ORIGINAL PAPER

Effects of invasive Pacific red lionfish *Pterois volitans* versus a native predator on Bahamian coral-reef fish communities

Mark A. Albins

Abstract The recent irruption of Pacific red lionfish (*Pterois volitans*) on Caribbean and Atlantic coral reefs could prove to be one of the most damaging marine invasions to date. Invasive lionfish are reaching densities much higher than those reported from their native range, and they have a strong negative effect on the recruitment and abundance of a broad diversity of native coral-reef fishes. Otherwise, little is known about how lionfish affect native coral-reef communities, especially compared to ecologically similar native predators. A controlled field experiment conducted on small patch-reefs in the Bahamas over an 8-week-period demonstrated that (1) lionfish caused a reduction in the abundance of small native coral-reef fishes that was 2.5 ± 0.5 times (mean $\pm$ SEM) greater than that caused by a similarly sized native piscivore, the coney grouper *Cephalopholis fulva* (93.7 vs. 36.3 % reduction); (2) lionfish caused a reduction in the species richness of small coral-reef fishes (loss of 4.6 ± 1.6 species), whereas the native piscivore did not have a significant effect on prey richness; (3) the greatest effects on the reef-fish community, in terms of both abundance and richness, occurred when both native and invasive predators were present; and (4) lionfish grew significantly faster (>6 times) than the native predator under the same field conditions. These results suggest that invasive lionfish have stronger ecological effects than similarly sized native piscivores, and may pose a substantial threat to native coral-reef fish communities.

Keywords Invasive species · Coral reefs · Predation · Community structure · Piscivory · Marine fishes

Introduction

Some of the most damaging biological invasions, in terms of loss of native species and disruption of ecosystems, have resulted from the introduction of non-native predatory freshwater fishes (e.g., Ogutu-Ohwayo 1990; Thomas 1993; Jackson 2002; Pyke 2008). Introductions of non-native predatory diadromous fishes have also resulted in invasions that have negatively affected native communities and ecosystems (e.g., Christie 1974; Simon and Townsend 2003).

In contrast, while some strictly marine fishes have been introduced into new ecosystems by humans, both intentionally and unintentionally, relatively few of these introductions have resulted in the establishment of self-sustaining, reproductive populations (Baltz 1991; Randall 1987). Examples of marine fishes which have become established after introduction include the

M. A. Albins (✉)
Department of Zoology, Oregon State University, 3029 Cordley Hall, Corvallis, OR 97331, USA
e-mail: albinsm@science.oregonstate.edu

peacock grouper (*Cephalopholis argus*) and the blue-lined snapper (*Lutjanus kasmira*), both of which were introduced intentionally to the Hawaiian archipelago in the 1950s in an attempt to augment nearshore fisheries (Randall 1987). *C. argus* now constitutes more than 80 % of the large piscivore biomass on some reefs in the main Hawaiian Islands (Dierking et al. 2009), and *L. kasmira* has become one of the most numerous reef fishes across a large part of the Hawaiian archipelago (Randall 1987; Friedlander et al. 2002).

Very few studies have examined the effects of introduced marine fishes on native communities (Helfman 2007). Most such studies were conducted decades after the introductions occurred and were restricted to observational rather than experimental approaches. Thus, while some evidence exists that introduced marine fishes, when successful, may cause deleterious changes in native ecosystems (Friedlander et al. 2002; Bariche et al. 2004; Goren and Galil 2005; Schumacher and Parrish 2005; Dierking et al. 2009), unequivocal causal linkages between these introductions and observed changes in native systems are lacking (*but see* Albins and Hixon 2008).

Few marine fish introductions have resulted in range expansions as rapid or extensive as that recently demonstrated by lionfish (*Pterois volitans*) in the Western Atlantic and Caribbean. Lionfish were initially introduced, likely via the aquarium trade, to coastal waters of southeast Florida in the mid-to-late 1980s (Semmens et al. 2004). Since the early 2000s, their range has expanded rapidly throughout the tropical and sub-tropical Western Atlantic Ocean and Caribbean Sea (Schofield 2009, 2010). In addition to their rapid range expansion, invasive lionfish are of particular concern for several reasons. Lionfish in the Atlantic demonstrate high individual growth and reproductive rates (Morris and Whitfield 2009) and high population growth rates (Albins and Hixon 2011). They are reaching higher densities (nearly five times greater) in the invaded range (Green and Côté 2009) than have been reported from their native Pacific range (Kulbicki et al. 2012). Invasive lionfish also appear to reach larger maximum sizes in the invaded range (Whitfield et al. 2007) than have been reported from their native Pacific (Randall et al. 1990).

Novel traits of introduced predators and naïveté of native prey to such traits are generally thought to contribute to predator invasion success and may result in strong relative effects of invasive predators on native prey (Sih et al. 2010). Invasive mammalian and avian predators across a variety of systems have been shown to have stronger effects on native prey than do native predators (Salo et al. 2007). However, at least one study of an invasive predatory freshwater fish has found the opposite (Baber and Babbitt 2003), indicating that in some situations, non-native predators may be relatively poorly adapted to capture and consume certain native prey.

Lionfish demonstrate a suite of predatory characteristics and behaviors that is novel in the invaded system, and which may confer a high degree of predatory efficiency relative to native piscivores (Albins and Hixon 2011; Albins and Lyons 2012). A combination of slow stalking movements, cryptic coloration, elongated fin rays, and numerous spine-like and fleshy projections on the head and face, may provide crypsis, or cause lionfish to appear like a harmless plant or invertebrate, resulting in reduced prey vigilance (Albins and Hixon 2011). When hunting, lionfish slowly approach prey with their large fan-like pectoral fins flared and held perpendicular to their body (Allen and Eschmeyer 1973). Prey are often herded into a corner and consumed with a rapid strike (Albins and Hixon 2011). When approaching prey, lionfish occasionally direct jets of water at the prey fish. This recently documented predatory behavior of *P. volitans* appears to be unique among piscivores, may confuse the lateral-line sensory system of prey and/or may increase the incidence of head-first capture (Albins and Lyons 2012). Prey species that have coexisted with predator species over long periods are likely to evolve traits that reduce the risk of predation. In contrast, prey encountering a newly introduced alien predator with novel characteristics, such as lionfish with their unique morphology and predatory behaviors, may not recognize the invader as a threat and may lack morphological or behavioral traits to reduce risk.

Lionfish consume a broad diversity of native Atlantic coral-reef fishes (Albins and Hixon 2008; Morris and Akins 2009) and appear to have strong effects on native prey. A previous field experiment demonstrated that single lionfish are capable of reducing overall recruitment of native coral-reef fishes to small patch-reefs by nearly 80 % over short time periods (Albins and Hixon 2008) and an observational study has documented 65 % reductions in the biomass of fish prey on invaded reefs (Green et al. 2012).

Such large reductions in populations of small fishes could have detrimental effects on native coral-reef communities in a variety of ways (Albins and Hixon 2011). First, if lionfish reduce the number of juveniles substantially, then they could have a negative effect on realized adult abundances of a wide range of species. Second, lionfish could have substantial indirect negative effects on native piscivores by reducing prey availability. While native piscivore populations are already severely reduced across a majority of the Caribbean due to overfishing, relatively healthy populations still exist in remote locations with low human populations and inside some marine reserves (Stallings 2009). Invasive lionfish have reached some of the most remote reefs and readily enter reserves. Therefore, potential competitive interactions between lionfish and native piscivores could inhibit conservation and stock rebuilding efforts for these species. Third, if lionfish cause reductions in the survival of juvenile herbivorous fish, then the invasion could have far reaching, destabilizing effects on entire coral-reef ecosystems by reducing herbivory, thereby allowing seaweeds to outcompete or otherwise inhibit reef-building corals (Mumby et al. 2006). Additionally, lionfish could have broad effects on coral-reef ecosystems by consuming other ecologically important species, such as cleaners, the loss of which could result in reduced reef fish abundance and diversity (Losey et al. 1999; Côté 2000).

This potential for lionfish to cause indirect destabilizing effects on native coral reefs is of particular concern because these ecosystems have already been substantially degraded by a suite of disturbances, including overfishing, pollution, and climate change (Mora 2008). In short, what is currently known of the ecology of lionfish suggests that this predator could manifest one of the most damaging marine-fish invasions to date (Sutherland et al. 2010; Albins and Hixon 2011).

While a previous field experiment demonstrated that lionfish caused reductions in the abundance of prey-sized native fishes (Albins and Hixon 2008), that study did not provide an explicit frame-of-reference for evaluating the magnitude of the lionfish effect. The question remains how the effect of invasive lionfish compares to that of similarly sized native predators. Additionally, the effects of lionfish on aspects of community composition other than overall abundance (such as species richness, evenness, and diversity)

have not yet been examined. The current study explores the effects of lionfish on native reef-fish communities relative to those of a common, similarly sized, native predator, the coney grouper (*Cephalopholis fulva*). This study addresses the following questions: (1) How do the effects of lionfish on native reef-fish communities compare to those of a similarly sized native predator? (2) What are the combined effects of invasive lionfish and the native predator on native reef-fish communities? (3) Does the presence of lionfish affect the growth rates of the native predator (and vice versa)? (4) How do growth rates compare between invasive and native predators under identical field conditions?

Materials and methods

Study site and experimental design

The study systems were communities of small (≤ 5 cm total length [TL]) native fishes on coral patch-reefs near Lee Stocking Island, Bahamas. I used an existing matrix of 32 live-coral patch reefs, each approximately 4 m², which were translocated in the early 1990s and are now essentially natural features (Carr and Hixon 1995; Hixon and Carr 1997). These experimental reefs are separated from the nearest natural reefs by at least 1 km and from each other by about 200 m (Fig. 1). The degree of spatial isolation among reefs, coupled with relatively featureless intervening habitat (flat, sandy, seagrass beds), meant that the resident reef-fish communities could be treated as independent replicates (i.e., negligible juvenile and adult movement among reefs) subject to regional levels of larval settlement.

I conducted a baseline census of all fishes on all 32 reefs at the beginning of the summer of 2008. I then selected a subset of reefs (n = 20) and separated them into five blocks of four reefs each. Blocks were based on similarity of the pre-existing reef-fish communities as determined by the number of individuals in major groups of strong interactors, including resident piscivores and territorial damselfishes. Because this was an experimental manipulation of native and invasive piscivores, I first removed all resident adult piscivores from the experimental reefs (after removals, no immigrant resident piscivores were observed on experimental reefs during the study). I then randomly
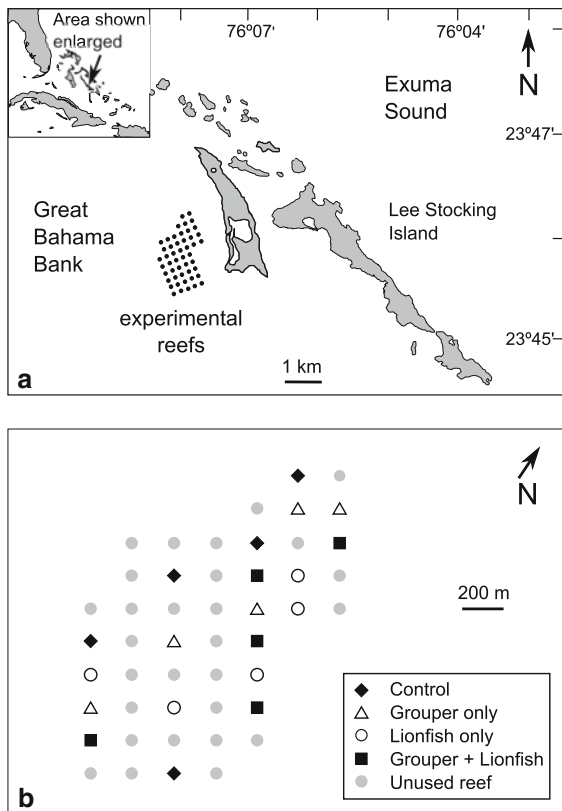
Fig. 1 **a** Matrix of patch reefs near Lee Stocking Island, Bahamas. **b** Experimental design showing treatment assignments. *Grey symbols* represent unused reefs. Map redrawn from Almany (2003)

assigned four different predator treatments to the four reefs in each of the five blocks.

The treatments were (1) a single native grouper, (2) a single invasive lionfish, (3) one grouper and one lionfish together, and (4) a predator-free control. While predator-free patch reefs are naturally rare in this system, the experimental control reefs provided a baseline against which to estimate, and thus compare the effects of the native and invasive predators. The experimental design deliberately confounded the number of resident predators with predator identity because that is the nature of this invasion: a new species was added to the existing native community. Before the lionfish invasion, it would have been typical to find patch reefs with one or two small resident coney grouper; now it is more typical to find one or two small lionfish on such reefs in addition to the original resident piscivores. Therefore, the single native-predator treatment could be viewed as a simplified pre-invasion food

web, while the combined predator treatment represented the current post-invasion situation common to reefs in the Bahamas, a situation likely to become the norm across the majority of Western Atlantic and Caribbean coral reefs (Morris and Whitfield 2009; Schofield 2009, 2010). The lionfish-only treatment provided a comparison of effect sizes between the two predator species, and could also be interpreted to represent a possible future scenario where lionfish have excluded or replaced native predators.

Resident-predator treatments were established by transplanting onto the experimental reefs from other reefs far from the study sites. Predators were captured using small hand nets, held in buckets, and transplanted as quickly as possible with as little handling as possible. There were no obvious indications of handling effects, as post-transplant predator behaviors appeared normal. However, handling effects were not examined explicitly.

In order to examine predator growth rates, I measured (to the nearest 0.1 cm TL) and wet weighed (to the nearest 0.1 g) all transplanted predators at the beginning and again at the end of the experiment. All predators in each block were of similar size at the outset of the experiment. The average length of transplanted lionfish ($\pm$ SEM) was 7.1 ± 0.4 cm TL, and their average mass was 4.0 ± 0.5 g. Transplanted grouper were, on average, 7.0 ± 0.3 cm TL, and weighed, on average, 4.7 ± 0.7 g. At the end of the experiment, all native coney grouper were released, and all lionfish were euthanized for further study.

The coney grouper was chosen as a model native predator for several reasons. First, it is a common species in the region and is readily collected and transplanted onto experimental reefs (e.g., Stallings 2008). Second, it is comparable in size to lionfish, both in terms of maximum adult size and size of individuals available in the study area. Third, its diet is similar to that of lionfish, consisting primarily of small reef fishes, and secondarily of small reef invertebrates (Randall 1967). Finally, and most importantly, several previous experiments had demonstrated that the coney is an effective predator of small reef fishes in the study system (Almany 2003, 2004a, b; Stallings 2008).

Following predator transplants, I monitored the community of small native coral-reef fishes on all experimental reefs at ca. 1 week intervals for 8 weeks during the summer 2008 recruitment period (July–September). Censuses were conducted by two divers using SCUBA,

who counted and sized all fishes ≤5 cm TL on each reef following methods described by Hixon and Beets (1989, 1993). I assumed that variation in natural processes affecting reef-fish abundance and community composition—including settlement, resource availability, and predation by transient predators, etc.—would be distributed among experimental reefs with negligible bias. Therefore, I attributed observed differences in reef-fish abundance and community composition arising over the course of the experiment to the predator treatments themselves (e.g., the mean difference in the change in abundance of small fish between lionfish-only reefs and predator-free control reefs represented mortality caused by the lionfish).

During the summer months in this region, coral-reef fishes settle (i.e., make the transition from pelagic larvae to reef-dwelling juveniles) in relatively large numbers. During the winter months, fish abundances typically decline as mortality exceeds recruitment. Since this experiment ran through the summer, I expected to see increasing numbers of new recruits, resulting in a positive change in abundance of small native fishes, on all reefs over the course of the experiment. "Recruitment" in this context is defined as an observable increase in the abundance of juvenile reef fishes due to larval settlement (Jones 1991). I also expected other changes in the community, such as changes in species diversity, to be driven primarily by recruitment, with differences among treatments reflecting the effects of different predators on small–bodied species and on post-settlement juveniles of both small-bodied and large-bodied species.

Statistical analyses

Community response variables included change in abundance (ΔN), change in species richness (ΔS), change in species evenness (ΔJ), and change in species diversity ($\Delta H'$) of small (≤ 5 cm TL) native fishes. I calculated ΔN for each reef census as the abundance of each species of reef fish minus the abundance of that species at the baseline census for that particular reef, totaled across species:

$$\Delta N_{ti} = \sum_{j=1}^{s} n_{tij} - n_{0ij} \tag{1}$$

where ΔN_{ti} was the change in abundance for reef i at census t, and n_{tij} was the abundance of species j on reef i at census t. Therefore, ΔN represented the overall change in abundance for all species on each reef between the baseline census and each consecutive census. The change in species richness (ΔS) was calculated for each reef as the change in the number of species of small fish between the baseline census and each consecutive census. Similarly, ΔJ and $\Delta H'$ were calculated as the change in Pielou's J (Pielou 1966), and the change in the Shannon-Wiener index H' (Pielou 1966) between the baseline census and each consecutive census. I also examined the differences in baseline abundance, richness, evenness, and diversity of small native reef fishes among reefs assigned to the four predator treatments at the beginning of the experiment (before establishment of predator treatments).

I used linear mixed-effects models (LMM), with two categorical explanatory variables, predator treatment and time step, and a random intercept for each experimental reef, to draw inferences regarding the effects of predator treatments on the four community-change indices (ΔN, ΔS, ΔJ, and $\Delta H'$) over the course of the experiment. I chose to include time step as a categorical variable, rather than a continuous variable, because I did not want to assume a linear relationship between the response variables and time. I used reef, rather than block, as the random term in the models due to the nested nature of the data (multiple observations of each reef across time steps). Likelihood Ratio Tests (LRT) with a correction for testing-on-the-boundary (Verbeke and Molenberghs 2000) indicated that inclusion of the random reef term resulted in significantly better fits for each of the response variables (Online Resource 1).

Initial visual examination of the standardized residuals from LMMs for each of the response variables indicated departures from the assumptions of homogeneity of variance and independence. Based on this graphical evidence, I fit three alternative LMMs for each response variable, one incorporating heteroscedasticity among treatments, one incorporating temporal autocorrelation among observations within each reef (using the AR(1) autoregressive model), and one incorporating both of these variance and correlation structures. I compared the resulting models using Akaike's Information Criterion (AIC) and used the optimal models for hypothesis testing (Online resource 1). Visual examination of standardized residuals from the final optimal models indicated that all statistical assumptions, including homogeneity, independence, and normality, were met.

I used t-tests within this *LMM* framework, to evaluate six a priori hypotheses regarding differences in each of the response variables among the four predator treatments at the end of the experiment. I also fit similar models to those described above, but with abundance, richness, evenness, and diversity (rather than the *change* in each of these) as response variables in order to evaluate whether these metrics differed among reefs assigned to the four predator treatments at the baseline census (before establishment of predator treatments).

I used a generalized least squares model (*GLS*) with two categorical variables, *species* (lionfish or grouper) and *treatment* (presence vs. absence of the other predator), to draw inferences about differences in length growth rates. I used an *LMM* with the same fixed structure, but with random intercepts for each reef, to draw inferences about differences in mass growth rates. Inclusion of a random term for *reef* was not found to improve the model fit based on corrected *LRT*s for length growth, but inclusion of a random term for *reef* provided the best fit for mass growth (Online Resource 1). Visual examination of residuals indicated increasing variance with fitted values and heteroscedasticity between *species* for length growth and between both *species* and *treatment* for mass growth. Incorporation of heteroscedasticity in each of the models provided better fits, based on *AIC*, than did equal variance models (Online Resource 1). Examination of the residuals from the optimal models suggested that all assumptions including homogeneity, independence, and normality, were met. Once the best fitting models in terms of random effects and variance structures were selected, I refit each model using Maximum Likelihood estimation, and used *LRT*s to test for significance of the *species* and *treatment* terms and to reduce the models in a backwards-selection procedure described in Zuur et al. (2009).

To further evaluate the effects of the four predator treatments on the native reef-fish community, I used a combination of multivariate ordination, using non-metric multidimensional scaling (NMDS, Kruskal and Wish 1978; McCune and Grace 2002), and a permutation-based Multivariate Analysis of Variance (perMANOVA, McArdle and Anderson 2001), with 1,000 permutations constrained within experimental blocks. I ran this analysis once for all experimental reefs at the beginning of the experiment (before establishment of predator treatments), and again for all experimental reefs at the conclusion of the experiment (week 8). Before conducting the NMDS ordinations and perMANOVAs, I transformed the original community matrices using a log transformation ($\log[x + 1]$) to moderate the influence of dominant species in relation to rarer species. I chose not to relativize by species in order to avoid giving rare species an inordinate influence on the outcome. I also chose not to relativize by sample units to avoid losing information about differences in total abundance of native fish among the experimental reefs. I used Bray-Curtis distances for both the NMDS ordinations and perMANOVA hypothesis testing (Bray and Curtis 1957). NMDS ordination routines followed the guidelines outlined in McCune and Grace (2002) and included multiple random starts (up to 20, with up to 50 iterations each) at varying levels of dimensionality (1–5 axes) to ensure that the global solution was reached, and that the choice of dimensionality was appropriate. I also used Monte-Carlo tests based on 50 runs with randomized data to ensure that the ordinations were extracting stronger axes than would be expected by chance (McCune and Grace 2002). For ease of interpretation, the ordination for the final census data was rotated for maximum correlation between the change-in-abundance (ΔN) and the first axis.

All statistical analyses were conducted in the *R* software environment (*R* Development Core Team 2011) and used the associated packages *MASS* (Venables and Ripley 2002), *nlme* (Pinheiro et al. 2011) and *vegan* (Oksanen et al. 2011). Evaluation of *LMM*s and selection of appropriate random structures followed the guidelines and procedures described in Zuur et al. (2009). For all hypothesis testing, *p* values less than 0.05 were considered to represent strong evidence against the null hypotheses, whereas *p* values between 0.05 and 0.10 were considered to represent marginal evidence against the null hypotheses. A comparison of univariate and multivariate responses indicated that communities of small native reef-fishes at the beginning of the experiment were essentially similar among experimental reefs assigned to the four treatments (see Online Resource 2 and Fig. 4a).

Results

Native reef-fish abundance

Over the course of the 8 week experiment the abundance of small native reef fish (≤ 5 cm TL) increased by 66.6 ± 10.4 fish per reef (*mean* $\pm$ *SEM*) on predator-free control reefs (Fig. 2), increased somewhat less on native grouper reefs (42.4 ± 6.1 fish per reef), and remained near baseline levels on lionfish reefs (4.2 ± 5.8 fish per reef) and combined predator reefs (-5.8 ± 6.8 fish per reef). Compared to predator-free controls, single lionfish reduced the change-in-abundance (ΔN) by 62.4 ± 11.9 fish per reef (t = 5.25, $p < 0.001$), representing an average reduction of 93.7 %. ΔN on native-grouper-only reefs was 24.2 ± 12.0 fish per reef lower, on average, than ΔN on control reefs, an effect that was marginally significant (t = 2.01, $p = 0.061$). The negative effect of lionfish on ΔN was 2.6 ± 0.5 times stronger than the effect of the native predator (t = 4.52, $p < 0.001$). Compared to reefs with native grouper only, net recruitment to reefs with both predators present was reduced by 48.2 ± 9.2 fish per reef (t = 5.26, $p < 0.001$).

Most of the overall change in abundance on predator-free control reefs (ΔN) was due to increases in the abundance of two common species, bridled goby *Coryphopterus glaucofraenum* and beaugregory damselfish *Stegastes leucostictus*. Fourteen other species in ten different families contributed to the increase (Table 1, Online Resource 3). These included three herbivores—redband parrotfish *Sparisoma aurofrenatum*, stoplight parrotfish *S. viride*, and doctorfish *Acanthurus chirurgus*—and one facultative cleaner—Spanish hogfish *Bodianus rufus*. Of these sixteen contributors, the average change in abundance of fifteen species (including all three herbivores and *B. rufus*) was lower on both lionfish-only reefs and reefs with both predators present than on control reefs. The exception was goldspot goby *Gnatholepis thompsoni*, which increased slightly more on lionfish reefs and combined predator reefs than on control reefs. The mean change in abundance of twelve of the sixteen species, including two of the three herbivores and *B. rufus*, was also lower on grouper-only reefs than on control reefs. A notable exception included *S. viride*, which increased substantially more on grouper-only reefs than on control reefs.
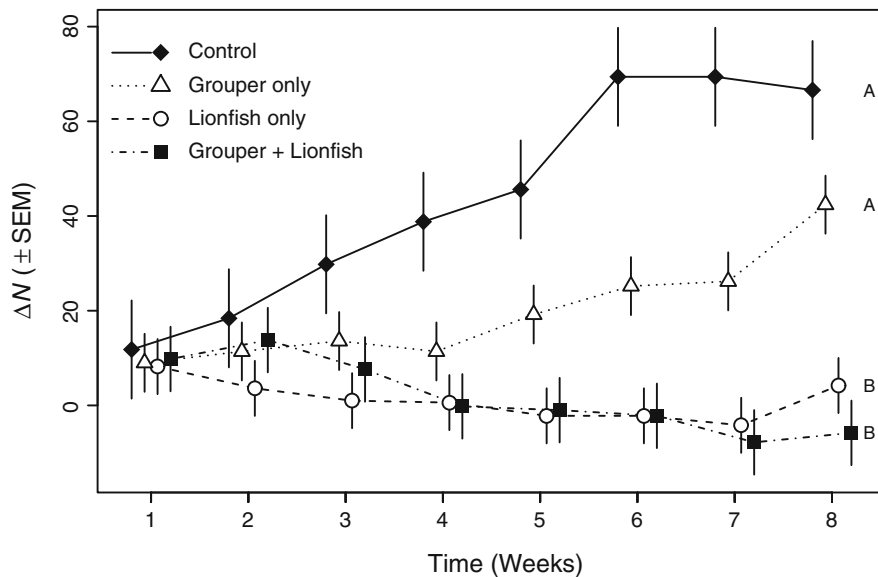

Fig. 2 Change in abundance ΔN (mean $\pm$ SEM) of small fish (≤ 5 cm TL) on experimental coral patch-reefs under four different predator treatments: predator-free controls (*solid diamonds*), native grouper only (*open triangles*), invasive lionfish only (*open circles*), and combined grouper + lionfish (*solid squares*). N = 5 patch reefs per treatment. *Values* represent the change in abundance between the baseline census (before establishment of predator treatments) and each subsequent weekly census. *Letters* on the *right side of the plot* indicate the results of pairwise comparisons among the treatments at the final census (matching *letters* indicate a *p*-value >0.05). *Symbols* are offset along the x-axis to facilitate viewing

Table 1 Mean change in abundance (individuals per reef) of small native coral-reef fishes on predator-free control reefs ($\Delta N_{control}$) over the course of the 8-week experiment and the effect of each predator treatment on the mean change in abundance for each reef-fish species

Family	Species	Control ($\Delta N_{control}$)	Grouper effect ($\Delta N_{grouper} - \Delta N_{control}$)	Lionfish effect ($\Delta N_{lionfish} - \Delta N_{control}$)	Combined effect ($\Delta N_{grouper+lionfish} - \Delta N_{control}$)
Gobiidae	*Coryphopterus glaucofraenum*	35.2	−12.4	−30.4	−32.6
Pomacentridae	*Stegastes leucostictus*	18.2	−14.2	−19.6	−19.6
Gobiidae	*Gnatholepis thompsoni*	5.0	0.6	1.2	1.2
Labrisomidae	*Malacoctenus macropus*	4.0	−3.8	−4.4	−6.6
Scaridae	*Sparisoma aurofrenatum*	4.0	−0.6	−2.0	−1.6
Scaridae	*Sparisoma viride*	1.8	4.8	−3.4	−5.2
Labridae	*Halichoeres pictus*	1.8	−0.6	−1.8	−1.8
Acanthuridae	*Acanthurus chirurgus*	0.6	−0.6	−0.6	−0.8
Pomacentridae	*Stegastes partitus*	0.6	0.0	−0.4	−1.4
Tetraodontidae	*Canthigaster rostrata*	0.6	−0.6	−0.8	−0.4
Gobiidae	*Priolepis hipoliti*	0.2	0.0	−0.4	−0.2
Labridae	*Halichoeres poeyi*	0.2	−0.6	−0.6	−0.2
Serranidae	*Serranus tigrinus*	0.2	−0.2	−0.2	−0.2
Haemulidae	*Haemulon* sp. (juvenile)	0.2	−0.2	−0.2	−0.2
Scorpaenidae	*Scorpaena plumieri*	0.2	−0.2	−0.2	−0.2
Labridae	*Bodianus rufus*	0.2	−0.4	−0.2	−0.2
Scaridae	*Cryptotomus roseus*	0.0	0.0	0.0	−0.4
Gobiidae	*Gobiosoma genie*	0.0	−0.2	−0.2	−0.2
Pomacanthidae	*Holocanthus tricolor*	0.0	0.0	0.0	−0.2
Holocentridae	*Sargocentron coruscum*	0.0	0.0	0.0	−0.2
Gobiidae	*Coryphopterus dicrus*	0.0	0.0	0.4	0.0
Labridae	*Halichoeres radiatus*	0.0	0.0	0.0	−0.4
Apogonidae	*Apogon binotatus*	0.0	0.0	0.4	−0.2
Acanthuridae	*Acanthurus coeruleus*	0.0	0.0	0.0	0.2
Apogonidae	*Apogon townsendi*	0.0	0.2	0.2	0.0
Apogonidae	*Apogon maculatus*	0.0	0.0	0.0	0.2
Serranidae	*Epinephelus guttatus*	0.0	0.0	0.0	−0.2
Pomacanthidae	*Holacanthus ciliaris*	0.0	0.0	−0.2	0.0
Holocentridae	*Holocentrus adscensionis*	0.0	−0.6	0.0	−0.4
Labridae	*Halichoeres maculipinna*	−0.2	−0.2	−0.2	−1.4
Serranidae	*Cephalopholis cruentatus*	−0.2	0.2	0.2	0.2
Pomacentridae	*Stegastes variabilis*	−0.2	0.2	0.2	0.2
Labrisomidae	*Malacoctenus macropus*	−0.2	0.2	0.2	0.0
Haemulidae	*Haemulon plumierii*	−0.4	0.4	0.2	−0.2
Labridae	*Thalassoma bifasciatum*	−0.4	0.4	−2.2	0.0
Callionymidae	*Paradiplogrammus bairdi*	−0.6	0.2	0.2	0.4
Scaridae	*Scarus taeniopterus*	−0.6	1.0	0.4	−0.8
Scaridae	*Sparisoma atomarium*	−0.6	0.4	−0.2	0.0
Labridae	*Halichoeres garnoti*	−0.8	1.0	0.0	−1.0
Pomacentridae	*Chromis cyanea*	−2.2	2.0	2.2	2.2
Total		66.6	−23.8	−62.4	−72.2

The treatment effects are calculated as the difference between mean change in abundance on control reefs at week 8 ($\Delta N_{control}$) and mean change in abundance on grouper only ($\Delta N_{grouper}$), lionfish only($\Delta N_{lionfish}$), and grouper + lionfish ($\Delta N_{grouper+lionfish}$) treatment reefs at week 8 (e.g., grouper effect = $\Delta N_{grouper} - \Delta N_{control}$). Table is sorted by increasing change in abundance on control reefs. *Haemulon melanurum*, *Malacoctenus triangulatus*, *Pseudupeneus maculatus*, and *Paralichthys albigutta* were also counted during reef censuses, but did not change in mean abundance over the course of the experiment on any of the four treatments

Predator growth rates

Lionfish growth rates were >6 times greater, in terms of both length (t = 9.56, $p < 0.001$) and mass (t = 11.38, $p < 0.001$), than growth rates of coney grouper under the same field conditions. Over the course of the experiment, lionfish increased in length by 0.80 ± 0.06 mm per day and in mass by 0.26 ± 0.02 g per day, while grouper increased in length by 0.13 ± 0.02 mm per day and in mass by 0.04 ± 0.01 g per day. By the end of the 8 week experiment, lionfish were therefore, on average, 11.6 cm TL and 18.6 g, whereas native grouper were 7.7 cm TL and 6.9 g. Lionfish did not appear to have an effect on growth rates of native grouper, and grouper had no detectable effect on lionfish growth rates (length: L-ratio$_{5,4}$ = 0.01, $p = 0.936$; mass: L–ratio$_{8,7}$ = 0.22, $p = 0.642$).

Native reef-fish richness, evenness and diversity

The species richness of small reef fishes increased by 3.4 ± 1.1 species on predator-free control reefs over the summer recruitment period, remained similar to baseline conditions on grouper only (1.0 ± 1.1 species) and lionfish only reefs (−1.2 ± 1.1 species), and dropped by 5.4 ± 1.1 species on combined grouper + lionfish reefs (Fig. 3a). Compared to controls, lionfish caused a reduction in ΔS of 4.6 ± 1.6 species (t = 2.84, $p = 0.011$). The mean of ΔS was 2.4 ± 1.6 species lower on grouper-only reefs than control reefs. However, this grouper effect was not significant (t = 1.48, $p = 0.157$). The effect of lionfish on ΔS was, on average, 1.9 ± 0.7 times larger than the effect of native grouper, although the difference between the two effect sizes was not significant (t = 1.36, $p = 0.193$). However, the effect of lionfish and grouper together was 2.7 ± 0.7 times stronger than the effect of grouper alone (t = 3.95, $p = 0.001$), resulting in a net reduction in ΔS of 6.4 ± 1.6 species compared to grouper-only reefs.

Over the course of the experiment, species evenness dropped by 0.12 ± 0.03 on the predator-free control reefs, changed little on the grouper-only (−0.04 ± 0.04) and lionfish-only reefs (−0.01 ± 0.04), and dropped by 0.14 ± 0.03 on the combined predator reefs (Fig. 3b). Compared to controls, lionfish-alone caused an increase of 0.10 ± 0.05 in ΔJ (t = 2.27, $p = 0.037$). On the grouper-alone reefs, ΔJ was

0.08 ± 0.05 higher than on the control reefs, and the difference between the two treatments was marginally significant (t = 1.76, $p = 0.096$). While each of the predator species alone appeared to have a positive effect on ΔJ, the combined native-invasive predator treatment resulted in drop in ΔJ of 0.13 ± 0.03, similar to that observed on the predator-free control reefs. Compared to the effect of grouper alone, the combined predator treatment caused a marginally significant reduction in ΔJ of 0.10 ± 0.05 (t = 2.07, $p = 0.054$).

The Shannon-Wiener species diversity index (H') remained relatively constant over the course of the experiment on predator-free control reefs (−0.06 ± 0.13), grouper-only reefs (−0.01 ± 0.13), and lionfish-only reefs (−0.1 ± 0.13), but declined by 0.73 ± 0.13 on combined grouper + lionfish reefs (Fig. 3c). Neither grouper alone (t = 0.27, $p = 0.791$) nor lionfish alone (t = 0.22, $p = 0.826$) caused differences in $\Delta H'$ compared to predator-free controls. However, the combined native-invasive predator treatment caused a reduction in $\Delta H'$ of 0.72 ± 0.18 compared to the native-only treatment (t = 4.02, $p = 0.001$).

Multivariate community response

An NMDS ordination of communities at the beginning of the experiment illustrated a high degree of overlap among reefs across the four treatments (final stress = 18.07, linear r^2 = 0.83, Monte-Carlo $p = 0.02$, Fig. 4a). Results of a perMANOVA suggested that no pronounced community differences existed among treatment groups at the beginning of the experiment (pseudo-F$_{16,3}$ = 0.67, $p = 0.890$).

In contrast, an ordination of the small reef-fish communities at the end of the experiment illustrated clear differences among the four predator treatments in terms of species composition and relative abundances (final stress = 12.81, linear r^2 = 0.92, Monte-Carlo $p = 0.02$, Fig. 4b). These differences were corroborated by the results of a perMANOVA (pseudo-F$_{16,3}$ = 2.48, $p = 0.006$). The four predator treatment groups were distributed in a fairly clear pattern within the ordination space. Predator-free control reefs did not overlap with any of the three predator-addition treatments. Reefs in each of the single-predator treatments (lionfish-only and grouper-only) occupied distinct areas of the plot with a small degree of overlap, while reefs in the combined-predator treatment
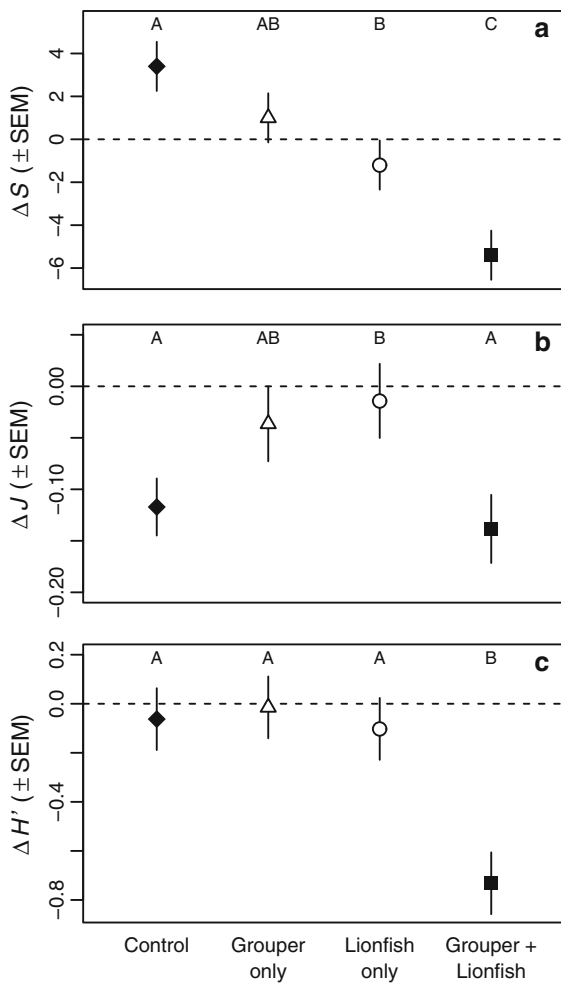
Fig. 3 Changes (mean ± SEM) in **a** species richness ΔS, **b** species evenness ΔJ, and **c** species diversity ΔH' of small fish (≤5 cm TL) on experimental coral patch-reefs under four different predator treatments: predator-free controls (*solid diamonds*), native grouper only (*open triangles*), invasive lionfish only (*open circles*), and combined grouper + lionfish (*solid squares*). N = 5 patch reefs per treatment. The experiment ran for 8 weeks; values represent the change in each metric between the baseline census (before establishment of predator treatments) and the final census. *Letters* at the *top of the plot* indicate the results of pairwise comparisons among the treatments at the final census (matching letters indicate a *p*-value >0.05)

occupied a similar range to lionfish-only reefs along axis-1, yet were distributed much more broadly across axis-2 than any of the other treatments. Of the thirty species present on experimental reefs at the end of the experiment, twelve species from six different families—including the two most commonly recruiting

species (*Coryphopterus glaucofraenum* and *Stegastes leucostictus*), two herbivores (*Sparisoma viride* and *Acanthurus chirurgus*), and two facultative cleaners (bluehead wrasse *Thalassoma bifasciatum* and *Bodianus rufus*)—had strong positive correlations (>0.3) with the first NMDS axis, whereas only one species (barred cardinalfish *Apogon binotatus*) had a strong negative correlation (<−0.3) with this axis (Online Resource 4). Two species (*T. bifasciatum* and *Gnatholepis thompsoni*) had strong positive correlations (>0.3) with the second NMDS axis, whereas two species (sharpnose puffer *Canthigaster rostrata* and flamefish *Apogon maculatus*) had strong negative correlations with this axis (Online Resource 4).

Discussion

Native reef-fish abundance

This field experiment demonstrated that reductions in the abundance of small native fishes on patch reefs caused by lionfish were substantially greater than those caused by a similarly sized native predator. Native fish abundance was also much lower in the combined-predator treatment than in the native-grouper treatment, suggesting that large reductions in the abundance of small fishes can be expected on coral reefs invaded by lionfish, at least during the summer recruitment period.

The increase in numbers of small fish observed on predator-free control reefs and on grouper-only reefs was primarily due to a large pulse of natural settlement of larval fishes, which typically occurs during the summer months in this region. Recruitment was dominated by two species in particular (*Coryphopterus glaucofraenum* and *Stegastes leucostictus*), with a broad diversity of fishes (including three herbivorous species and one cleaner) also contributing to the overall increase. The presence of a single, small lionfish on a patch reef effectively attenuated this local recruitment pulse to nearly zero, and this negative effect was spread across a majority of the most commonly recruiting species, including those in ecologically important groups.

Such a major reduction in the recruitment of a broad diversity of native reef fishes, if widespread in the system as a whole, could have strong direct demographic consequences for native fish populations. The
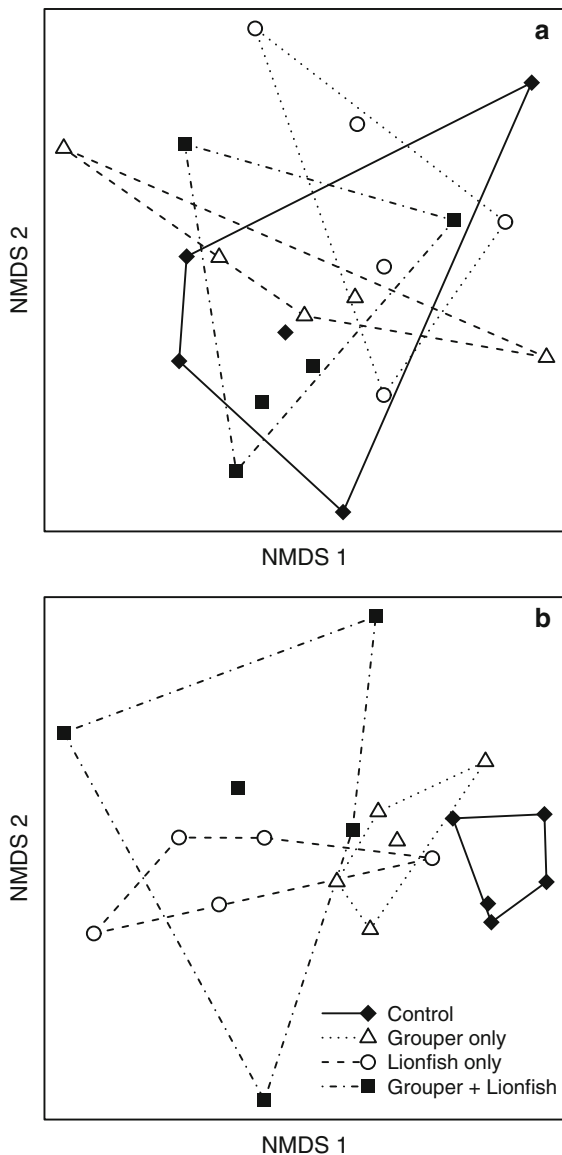
Fig. 4 Non-metric multidimensional scaling ordinations of experimental reefs in species space **a** at the beginning of the experiment (*baseline census*) and **b** at the end of the experiment (*final census*) with minimum convex hull polygons for each predator treatment group: predator-free controls, native grouper only, invasive lionfish only, and combined grouper + lionfish. For ease of interpretation, the ordination for the final census has been rotated for maximum correlation between axis one and overall change in abundance. See supplementary materials (Table 4) for a list of species-specific linear correlations with each NMDS axis

severity of these demographic consequences will, at least in part, be determined by species-specific population growth sensitivities to increased rates of early

post-settlement mortality. Early post-settlement mortality rates in most coral-reef fishes are naturally very high due to predation, represent a disproportionately large component of overall mortality, and can have strong effects on adult population densities as well as the structure of reef-fish communities (Carr and Hixon 1995; Hixon and Jones 2005; Almany and Webster 2006). This study demonstrates that lionfish are consuming large numbers of small native fish relative to a similarly sized native predator. If the tremendous increases in early mortality of native fishes caused by lionfish translate into reduced adult populations of ecologically important species such as herbivores, then the lionfish invasion could possibly have far-reaching and destabilizing consequences for coral-reef ecosystems (Albins and Hixon 2011).

Invasive vs. native predator growth rates

In addition to the fact that lionfish consumed native reef fishes at substantially higher rates than the native grouper in this study, they also grew over six times faster (in both length and mass). Lionfish growth rate estimates from the current study were nearly identical to those observed in a separate mark-recapture study of juvenile invasive lionfish on non-experimental reefs in the same region (Kindinger et al. unpublished data, Pusack et al. unpublished data). The relatively rapid growth rates of lionfish documented in this study, along with evidence that lionfish consume juvenile groupers (Morris and Akins 2009) suggests the possibility that cohorts of lionfish may grow large enough, quickly enough, to become predators of contemporaneous cohorts of native groupers.

Despite a clear demonstration that lionfish caused large reductions in the density of reef-associated prey fish, grouper maintained equivalent growth rates in the presence and absence of lionfish over the course of the experiment. It is possible that, in the presence of lionfish, grouper may have compensated for reduced availability of reef-associated prey fish by consuming alternative prey (e.g., invertebrates or non-reef-associated fish). While such alternative prey may have allowed the maintenance of normal somatic growth rates in grouper over the 8 wk experiment, these are likely to represent lower-quality or higher-risk food sources and may not support equivalent long-term growth or reproduction. Therefore, the lack of direct evidence for short-term competition between lionfish

and grouper in terms of individual growth rates should not be taken as evidence against the likelihood of long-term competitive interactions.

The potential for lionfish to both compete with and consume native predators is reason for concern as such simultaneous negative interactions have been implicated in exacerbating the effects of other invasive predatory fishes on natives (Mills et al. 2004). Native predators are severely overfished in many locations across the Caribbean, especially in areas with high human population densities (Stallings 2009). Although some native predators maintain relatively healthy populations in remote locations and within some protected areas, lionfish may represent an additional threat to these already imperiled species, a threat that will neither respond to fisheries regulations nor be limited by remoteness or the boundaries of marine protected areas. It will therefore be important to continue to investigate the effects of lionfish on native predators, particularly those with high ecological or economic importance.

Native reef-fish richness, evenness, and diversity

The effects of predators on prey community composition are highly context dependent (see review by Hixon 1986 for fishes). In several classic examples, predation has been found to disproportionately target competitively dominant prey species, thereby favoring competitive subordinates and leading to increased prey diversity (Paine 1966; Connell 1971). At least one introduced freshwater piscivore has been found to have a similar effect, causing a decrease in the abundance of common species and a concomitant increase in the abundance of rare species, effectively increasing prey community evenness (He and Kitchell 1990). In contrast, a study of coral-reef fish found that generalist piscivores disproportionately consumed rare prey species, thereby causing local reductions in prey species richness (Almany and Webster 2004).

In this study, lionfish caused a reduction in the local richness of native species, whereas native grouper did not. Additionally, lionfish and grouper together (the post-invasion treatment) caused a substantial reduction in species richness compared to grouper alone (the pre-invasion treatment). It is important to note that species richness may have been slightly higher on the combined predator treatment reefs than on the grouper-only reefs at the beginning of the experiment (Online Resource 2). Despite this caveat, the experimental results indicate that one of the ultimate effects of the lionfish invasion may be substantial reductions in the number of native fish species on invaded reefs.

Species evenness decreased on predator-free control reefs over the course of the experiment, likely due to high recruitment of common species and a resulting increase in the difference between the density of common and rare species. Compared to controls, lionfish caused an increase in evenness on experimental reefs over the course of the experiment. Increased evenness in the presence of lionfish resulted from a combination of reduced abundance of common species, and reduced numbers of rare species (due to extirpations). While the effect of native grouper on the change in prey evenness was not statistically significant, the mean effect was positive (similar to the lionfish effect). However, patterns of evenness in the combined-predator treatment were more similar to those in the control treatment than to either of the single-predator treatments. This non-additive effect of the two predators on evenness is difficult to explain. One speculative explanation is that, in combination, the two predators reduced the abundance of common species so greatly that it became inefficient for one or both predators to target these species, thus causing a shift to less common prey species (i.e., switching behavior, Murdoch 1969). This increased predation on less common species may have resulted in the observed increase in the difference in abundance between common and less common species (i.e., a decrease in evenness). It also appears that at least one species (*Gnatholepis thompsoni*) may be resistant to one or both predators. This goby is one of the few species for which final abundance was actually higher on combined predator reefs than on control reefs (Table 1, Online Resource 3). The resulting numerical dominance of this single species could have contributed to the relative drop in evenness observed for this treatment.

Species diversity (richness and evenness combined) did not change on control reefs or for either of the single-predator treatments (lionfish-only and grouper-only) over the course of the experiment. Diversity remained relatively constant on the control reefs because increases in species richness were offset by decreased evenness. Diversity also remained relatively constant on both single-predator treatments because the converse was true—losses of species

richness were offset by increased evenness. However, diversity was reduced on the combined predator treatment reefs compared to the other treatments because both richness and evenness declined in this treatment.

Multivariate community response

Comparison of the ordination from the baseline census (which showed no pronounced differences among experimental communities) to the ordination from the final census demonstrated that the communities in the four treatments diverged substantially over the course of the experiment. Linear correlations of reef-fish species with axis 1 from the final ordination indicated that native grouper had a moderate effect on the abundance of common species (causing a small shift towards the negative end of axis 1), whereas lionfish had a stronger effect on those species (causing a larger shift to the negative end of the axis). The list of species that had positive correlations with this axis, and were thus negatively affected by lionfish, included the most commonly recruiting species as well as two herbivores and two cleaners, suggesting that the lionfish invasion may have a negative effect on these ecologically important species. It is likely that the broad distribution of the combined-predator reefs along the second axis was primarily driven by an increasing influence of rare species as the abundances of common species were drastically reduced by the combined effects of the two predators.

Conclusions

This study establishes a causal relationship between an invasive predator and changes in the native prey community relative to an ecologically similar native predator. Such studies are quite rare and are valuable, first, adding to our limited knowledge regarding the mechanisms by which invasive predators affect native prey communities, and second, determining the appropriate management approach to a particular invasion.

The primary conclusion of this study is that invasive lionfish are not ecologically equivalent to coney grouper, a similarly sized native piscivore. Under the same field conditions, lionfish grew at substantially faster rates, and had stronger effects on

native coral-reef fish communities, reducing both overall abundance and local species richness. Novel characteristics and behaviors of lionfish and naïveté of native prey to these traits may contribute to the relative strength of these effects. Large reductions in the abundance of small native coral reef fishes due to lionfish predation may alter native reef-fish community composition, and may have important and far-reaching consequences for coral-reef ecosystems. Coral reefs and associated fishes are threatened by a wide range of perturbations, including overfishing, climate change, and habitat destruction (Mora 2008). Invasive species in general, and lionfish in particular, represent an additional threat to these ecosystems.

These results indicate that managers tasked with mitigating the invasion should anticipate strong direct and indirect effects between lionfish and native species. However, it should be emphasized that the effects reported here were caused by juvenile lionfish, and were measured over small spatial and temporal scales. Given that ecological processes are often temporally and spatially scale-dependent (Levin 1992), the question remains whether and how the lionfish invasion will affect reef-fish communities on large contiguous reefs over longer time periods. To gain a more complete understanding of the overall consequences of the lionfish invasion, it will be important to assess their effects at more management-relevant temporal and spatial scales.

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