individuals/ha) (F) for each survey year. Boxes indicate the first and third quartiles with the median shown by the thicker transecting line. Mean values are indicated by the filled black dots.

From 2009 to 2013, 46 species of fish in the 0–5 cm size class and 77 species of fish in the 6–10 cm TL size class were observed, 33 of which have been previously documented as prey species for lionfish (Table S2). The most abundant documented lionfish prey in the 6–10 cm size class were damselfish (Pomacentridae), wrasses (Labridae), and parrotfish (Scaridae), accounting for ~34%, ~33%, and ~26% of the total density of small prey fish in this size class, respectively. The density and species richness of all potential prey fish, as well as the density of the most abundant families, fluctuated over time, but were generally higher after 2009 (Fig. 2).

We found no significant relationship between lionfish density and total density and species richness of potential prey fishes, or the density of small wrasses and parrotfish (Fig. 3, Table S3). The one exception was a marginal negative relationship between the densities of damselfish and lionfish (Fig. 3, Table S3). Total and family-specific density and species richness of all potential prey fish increased over time (Fig. 3, Table S3). The effect of year was ~2–5 times greater than the effect of lionfish density on the total density and species richness of prey fishes and the density of small wrasses and parrotfish (Table S3).

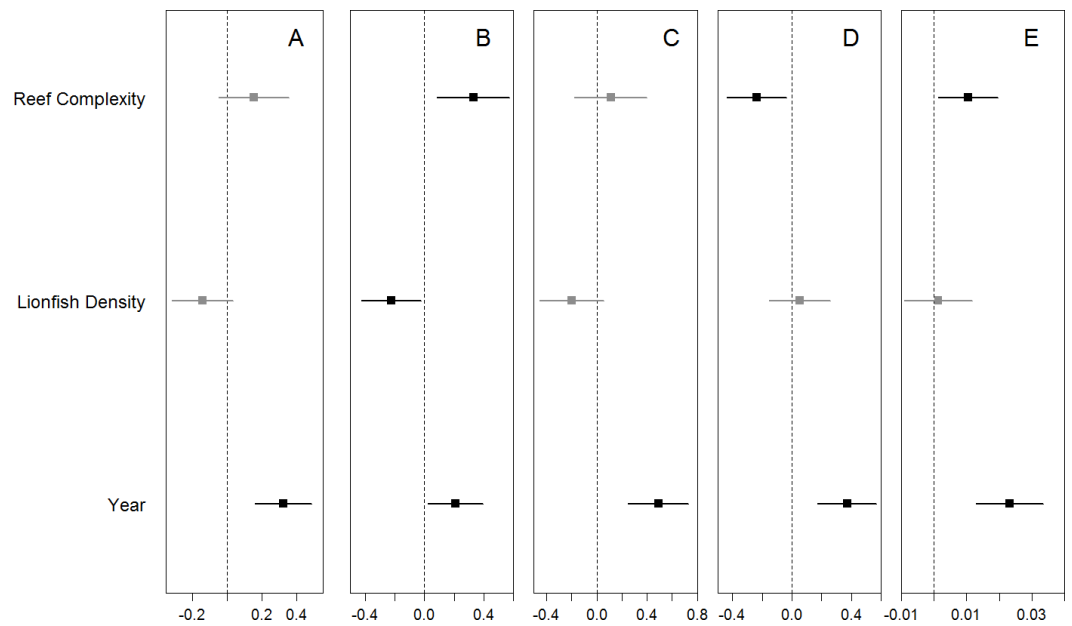


Figure 3 Coefficient estimates (mean \pm 95% confidence interval) for each model. The site-averaged abundance of all potential prey fish (A), the abundance of the most common families (Pomacentridae, Labridae, and Scaridae B–D, respectively), as well as species richness (E) of potential prey fish were each modeled with the predictors of interest (lionfish abundance and years since the lionfish invasion) as well as site-specific reef complexity. Significant coefficient estimates are shown in black while non-significant coefficients are shown in gray (details in Table S3).

The density of small damselfish and parrotfish, as well as the total species richness of potential prey fish, were related to reef complexity, where species richness and damselfish density increased, while parrotfish density decreased with increasing reef complexity (Fig. 3, Table S3). Similarly, none of the prey fish responses were related to lionfish densities when transect level data was used, and year had a positive effect of ~ 2 – 11 times greater than that of lionfish density (Text S2, Table S3). In addition, the density of small prey fish was not significantly different between “high” and “low” lionfish densities, regardless of the categorical threshold density used (25–10 individuals/ha) (Fig. S3). Results were similar for models of prey fish < 5 cm TL when modeled separately, or combined with prey fish 6–10 cm with year having a positive effect ~ 2 – 3 times greater than lionfish density while lionfish density was not related to prey fish density (Text S1, Fig. S4, Table S4).

The PERMANOVA analyses indicated that the community composition of potential prey species changed over time (p -value = $1.0e^{-6}$), but was not related to lionfish density (p -value = 0.54). The NMDS plot of prey species abundance showed that prey fish communities in 2009 were substantially different from prey communities in 2010, 2012, and 2013, which all clustered together (Fig. 4A). However, this separation was not observed on the NMDS plot of prey species using presence/absence data (Fig. 4B), indicating that there was a change prey abundance over time rather than a change in species identity.

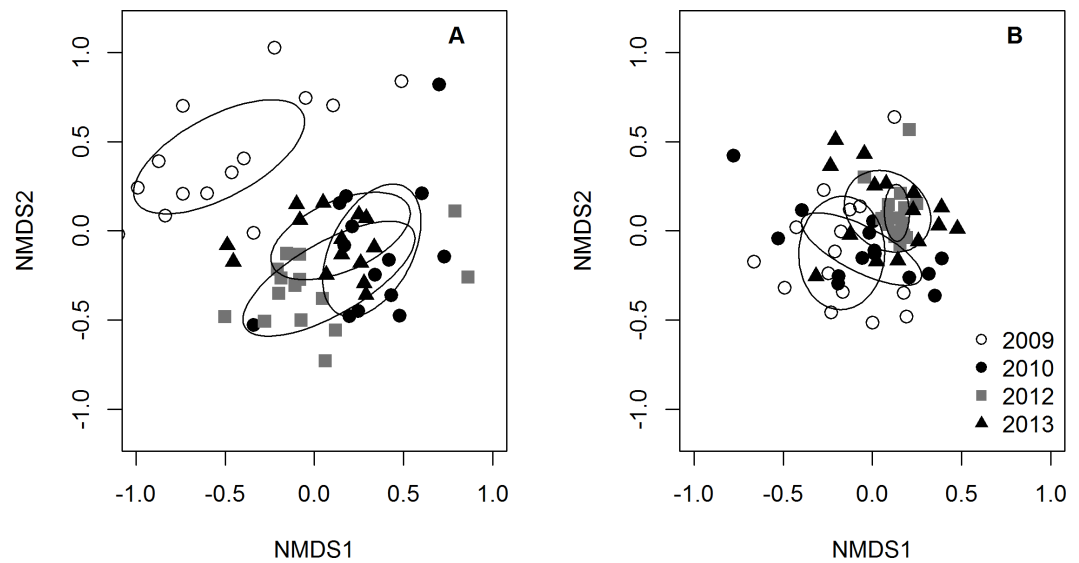


Figure 4 NMDS plots of small prey fish community composition. Community composition was visualized using (A) prey species abundance (density) and (B) prey species presence/absence. Each point represents the average community composition across all transects from each site for each year surveyed. Ellipses are standard deviations of the mean for each year. When using density data, 2009 is distinct from all other years (A) whereas there are no differences between years when using presence/absence data (B).

DISCUSSION

Lionfish density varied greatly across years and sites during our four year, sixteen site study (Fig. S2). We used this variation as a “natural experiment” (i.e., as lionfish density treatments) via a modified BACI design to quantify the effects of invasive lionfish on the community structure of 33 native prey species within the context of natural environmental variability. Despite the broad assumption that lionfish are one the greatest threats to Caribbean reefs, we found no evidence of a general, negative effect on native prey fishes. In fact, total small prey density and species richness *increased* after 2009 (Fig. 2). We also found that species composition shifted over time due to a temporal change in abundance, rather than a change in presence/absence patterns (Figs. 4A–4B). As Belizean reefs are classified as a larval sink (Roberts, 1997), this shift in prey fish abundance could have been due to a larval settlement pulse that coincided with the arrival of lionfish to the region. Alternatively, inter-annual variability in abiotic factors could have increased post-settlement survival (i.e., recruitment) in 2010.

Our finding that lionfish had no apparent effect on native prey communities four years post-invasion is not concordant with most past work. For example, several small-scale manipulations on artificial reefs or isolated patch reefs have documented effects on prey density (Albins & Hixon, 2008; Albins, 2013; Albins, 2015), as have at least two uncontrolled (i.e., the design did not include sites without lionfish for comparison) single site observational studies (Lesser & Slattery, 2011; Green et al., 2012). In contrast, the only previously published, controlled study quantifying community-level responses to naturally occurring lionfish densities on coral reef habitats found the density and richness of native fish

assemblages did not change along ~ 1.5 km of reef within the marine protected area of Archipelago Los Roques National Park in Venezuela (*Elise et al., 2014*).

There are at least four explanations for why the results of lionfish impact studies have been so variable. First, lionfish density—which varies substantially among studies—could strongly influence the effects on native prey and thus study outcomes. Many of the small-scale experimental tests of whether lionfish affects prey populations have used unnaturally high lionfish densities as treatments. For example, *Albins (2013)* added one lionfish to each replicate 4 m^2 artificial reef, which is equivalent to $2,500$ individuals/ha—nearly an order of magnitude greater than the Caribbean record (393.3 ± 144.4 individuals/ha, mean \pm SD, *Green & Côté, 2014*) and ~ 150 times higher than average post-invasion density (16.3 ± 5 individuals/ha) across the BBR (this study). Likewise, using densities of $10,000$ and $3,333$ lionfish/ha, *Albins & Hixon (2008)* found a large decline (79%) in the recruitment of native fishes compared to artificial reefs without lionfish. Besides being an extreme and unrealistic treatment level, such lionfish densities would not be stable because prey would quickly be depleted. Less extreme lionfish densities, experimentally maintained at the maximum recorded density (~ 300 /ha), resulted in more modest declines in abundance and richness of small prey (<10 cm TL) and no effect on 10 – 20 cm (TL) prey (*Albins, 2015*). And in Los Roques National Park, Venezuela, natural lionfish densities of 121 ± 164 individuals/ha had no effect on native prey communities (*Elise et al., 2014*). Likewise, we found no lionfish effects in our regional scale study, in which average post-invasion density was even lower.

The effects of lionfish likely become apparent at different densities (i.e., thresholds), depending on the prey fish community or reef habitat. On patch reefs, the effect of lionfish on the biomass of small prey individuals can be limited if lionfish densities are reduced below a reef-specific threshold (*Green et al., 2014*). The lionfish densities across our sites post-invasion (2012 and 2013) were lower than the threshold of lionfish density (mean \pm SE; $\sim 138.9 \pm 14.7$ individuals/ha) predicted to prevent declines in prey fish on patch reefs in Eleuthera, Bahamas (*Green et al., 2014*). While threshold densities surely vary across habitats, site-specific “thresholds” for our larger fore-reef sites are likely higher than those estimated for smaller patch reefs. This is because reef fish communities are naturally more variable (*Mellin et al., 2010*) and may be more strongly structured by recruitment on isolated patch reefs than on contiguous reef systems (*Ault & Johnson, 1998*). Therefore, it is likely that lionfish densities on our sites were lower than the site-specific “threshold” levels, which could explain why the predicted effects of lionfish were not apparent in our study. Clearly, had densities been far greater (e.g., >300 /ha) across the fore-reefs of the BBR we may have seen larger effects on native prey.

Shortly following the arrival of lionfish in Belize, various management actions were initiated including awareness programs, lionfish fishing tournaments, and market-based approaches (*Searle, Chacon & Bach, 2012; Chapman et al., 2016*). It is possible that these lionfish management strategies have helped control lionfish densities in Belize, at least at sites frequently visited by tourists and dive guides (*Searle, Chacon & Bach, 2012*). However our observed lionfish densities along the BBR are not atypical. In fact, lionfish densities in Belize are comparable to those reported on similar reef habitats in Mexico, Cuba (Bay of Pigs), The Bahamas (San Salvador and Abaco), Colombia, and Venezuela (*Agudo &*

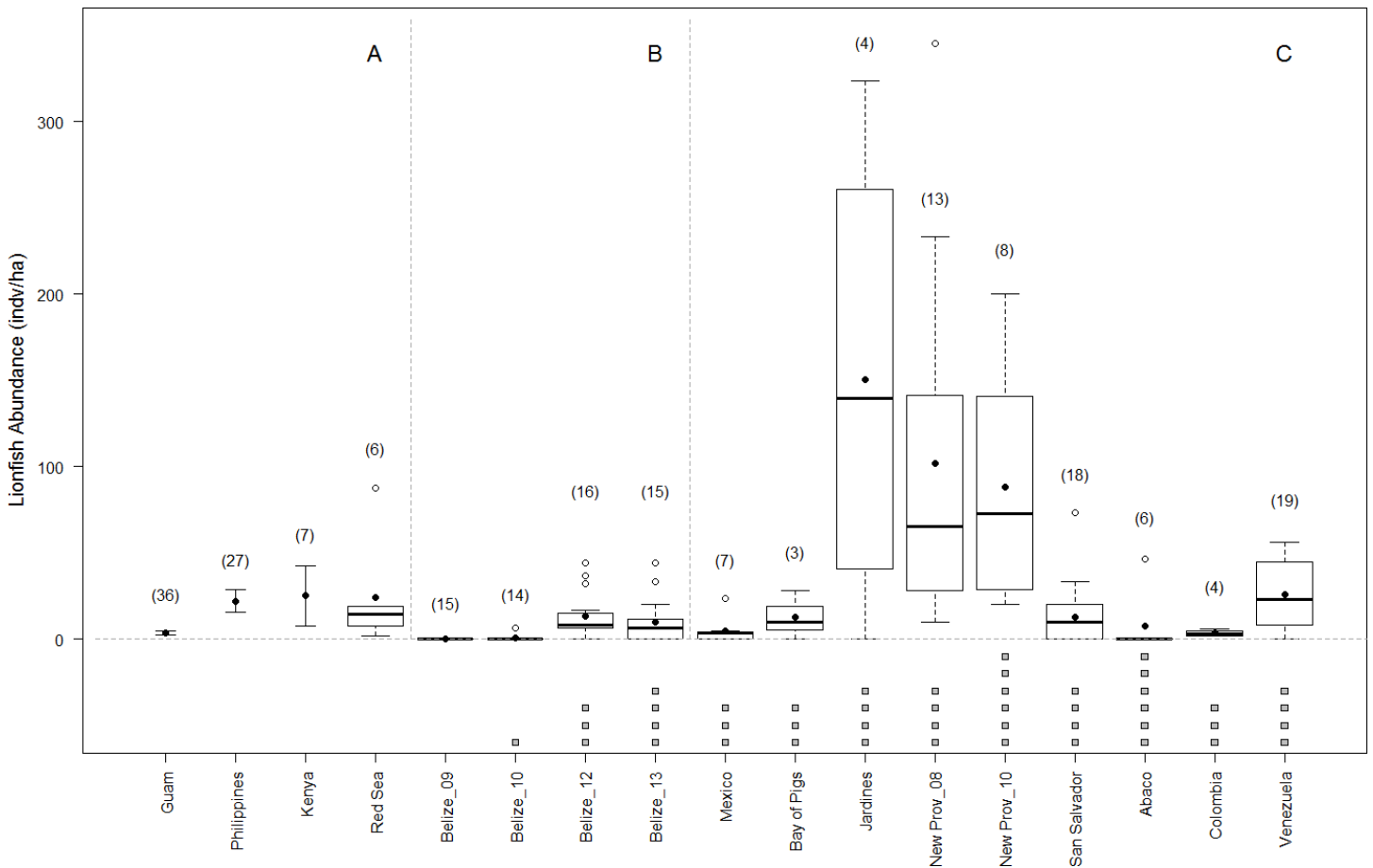


Figure 5 Lionfish abundance on reefs in native and invaded range. Lionfish abundance values published for similar reef habitats and similar depth ranges across the native (A) and invaded range (this study, and other studies B–C, respectively) showing boxplots of site-level data when available. Averages are shown in solid circles. When site-level data was not available, averages are transected by error bars showing published standard deviation. Number of sites surveyed within each region are shown in parentheses. Below the axis, grey boxes indicate number of years since the invasion at the time of the survey of invaded regions. Sources for lionfish density values include (Kulbicki et al., 2011; Agudo & Salas, 2014; Cure, McIlwain & Hixon, 2014; Valdivia et al., 2014; Bayraktarov et al., 2014; McTee & Grubich, 2014; Anton, Simpson & Vu, 2014).

Salas, 2014; Valdivia et al., 2014; Bayraktarov et al., 2014; Anton, Simpson & Vu, 2014), and may be more representative of the Caribbean region than the often-cited densities of New Providence, Bahamas (Green & Côté, 2009) (Fig. 5). Future experiments should focus on realistic density values to better determine the density-dependence of lionfish predation effects (Green et al., 2014) and the threshold below which local management actions (e.g., culling) are likely unnecessary.

Second, lionfish effects could be habitat dependent. Lionfish have invaded a wide range of habitat-types and depth ranges including estuaries, seagrass beds, mangroves, mesophotic reefs, and shallow patch reefs (Barbour et al., 2009; Claydon, Calosso & Traiger, 2011; Jud et al., 2011; Nuttall et al., 2014; Layman, Jud & Nichols, 2014), yet their impacts in these and other invaded habitats is largely unknown (although see an example on one mesophotic reef in Lesser & Slattery, 2011). It is possible that the relative effect of lionfish varies among habitats and could be greater where lionfish densities are especially high, e.g., on deep reefs

(Claydon, Calosso & Traiger, 2011; Lesser & Slattery, 2011; Nuttall et al., 2014; Pinheiro et al., 2016), or where juvenile fish recruit, i.e., mangroves and seagrass beds. Even independent of density, the effects of lionfish could vary among habitat types due to differences in benthic complexity and structure and thus the availability of refugia for prey. Unlike previous shallow-water experiments (mainly performed on sand flats or patch reefs), our study was on deeper, far more physically complex and contiguous fore-reef environments. Effects are also likely dependent on prey productivity, recruitment or immigration from adjacent habitat patches. Most studies reporting effects on native communities have been performed in relatively homogeneous and isolated shallow, patch reef habitats—likely increasing predation and reducing immigration rates relative to a typical fore-reef environment. This could exaggerate predation effects and could explain the contrasting outcomes of different approaches, e.g., effects of lionfish on prey populations could be offset in more connected habitats by recruitment or immigration from surrounding areas (Ault & Johnson, 1998).

The third explanation is that other biotic and abiotic factors that influence prey population dynamics could have stronger effects than lionfish predation in a natural heterogeneous setting. Prey populations are naturally regulated by bottom-up forces such as resource availability, top-down forces such as predation, inter- and intra-specific competition, and stochastic processes such as variability in recruitment or environmental disturbances (Sale, 1977; Shulman, 1984; Jones, 1986; Hunter & Price, 1992; Power, 1992). For example, our results indicate habitat complexity had up to five times greater effect on the density and richness of some families of small reef fishes than lionfish densities. Additionally, we found that the species richness and total prey density, as well as the density of small damselfish, wrasses, and parrotfish increased over time, suggesting that reef fish communities were more strongly structured by inter-annual variability (e.g., annual changes in recruitment or environmental conditions) than by lionfish predation. Such spatiotemporal heterogeneity is generally eliminated in a small-scale, short-term experiment, e.g., where all replicate habitat patches are identical, all other factors that could influence prey population dynamics are held constant, etc. Although these experiments allow us to evaluate the potential role of a given factor, inferences that can be drawn from the results are limited. Such experiments test whether lionfish *could* affect prey communities, not whether they actually do within natural contexts. For example, during experiments that demonstrated a significant effect on reef fish recruits, lionfish comprised ~50–100% of the total predator biomass (Albins & Hixon, 2008; Albins, 2013). In contrast, in our study lionfish were only ~10% of the total potential predator biomass post-invasion (in 2012 and 2013) (Fig. S5, Table S5, Text S3).

The relative importance of lionfish predation compared to natural abiotic and biotic factors in structuring reef fish communities may vary between contexts. For example, lionfish had no detectable effect on reef fish communities on healthy reef fish communities in the Archipelago Los Roques National Park in Venezuela (Elise et al., 2014), suggesting that lionfish are less likely to have apparent impacts in more intact reef ecosystems. The Belizean Barrier Reef is protected by one of the most extensive networks of marine protected areas in the Caribbean (Healthy Reefs Initiative, 2014). These protected reefs may therefore have healthier reef fish assemblages (although see Cox et al., 2017) and be less likely to be measurably affected by invasive lionfish compared to more degraded reef systems.

The fourth, and more overarching, potential explanation is that the effects of lionfish may vary with time since invasion in combination with previously discussed factors. For example, the threshold density at which lionfish measurably effect prey fish is influenced by both lionfish density and prey productivity (*Green et al., 2014*). Therefore, the impacts of lionfish may become apparent if prey productivity decreases or lionfish density increases over time on our study sites. Additionally, a longer time period may be required for impacts of lionfish to become apparent in certain contexts such as complex habitats with ample prey refugia, interconnected reef systems, larval sink ecosystems, or ecosystems with healthy, intact native communities.

In summary, our results suggest that fish communities appear unaffected by lionfish across the sites surveyed along the BBR. In contrast to the outcome of small-scale experiments, larger-scale field studies based on BACI designs have failed to detect negative effects of lionfish predation on native reef fish communities. This could be due to differences in scale, habitat, location, or lionfish density. Future studies of lionfish impacts should focus on quantifying the context dependency of impacts across a range of habitats and lionfish densities, and ideally relative to other threats including fishing, pollution, and climate change.

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Competing Interests

John F. Bruno is an Academic Editor for PeerJ. The remaining authors declare that they have no competing interests.

Author Contributions

- Serena Hackerott conceived and designed the experiments, performed the experiments, analyzed the data, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.
- Abel Valdivia conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, reviewed drafts of the paper.
- Courtney E. Cox conceived and designed the experiments, performed the experiments, contributed reagents/materials/analysis tools, prepared figures and/or tables, reviewed drafts of the paper.
- Nyssa J. Silbiger analyzed the data, prepared figures and/or tables, reviewed drafts of the paper.
- John F. Bruno conceived and designed the experiments, performed the experiments, contributed reagents/materials/analysis tools, reviewed drafts of the paper.

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Data Availability

The following information was supplied regarding data availability:

GitHub: <https://github.com/johnfbruno/Rcode-and-data-for-Hackerott-et-al>.

Supplemental Information

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REFERENCES

- Agudo EA, Salas EK. 2014.** Lionfish abundance, size structure and spatial distribution along the Venezuelan coast (*Pterois volitans*, Pteroinae: Scorpaenidae). *Revista de Biología Tropical* **62**:151–158 DOI [10.15517/rbt.v62i0.15910](https://doi.org/10.15517/rbt.v62i0.15910).
- Albins MA. 2013.** Effects of invasive Pacific red lionfish *Pterois volitans* versus a native predator on Bahamian coral-reef fish communities. *Biological Invasions* **15**:29–43 DOI [10.1007/s10530-012-0266-1](https://doi.org/10.1007/s10530-012-0266-1).
- Albins MA. 2015.** Invasive Pacific lionfish *Pterois volitans* reduce abundance and species richness of native Bahamian coral-reef fishes. *Marine Ecology Progress Series* **522**:231–243 DOI [10.3354/meps11159](https://doi.org/10.3354/meps11159).
- Albins MA, Hixon MA. 2008.** Invasive Indo-Pacific lionfish *Pterois volitans* reduce recruitment of Atlantic coral-reef fishes. *Marine Ecology, Progress Series* **367**:233–238 DOI [10.3354/meps07620](https://doi.org/10.3354/meps07620).
- Albins MA, Hixon MA. 2011.** Worst case scenario: potential long-term effects of invasive predatory lionfish (*Pterois volitans*) on Atlantic and Caribbean coral-reef communities. *Environmental Biology of Fishes* **96**:1151–1157 DOI [10.1007/s10641-011-9795-1](https://doi.org/10.1007/s10641-011-9795-1).

- Albins MA, Lyons PJ. 2012.** Invasive red lionfish *Pterois volitans* blow directed jets of water at prey fish. *Marine Ecology Progress Series* **448**:1–5 DOI [10.3354/meps09580](https://doi.org/10.3354/meps09580).
- Almany GR, Webster MS. 2004.** Odd species out as predators reduce diversity of coral-reef fishes. *Ecology* **85**:2933–2937 DOI [10.1890/03-3150](https://doi.org/10.1890/03-3150).
- Anton A, Cure K, Layman C, Puntilla R, Simpson M, Bruno J. 2016.** Prey naiveté to invasive lionfish *Pterois volitans* on Caribbean coral reefs. *Marine Ecology Progress Series* **544**:257–269 DOI [10.3354/meps11553](https://doi.org/10.3354/meps11553).
- Anton A, Simpson MS, Vu I. 2014.** Environmental and biotic correlates to lionfish invasion success in Bahamian coral reefs. *PLOS ONE* **9**:e106229 DOI [10.1371/journal.pone.0106229](https://doi.org/10.1371/journal.pone.0106229).
- Arias-González JE, González-Gándara C, Luis Cabrera J, Christensen V. 2011.** Predicted impact of the invasive lionfish *Pterois volitans* on the food web of a Caribbean coral reef. *Environmental Research* **111**:917–925 DOI [10.1016/j.envres.2011.07.008](https://doi.org/10.1016/j.envres.2011.07.008).
- Ault TR, Johnson CR. 1998.** Spatially and temporally predictable fish communities on coral reefs. *Ecological Monographs* **68**:25–50 DOI [10.1890/0012-9615\(1998\)068\[0025:SATPFO\]2.0.CO;2](https://doi.org/10.1890/0012-9615(1998)068[0025:SATPFO]2.0.CO;2).
- Barbour AB, Montgomery ML, Adamson AA, Díaz-Ferguson E, Silliman BR. 2009.** Mangrove use by the invasive lionfish *Pterois volitans*. *Marine Ecology Progress Series* **401**:291–294 DOI [10.3354/meps08373](https://doi.org/10.3354/meps08373).
- Bates D, Maechler M, Bolker B, Walker S. 2014.** lme4: linear mixed-effects models using Eigen and S4. Available at <https://cran.r-project.org/web/packages/lme4/index.html>.
- Bayraktarov E, Alarcón-Moscoso J, Polanco FA, Wild C. 2014.** Spatial and temporal distribution of the invasive lionfish *Pterois volitans* in coral reefs of Tayrona National Natural Park, Colombian Caribbean. *PeerJ* **2**:e397 DOI [10.7717/peerj.397](https://doi.org/10.7717/peerj.397).
- Beisner BE, Ives AR, Carpenter SR. 2003.** The effects of an exotic fish invasion on the prey communities of two lakes. *Journal of Animal Ecology* **72**:331–342 DOI [10.1046/j.1365-2656.2003.00699.x](https://doi.org/10.1046/j.1365-2656.2003.00699.x).
- Beukers JS, Jones GP. 1998.** Habitat complexity modifies the impact of piscivores on a coral reef fish population. *Oecologia* **114**:50–59 DOI [10.1007/s004420050419](https://doi.org/10.1007/s004420050419).
- Bjornstad ON. 2013.** ncf: spatial nonparametric covariance functions. Available at <https://cran.r-project.org/web/packages/ncf/index.html>.
- Bruno JF, Fridley JD, Bromberg KD, Bertness MD. 2005.** Insights into biotic interactions from studies of species invasions. In: Sax DF, Stachowica JJ, Gaines SD, eds. *Species invasions: insights into ecology, evolution and biogeography*. Sunderland: Sinauer Press, 13–40.
- Chapman JK, Anderson LG, Gough CLA, Harris AR. 2016.** Working up an appetite for lionfish: a market-based approach to manage the invasion of *Pterois volitans* in Belize. *Marine Policy* **73**:256–262 DOI [10.1016/j.marpol.2016.07.023](https://doi.org/10.1016/j.marpol.2016.07.023).
- Claydon JAB, Calosso MC, Traiger SB. 2011.** Progression of invasive lionfish in seagrass, mangrove and reef habitats. *Marine Ecology, Progress Series* **448**:119–129 DOI [10.3354/meps09534](https://doi.org/10.3354/meps09534).

- Côté IM, Green SJ, Morris Jr JA, Akins JL, Steinke D. 2013. Diet richness of invasive Indo-Pacific lionfish revealed by DNA barcoding. *Marine Ecology Progress Series* 472:249–256 DOI 10.3354/meps09992.
- Cox CE, Valdivia A, McField MD, Castillo KD, Bruno JF. 2017. Establishment of marine protected areas alone does not restore coral reef communities in Belize. *Marine Ecology Progress Series* 563:65–79 DOI 10.3354/meps11984.
- Crowder LB, Cooper WE. 1982. Habitat structural complexity and the interaction between bluegills and their prey. *Ecology* 63:1802–1813 DOI 10.2307/1940122.
- Cure K, McIlwain JL, Hixon MA. 2014. Habitat plasticity in native pacific red lionfish *pterois volitans* facilitates successful invasion of the Atlantic. *Marine Ecology Progress Series* 506:243–253 DOI 10.3354/meps10789.
- Dahl KA, Patterson III WF. 2014. Habitat-specific density and diet of rapidly expanding invasive red lionfish, *pterois volitans*, populations in the northern gulf of Mexico. *PLOS ONE* 9:e105852 DOI 10.1371/journal.pone.0105852.
- Darling ES, Green SJ, O’Leary JK, Côté IM. 2011. Indo-Pacific lionfish are larger and more abundant on invaded reefs: a comparison of Kenyan and Bahamian lionfish populations. *Biological Invasions* 13:2045–2051 DOI 10.1007/s10530-011-0020-0.
- Eby LA, Roach WJ, Crowder LB, Stanford JA. 2006. Effects of stocking-up freshwater food webs. *Trends in Ecology & Evolution* 21:576–584 DOI 10.1016/j.tree.2006.06.016.
- Elise S, Urbina-Barreto I, Boadas-Gil H, Galindo-Vivas M, Kulbicki M. 2014. No detectable effect of lionfish (*Pterois volitans* and *P. miles*) invasion on a healthy reef fish assemblage in Archipelago Los Roques National Park, Venezuela. *Marine Biology* 162:319–330 DOI 10.1007/s00227-014-2571-y.
- Fox J, Weisberg S. 2011. *An R companion to applied regression*. Thousand Oaks: Sage.
- Friedlander AM, Brown EK, Jokiel PL, Smith WR, Rodgers KS. 2003. Effects of habitat, wave exposure, and marine protected area status on coral reef fish assemblages in the Hawaiian archipelago. *Coral Reefs* 22:291–305 DOI 10.1007/s00338-003-0317-2.
- Gido KB, Brown JH. 1999. Invasion of North American drainages by alien fish species. *Freshwater Biology* 42:387–399 DOI 10.1046/j.1365-2427.1999.444490.x.
- Graham MH. 2003. Confronting multicollinearity in ecological multiple regression. *Ecology* 84:2809–2815 DOI 10.1890/02-3114.
- Green SJ, Akins JL, Maljković A, Côté IM. 2012. Invasive lionfish drive atlantic coral reef fish declines. *PLOS ONE* 7:e32596 DOI 10.1371/journal.pone.0032596.
- Green SJ, Côté IM. 2009. Record densities of Indo-Pacific lionfish on Bahamian. *Coral Reefs* 28:107–107 DOI 10.1007/s00338-008-0446-8.
- Green SJ, Côté IM. 2014. Trait-based diet selection: prey behaviour and morphology predict vulnerability to predation in reef fish communities. *Journal of Animal Ecology* 83(6):1451–1460 DOI 10.1111/1365-2656.12250.
- Green SJ, Dulvy NK, Brooks AML, Akins JL, Cooper AB, Miller S, Côté IM. 2014. Linking removal targets to the ecological effects of invaders: a predictive model and field test. *Ecological Applications* 24:1311–1322 DOI 10.1890/13-0979.1.

- Healthy Reefs Initiative.** 2014. Eco-audit of the Mesoamerican Reef countries. Available at <http://www.healthyreefs.org/cms/wp-content/uploads/2014/02/FINAL-ENGLISH-EcoAudit-2014.pdf>.
- Hunter MD, Price PW.** 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* 73:724–732.
- Jones GP.** 1986. Food availability affects growth in a coral reef fish. *Oecologia* 70:136–139 DOI 10.1007/BF00377123.
- Jud ZR, Layman CA, Lee JA, Arrington DA.** 2011. NOTE Recent invasion of a Florida (USA) estuarine system by lionfish *Pterois volitans*/*P. miles*. *Aquatic Biology* 13:21–26 DOI 10.3354/ab00351.
- Kindinger TL.** 2014. Behavioral response of native Atlantic territorial three spot damselfish (*Stegastes planifrons*) toward invasive Pacific red lionfish (*Pterois volitans*). *Environmental Biology of Fishes* 98(2):487–498 DOI 10.1007/s10641-014-0279-y.
- Kulbicki M, Beets J, Chabanet P, Cure K, Darling E, Floeter SR, Galzin R, Green A, Harmelin-Vivien M, Hixon M, Letourneur Y, Loma TL de, McClanahan T, McIlwain J, MouTham G, Myers R, O’Leary JK, Planes S, Vigliola L, Wantiez L.** 2011. Distributions of Indo-Pacific lionfishes *Pterois* spp. in their native ranges: implications for the Atlantic invasion. *Marine Ecology, Progress Series* 446:189–205 DOI 10.3354/meps09442.
- Layman CA, Allgeier JE.** 2011. Characterizing trophic ecology of generalist consumers: a case study of the invasive lionfish in the bahamas. *Marine Ecology, Progress Series* 448:131–141 DOI 10.3354/meps09511.
- Layman CA, Jud ZR, Nichols P.** 2014. Lionfish alter benthic invertebrate assemblages in patch habitats of a subtropical estuary. *Marine Biology* 161:2179–2182 DOI 10.1007/s00227-014-2491-x.
- Lesser MP, Slattery M.** 2011. Phase shift to algal dominated communities at mesophotic depths associated with lionfish (*Pterois volitans*) invasion on a Bahamian coral reef. *Biological Invasions* 13:1855–1868 DOI 10.1007/s10530-011-0005-z.
- Lönngstedt OM, McCormick MI.** 2013. Ultimate predators: lionfish have evolved to circumvent prey risk assessment abilities. *PLOS ONE* 8:e75781 DOI 10.1371/journal.pone.0075781.
- McClanahan TR.** 2014. Recovery of functional groups and trophic relationships in tropical fisheries closures. *Marine Ecology Progress Series* 497:13–23 DOI 10.3354/meps10605.
- McClanahan TR, Graham NAJ, Calnan JM, MacNeil MA.** 2007. Toward pristine biomass: reef fish recovery in coral reef marine protected areas in Kenya. *Ecological Applications* 17:1055–1067 DOI 10.1890/06-1450.
- McClanahan TR, Humphries AT.** 2012. Differential and slow life-history responses of fishes to coral reef closures. *Marine Ecology Progress Series* 469:121–131 DOI 10.3354/meps10009.

- McTee SA, Grubich JR. 2014. Native densities, distribution, and diurnal activity of red sea lionfishes (Scorpaenidae). *Marine Ecology Progress Series* 508:223–232 DOI 10.3354/meps10847.
- Mellin C, Huchery C, Caley MJ, Meekan MG, Bradshaw CJA. 2010. Reef size and isolation determine the temporal stability of coral reef fish populations. *Ecology* 91:3138–3145 DOI 10.1890/10-0267.1.
- Morris JA, Akins JL. 2009. Feeding ecology of invasive lionfish (*Pterois volitans*) in the Bahamian archipelago. *Environmental Biology of Fishes* 86:389–398 DOI 10.1007/s10641-009-9538-8.
- Nuttall MF, Johnston MA, Eckert RJ, Embesi JA, Hickerson EL, Schmahl GP. 2014. Lionfish (*Pterois volitans* [Linnaeus, 1758] and *P. miles* [Bennett, 1828]) records within mesophotic depth ranges on natural banks in the Northwestern Gulf of Mexico. *BioInvasions Records* 3:111–115 DOI 10.3391/bir.2014.3.2.09.
- Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O’Hare RB, Simpson GL, Solymos P, Stevens MHH, Wagner H. 2013. Package “vegan”. Available at <https://cran.r-project.org/web/packages/vegan/index.html>.
- Persson L, Eklov P. 1995. Prey refuges affecting interactions between piscivorous perch and juvenile perch and roach. *Ecology* 76:70–81 DOI 10.2307/1940632.
- Pinheiro HT, Goodbody-Gringley G, Jessup ME, Shepherd B, Chequer AD, Rocha LA. 2016. Upper and lower mesophotic coral reef fish communities evaluated by underwater visual censuses in two Caribbean locations. *Coral Reefs* 35:139–151 DOI 10.1007/s00338-015-1381-0.
- Polunin NVC, Roberts CM. 1993. Greater biomass and value of target coral-reef fishes in two small Caribbean marine reserves. *Marine Ecology Progress Series* 100:167–176 DOI 10.3354/meps100167.
- Power ME. 1992. Top-down and bottom-up forces in food webs: do plants have primacy. *Ecology* 73:733–746 DOI 10.2307/1940153.
- Roberts CM. 1997. Connectivity and management of caribbean coral reefs. *Science* 278:1454–1457 DOI 10.1126/science.278.5342.1454.
- Rocha LA, Rocha CR, Baldwin CC, Weight LA, McField MD. 2015. Invasive lionfish preying on critically endangered reef fish-Springer. *Coral Reefs* 34:803–806 DOI 10.1007/s00338-015-1293-z.
- Sale PF. 1977. Maintenance of high diversity in coral reef fish communities. *The American Naturalist* 111:337–359 DOI 10.1086/283164.
- Sax DF, Stachowicz JJ, Brown JH, Bruno JF, Dawson MN, Gaines SD, Grosberg RK, Hastings A, Holt RD, Mayfield MM, O’Connor MI, Rice WR. 2007. Ecological and evolutionary insights from species invasions. *Trends in Ecology & Evolution* 22:465–471 DOI 10.1016/j.tree.2007.06.009.
- Schofield P. 2009. Geographic extent and chronology of the invasion of non-native lionfish (*Pterois volitans* [Linnaeus 1758] and *P. miles* [Bennett 1828]) in the Western North Atlantic and Caribbean Sea. *Aquatic Invasions* 4:473–479 DOI 10.3391/ai.2009.4.3.5.

- Schofield P. 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. *Aquatic Invasions* 5:S117–S122
[DOI 10.3391/ai.2010.5.S1.024](https://doi.org/10.3391/ai.2010.5.S1.024).
- Searle L, Chacon N, Bach L. 2012.** The Belize lionfish management plan: an overview of the invasion, mitigation activities and recommendations. In: *ECOMAR technical publications no 1*. Belize City: ECOMAR.
- Shulman MJ. 1984.** Resource limitation and recruitment patterns in a coral reef fish assemblage. *Journal of Experimental Marine Biology and Ecology* 74:85–109
[DOI 10.1016/0022-0981\(84\)90039-X](https://doi.org/10.1016/0022-0981(84)90039-X).
- Simberloff D. 1981.** Community effects of introduced species. In: *Biotic crises in ecological and evolutionary time*. New York: Academic Press, 53–81.
- Valdez-Moreno M, Quintal-Lizama C, Gómez-Lozano R, García-Rivas M del C. 2012.** Monitoring an alien invasion: DNA barcoding and the identification of lionfish and their prey on coral reefs of the Mexican Caribbean. *PLOS ONE* 7:e36636
[DOI 10.1371/journal.pone.0036636](https://doi.org/10.1371/journal.pone.0036636).
- Valdivia A, Bruno JF, Cox CE, Hackerott S, Green SJ. 2014.** Re-examining the relationship between invasive lionfish and native grouper in the Caribbean. *PeerJ* 2:e348
[DOI 10.7717/peerj.348](https://doi.org/10.7717/peerj.348).
- Webster MS, Almany GR. 2002.** Positive indirect effects in a coral reef fish community. *Ecology Letters* 5:549–557 [DOI 10.1046/j.1461-0248.2002.00355.x](https://doi.org/10.1046/j.1461-0248.2002.00355.x).
- Wiles GJ, Bart J, Beck RE, Aguon CF. 2003.** Impacts of the brown tree snake: patterns of decline and species persistence in guam's avifauna. *Conservation Biology* 17:1350–1360 [DOI 10.1046/j.1523-1739.2003.01526.x](https://doi.org/10.1046/j.1523-1739.2003.01526.x).