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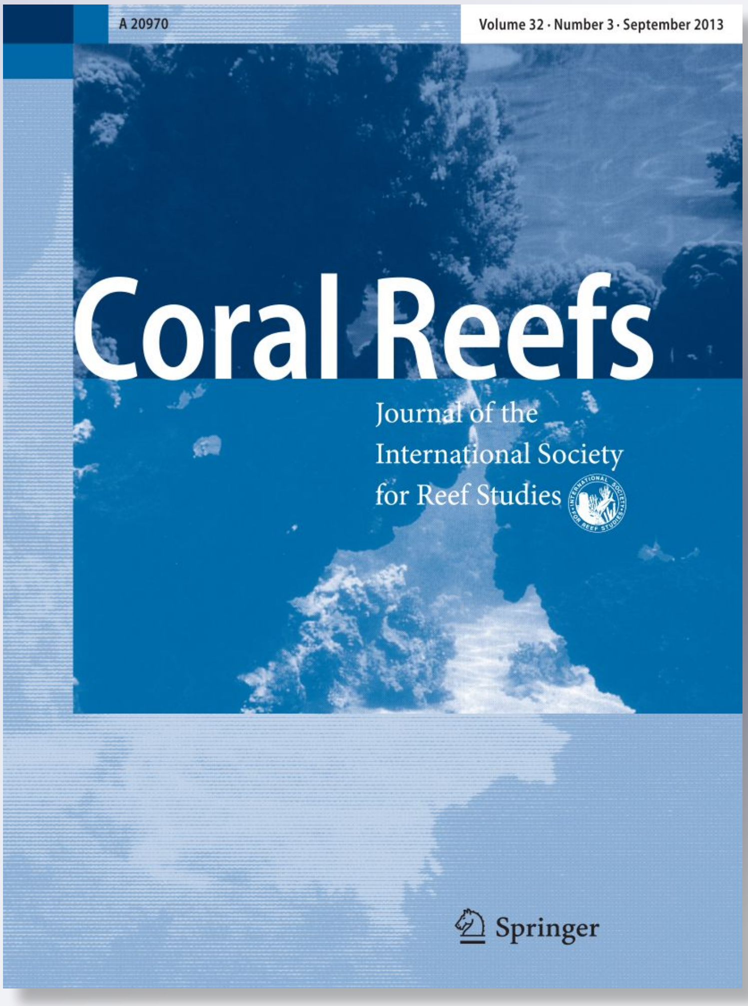

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NOTE

Is the lionfish invasion waning? Evidence from The Bahamas

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Abstract Indo-Pacific lionfishes (*Pterois volitans/miles*) have undergone rapid population growth and reached extremely high densities in parts of the invaded Atlantic. However, their long-term population trends in areas without active management programs are unknown. Since 2005, we have monitored lionfish abundance in the Exuma Cays of the central Bahamas on 64 reefs ranging in size from 1 to 4000 m^2. Lionfish densities increased from the first sighting in 2005 through 2009, leveled off between 2010 and 2011, and then began to decrease. By 2015, densities had noticeably declined on most of these reefs, despite a lack of culling or fishing efforts in this part of The Bahamas. There was no consistent change in lionfish size structure through time. We discuss possible causes of the decline, including reductions in larval supply or survival, hurricanes, interactions with native species, and intraspecific interactions. Further studies are required to determine whether the declines will persist. In the meantime, we recommend that managers continue efforts to control invasive lionfish abundances locally.

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Keywords Habitat scaling · Marine invasion · Population growth · Time series

Introduction

Indo-Pacific lionfishes (*Pterois volitans/miles*; hereafter lionfish) began a period of rapid population growth on Atlantic coral reefs in the early 2000s and have since spread throughout the tropical and subtropical western Atlantic (Whitfield et al. 2002; Schofield 2010; Ruttenberg et al. 2012; Dahl and Patterson 2014). Combined with their high population densities, lionfish are a concern due to their strong negative effects on native reef fishes via direct predation (reviews by Albins and Hixon 2013; Côté et al. 2013a). As a result, invasive lionfish are the focus of management efforts throughout the region, and in various local areas these efforts have reduced lionfish population densities and shifted size distributions downward (Frazer et al. 2012; de León et al. 2013).

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Tracking local abundances and body sizes of invasive species through time is essential to understand the dynamics of invasions (Bøhn et al. 2004; Simberloff and Gibbons 2004). However, there have been no investigations of long-term trends in invasive lionfish abundance and size in regions that lack control strategies. Therefore, we examined local populations of lionfish in the Exuma Cays, The Bahamas, to determine the patterns of lionfish abundance and size over the first 10 yr of the invasion in an area relatively free from human influence. The Bahamas is a hot spot of high lionfish abundances [up to approximately 400 ha^{-1} of continuous reef (Green and Côté 2009) and 8 m^{-2} on small artificial patch reefs (Benkwitt 2013)] and strong ecological effects at multiple spatial scales (Albins and Hixon 2008; Lesser and Slattery 2011; Green et al. 2012, 2014; Albins 2013, 2015; Benkwitt 2015, 2016; Ingeman and Webster 2015; Kindinger and Albins 2017). Importantly, no lionfish removal efforts have occurred in our remote study area, which is sparsely inhabited by humans.

We compared trends in the population densities of lionfish to those of Nassau grouper (*Epinephelus striatus*), a large native predator on these reefs. Nassau grouper are abundant in the study region, presumably in part due to low human population density corresponding to low fishing intensity (Stallings 2009). Nassau grouper were chosen as a comparison species because they are both potential predators (Maljković et al. 2008) and potential competitors (O'Farrell et al. 2014; Raymond et al. 2015) of lionfish. Therefore, we predicted that if the observed declines in lionfish abundances were caused by an increase in competition with or predation by native predators, then there may be an increase in Nassau grouper abundance as lionfish abundance decreased. On the other hand, if broad-scale processes (e.g., changes in abiotic conditions) were responsible for the observed changes in abundance of lionfish, then we expect Nassau grouper abundance and lionfish abundance to follow similar trajectories through time.

Materials and methods

To determine patterns of lionfish abundance and body size over the first decade of the invasion, we examined fish survey data collected in the Exuma Cays, The Bahamas, from when lionfish first arrived in the study area in 2005 through 2015. We surveyed reef-resident fishes at three spatial scales: (1) small patch reefs; (2) medium-sized patch reefs; and (3) large reefs (Fig. 1; Electronic supplementary material, ESM, Fig. S1).

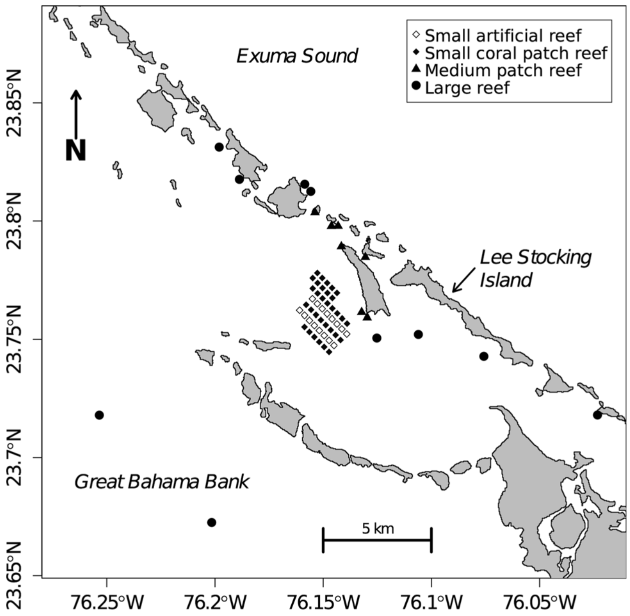

Fig. 1 Map of study area around Exuma Cays, The Bahamas

Small reefs included 32 coral patch reefs (ca. 6 m^2) as well as 16 artificial reefs (ca. 1 m^2) constructed of concrete blocks (Carr and Hixon 1997). These small reefs are arranged in a matrix on a sand and sea grass flat 3–6 m deep on the Great Bahama Bank, with 200 m between adjacent reefs and at least 1 km to the nearest large natural reef. As these reefs were often used in field experiments during summer recruitment seasons, we analyzed only censuses that were conducted before any manipulations each year. Surveys were conducted annually from June to August during 2005–2015, with the exception of 2006 and 2012–2014, years during which logistical constraints prevented surveys. A pair of trained observers recorded the abundance and visually estimated body size (to nearest cm total length, TL) of all resident fishes on each reef. Censuses consisted of divers slowly circling the reefs at distances of ∼3, ∼1, and 0 m and then using flashlights to thoroughly search all holes and crevices.

Medium-sized reefs comprised six natural coral patches (ca. 6 to 23 m^2, mean: 10.3 m^2). These reefs, ranging in depth from 2 to 4 m on sand and limestone bench, were each approximately 50 m from the nearest adjacent reef. Fish populations on these reefs were never manipulated, and all resident fishes were censused in 2006–2012 and 2015 following the same protocol as for the small reefs. Surveys were conducted annually in June or July except in 2006 when surveys were conducted in March.

At the largest scale, ten reefs (ca. 1400 to 4000 m^2) ranging in depth from 2 to 11 m were surveyed as part of a long-term lionfish manipulation experiment (Albins 2015) (see ESM for additional methods). All resident fishes in 400 m^2 survey areas (two 10 × 10 m plots and four 2 × 25 m^2 transects) were censused on each reef. For this analysis, we compared fish surveys that were conducted in

June 2009, before any lionfish manipulations, to surveys conducted in July/August 2015, 3 yr after the experiment of Albins (2015) was completed. Lionfish were never manipulated on one of these large reefs, which was isolated from other reefs (nearest reef ~5.5 km away). We examined a complete time series of surveys on this particular reef, including censuses conducted in both winter (November–February) and summer (June–August) of 2009, 2010, 2011, and in summer of 2012 and 2015.

To account for non-independence among repeated surveys on the same reefs, we used linear and generalized linear mixed-effects models to examine temporal trends in density and size of lionfish and Nassau grouper (Zuur et al. 2009). The size data were modeled using a normal distribution; residual plots indicated that the data met the assumptions of normality and homogeneity for both species. The density data violated the assumptions of normality and homogeneity, so abundance was modeled using a negative binomial distribution (log link) with reef area as an offset to account for differences in reef size (Zuur et al. 2009). Due to inconsistencies in the frequency of surveys among reef types, we conducted separate models for: (1) small artificial reefs, small natural patch reefs, and medium-sized patch reefs (surveyed approximately annually 2005–2015) with year, reef type, and a year–reef type interaction as fixed effects and reef as a random effect; (2) large reefs (surveyed in 2009 and 2015) with year as a fixed effect and reef as a random effect; and (3) the single large reef (surveyed approximately biannually 2009–2015) with year as a fixed effect and subsample as a random effect. Because we predicted that there would be a positive change in density in the years prior to peak density and a negative trend in density in the years after the peak, we conducted separate models for the years prior to the peak and after the peak for lionfish on small and medium reefs and the single large reef. To maintain consistency, we also conducted separate models for the years prior to and after the highest density for Nassau grouper. All statistical analyses were conducted in R version 3.0.2 (R Core Team 2013) with associated package lme4 (Bates et al. 2015).

Results and discussion

Lionfish densities on small and medium reefs increased by an estimated 70.6% per year (95% confidence interval, CI 69.6 to 71.7%) until peaking between 2010 and 2011, then subsequently declined by an estimated 16.6% per year (95% CI −5.7 to −26.3%) until the end of the study in 2015 (Fig. 2; ESM Table S1). On the single large reef, lionfish densities increased by an estimated 23.1% per year (95% CI 9.0–39.1%) until December 2011, then declined by an estimated 71.5% per year (95% CI −44.5 to −85.4%) until 2015 (Fig. 2; ESM Table S1). On all large reefs combined, there was a nonsignificant decline in lionfish density by an estimated 18.6% (95% CI −35.8 to 2.3%) between 2009 and 2015 (Fig. 2; ESM Table S1).

Prior to their peak densities in 2010–2011, density of Nassau grouper exhibited significant increases on small natural patch reefs (estimate: 13.2%, 95% CI 7.6–19.0%) and the single large reef (est: 65%, 95% CI 6.8–156.2%), marginal increases on medium-sized patch reefs (est: 15.7%, 95% CI 0.11–33.8%) and no significant temporal trend on small artificial reefs (est: −1.5%, 95% CI −7.8 to 5.2%) (Fig. 3; ESM Table S2). Nassau grouper also exhibited significant declines in density across several spatial scales after 2010–2011, but the magnitudes of decline were less than those observed for lionfish (Fig. 3; ESM Table S1). Density of Nassau grouper declined by an estimated 9.1% per year (95% CI −3.9 to −14.1%) on small and medium reefs, and by an estimated 28.6% per year (95% CI −0.4 to −48.7%) on the single large reef. On all large reefs combined, there was no significant change in Nassau grouper density between 2009 and 2015 (est: 0%, 95% CI −9.5–10.5%).

Prior to peak densities, mean lionfish size decreased on small natural patch reefs and on the single large reefs by an estimated 1.8 cm yr^{-1} (95% CI −0.26 to −3.4) and 1.7 cm yr^{-1} (95% CI −1.1 to −2.2), respectively (Fig. 2; ESM Table S1; ESM Figs. S2–S6). There was no significant trend in lionfish size on any other reef type before the peak nor was there a significant trend in lionfish size on any reef in the years following peak density (Fig. 2; ESM Table S1; ESM Figs. S2–S6). The only significant temporal trend in Nassau grouper size occurred on small and medium reefs prior to the peak, with mean body size decreasing by 0.49 cm yr^{-1} (95% CI −0.29 to −0.70; Fig. 3; ESM Table S2).

At present, these trends raise more questions than they answer. First, what caused the observed declines in lionfish densities? We can rule out direct removal of lionfish by humans given that there are no active culling programs or targeted lionfish fisheries in the area. If there were unreported removals, one would expect a shift in size distribution toward smaller individuals as population density decreased (Frazer et al. 2012; de León et al. 2013), which was not observed.

It is conceivable that a decline in larval recruitment limited population size. If lionfish recruited to the region from elsewhere, then reductions in spawning biomass of source populations due to lionfish fisheries in other areas may have lowered larval supply. However, modeling efforts suggest a high proportion of self-recruitment and local retention of lionfish larvae within The Bahamas (Johnston and Purkis 2015). Moreover, the closest annual lionfish fishing competition to the study area is over

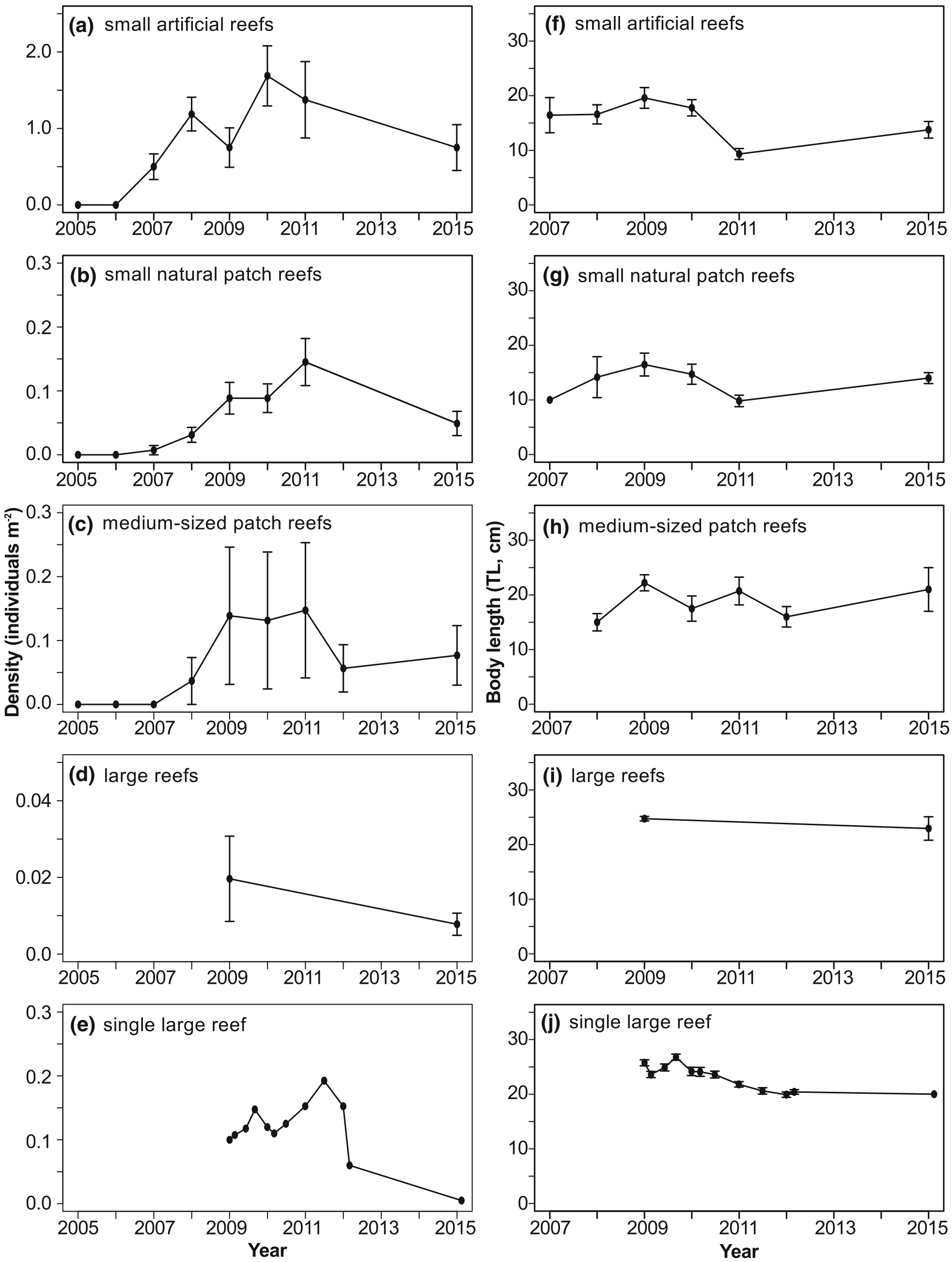

Fig. 2 Time series (mean ± SE) of densities (**a**–**e**) and lengths (**f**–**j**) of invasive lionfish on reefs of different sizes in the Exuma Cays, The Bahamas: **a**, **f** 16 small artificial reefs, **b**, **g** 32 small natural patch reefs, **c**, **h** 6 medium-sized patch reefs, **d**, **i** 10 large reefs and **e**, **j** single large reef. Note that *y*-axis scales vary among reef types

350 km away in Abaco, The Bahamas, and the intensity of fishing required to cause recruitment failure is extremely high (Morris et al. 2010; Barbour et al. 2011; Johnston and Purkis 2015). The likelihood of naturally caused reductions in larval supply or survival is difficult to evaluate due to a paucity of information on the early life stages of lionfish and the difficulty in finding new recruits of lionfish. In our surveys, lionfish recruits (<5 cm TL) were observed only on small reefs. However, recruitment limitation is a possibility given that the abundance of lionfish recruits on these reefs significantly increased until 2011 and then declined significantly after 2011 ($\chi^2 = 11.4$, $p < 0.001$; $\chi^2 = 14.0$, $p < 0.001$, respectively), mirroring patterns in overall abundance of lionfish through time. Furthermore, given the concurrent decline in Nassau grouper densities from 2010/2011 to 2015, regional decline in larval recruitment remains a possible explanation.

Similarly, broad-scale changes in abiotic conditions may explain the declines in both lionfish and Nassau grouper densities. While there may have been concurrent changes in abiotic conditions, the most extreme example was Hurricane Irene, which passed through the region in August 2011. Immediately following this Category 3 hurricane, lionfish were absent from many of the study reefs,

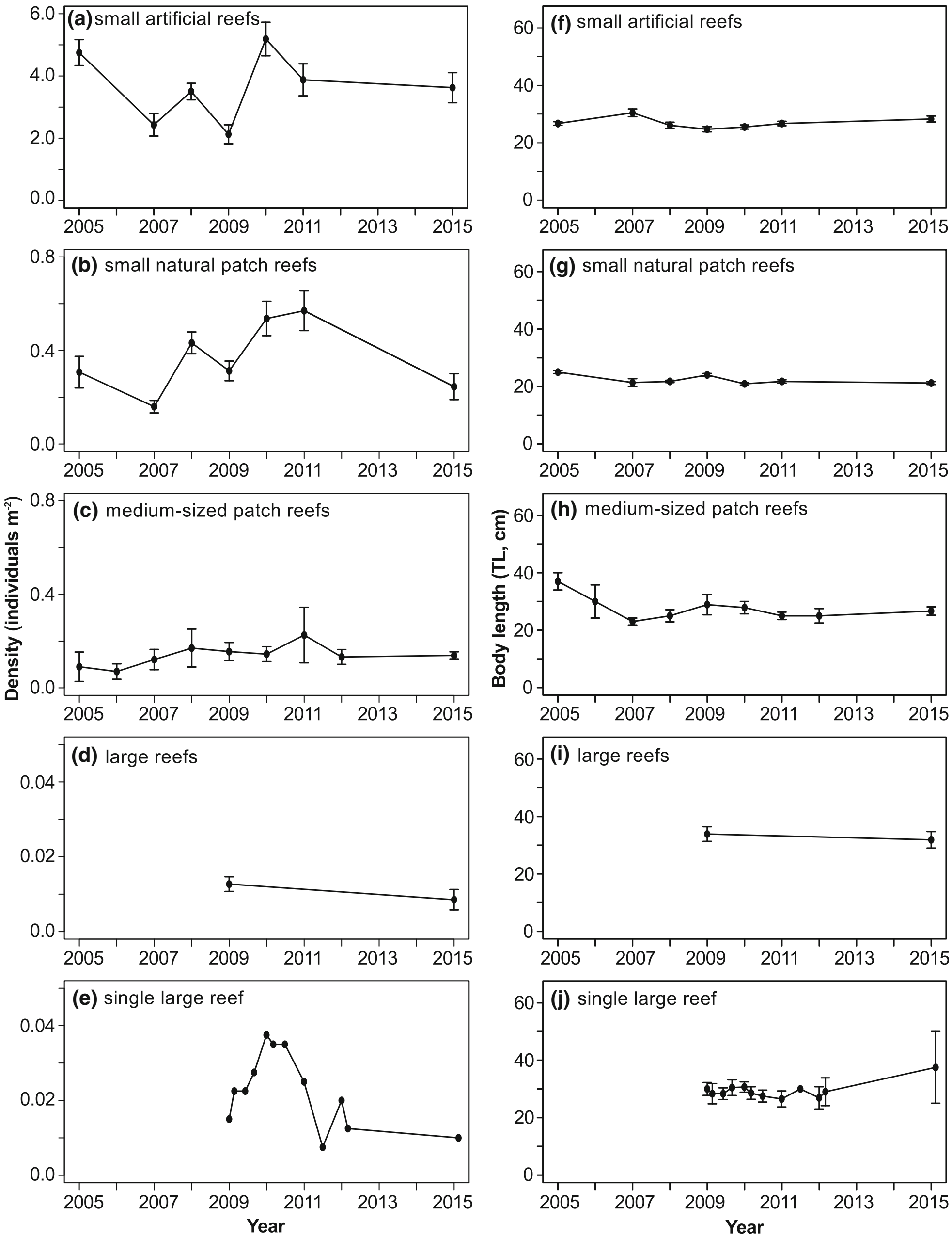

Fig. 3 Time series (mean ± SE) of densities (**a**–**e**) and lengths (**f**–**j**) of Nassau grouper on reefs of different sizes in the Exuma Cays, The Bahamas: **a**, **f** 16 small artificial reefs, **b**, **g** 32 small natural patch reefs, **c**, **h** 6 medium-sized patch reefs, **d**, **i** 10 large reefs and **e**, **j** single large reef. Note that *y*-axis scales vary among reef types

suggesting large-scale mortality and/or redistribution. However, one would expect lionfish to recover quickly after this disturbance given their rapid colonization (Dahl et al. 2016) and growth rates (Pusack et al. 2016), especially compared to Nassau grouper (Beets and Hixon 1994).

Interactions with native species could also be responsible for the observed declines. However, previous studies have indicated that lionfish are not substantially affected by native competitors (Albins 2013; Raymond et al. 2015) or predators (Hackerott et al. 2013; but see Ellis and Faletti 2016). Combined with the fact that abundances of Nassau grouper did not increase during the study, it is unlikely that increased competition or predation by native predators caused the declines in lionfish abundances. Similarly, lionfish are relatively free from parasites compared to native Atlantic reef fishes (Sellers et al. 2015; Tuttle et al. 2017). Nevertheless, the susceptibility of invasive species to native parasites can increase after establishment (Torchin and Mitchell 2004), and thus, the possibility that a recent infection by a parasite or disease caused the decline in lionfish cannot be eliminated.

Given that lionfish apparently interact with native competitors, predators, and parasites only weakly, intraspecific interactions among lionfish may be a more likely cause of the observed population declines.

Conspecifics have been found in the gut contents of lionfish from multiple regions (Valdez-Moreno et al. 2012; Côté et al. 2013b), suggesting that cannibalism among lionfish may occur naturally in the wild, albeit infrequently. Furthermore, lionfish at experimentally high densities exhibit slower growth rates likely due to intraspecific competition for food (Benkwitt 2013, 2015), which could be beginning to limit their population sizes. The observed decrease in lionfish size on some reefs as population density increased is consistent with this hypothesis and is similar to temporal trends in body size of other invasive species (Bøhn et al. 2004; Phillips and Shine 2005; Gutowsky and Fox 2011).

In addition to raising questions regarding the cause of these patterns, it is also unclear whether similar declines have occurred elsewhere. To our knowledge, there have been no other reported declines in lionfish abundances in areas without removal efforts. Additional studies of these phenomena are warranted to determine where such declines occur and whether these declines are temporary, permanent or cyclical. Importantly, given the preliminary nature of these patterns, management efforts to control the lionfish invasion should continue in earnest.

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