AN ABSTRACT OF THE DISSERTATION OF

Mark A. Albins for the degree of Doctor of Philosophy in Zoology presented on September 20, 2011.

Title: Effects of the Invasive Pacific Red Lionfish *Pterois volitans* on Native Atlantic Coral-reef Fish Communities

Abstract approved:

Mark A. Hixon

Predatory lionfishes (*Pterois volitans* and *P. miles*) were introduced to Florida waters during the mid to late 1980s, and eventually established self-sustaining breeding populations in the tropical western Atlantic. These invasive species are now widespread along the southeastern seaboard of the United States, across the Caribbean Sea, and in the Gulf of Mexico. In these regions, lionfish reach larger maximum sizes and higher abundances than they do in their native Pacific, suggesting that they have undergone ecological release. Invaded marine communities have thus far provided little if any biotic resistance.

Lionfish are generalist predators with high consumption rates, inhabit a broad range of habitats, are defended from predation by venomous spines, and are capable of long-range larval dispersal. It is possible that lionfish have direct effects on native communities, through consumption of native fishes and competition with native

predators, as well as indirect effects, such as overconsumption of herbivorous fishes that prevent seaweeds from outcompeting reef-building corals. There is also serious concern that invasive lionfish could act additively, or even synergistically, with existing stressors of coral-reef systems, such as overfishing and ocean warming, resulting in substantial negative consequences for native ecosystems and economically valuable fisheries.

The primary goal of this dissertation was to conduct a set of controlled, replicated field experiments to rigorously examine and measure the effects of lionfish on native reef-fish communities across a range of spatial and temporal scales. In the first experiment (Chapter 2), the net recruitment of native fishes to twenty small patch reefs was compared in the presence (n = 10) and absence (n = 10) of lionfish. This study demonstrated that lionfish reduced net recruitment, or change in abundance of small native fishes, by an average (± SEM) of 78.9 ± 32.2 % over 5 weeks, affecting 23 of 38 species recruiting to reefs in both treatments. In a second experiment (Chapter 4), I examined the effects of lionfish on patch-reef communities of small native fishes relative to, and in combination with, those of a similarly sized native predator, the coney grouper (*Cephalopholis fulva*). Four different predator treatments were established by transplanting predators (n = 5 reefs each). Treatments included a single small invasive lionfish, a single small native grouper, a grouper and a lionfish together, and predator-free controls. Compared to controls, invasive lionfish caused reductions (mean ± SEM) in abundance (93.7 ± 17.8 %) and

species richness (4.6 ± 1.6 species) of small native fishes. The negative effect of lionfish on abundance was 2.6 ± 0.5 times stronger than that of the native grouper. The greatest negative effects on abundance, species richness, evenness, and diversity of native fishes occurred when both lionfish and native grouper were present. Additionally, lionfish grew more than six times faster in both length and mass than did native grouper. A third experiment (Chapter 6) assessed the effects of lionfish on native reef-fish communities at spatial and temporal scales directly relevant to management and conservation efforts. Subsequent to baseline surveys, high- and low-density lionfish treatments were established on 10 large (1400 to 4000 m^2) isolated coral reefs. After initiation of treatments, quarterly surveys of the native reef-fish communities were conducted for approximately 14 months. Lionfish caused significant reductions (mean ± SEM) in density (up to 3.22 ± 0.95 fish m^{-2}), biomass (3.26 ± 1.10 g m^{-2}), and species richness (4.92 ± 2.09 species) of small (<10 cm TL) native fishes. However, these negative effects on prey-sized fishes had not yet translated into declines in larger size classes during the first 14 months of this experiment.

In addition to field experiments, this dissertation describes field and aquarium observations of a previously undocumented piscivorous behavior by invasive lionfish — blowing jets of water at prey fish — which may confer a high degree of predation efficiency, thus contributing to the dramatic success of the invasion (Chapter 5). Also provided is a review of the current state of knowledge about the lionfish invasion,

with speculation on the long-term effects of the invasion on coral-reef communities, and a brief discussion of potential mitigation measures (Chapter 3).

In sum, this research demonstrated that invasive lionfish have substantial negative effects on native communities of coral-reef fishes. In all cases, numerical reductions in small (prey-sized) native fishes caused by lionfish were substantial. Additionally, lionfish caused considerable reductions in native reef-fish species richness (via predation on rare species). These findings indicate that the lionfish invasion may have long-term, broad-scale impacts on the structure and function of coral-reef communities as a whole, potentially reducing the resilience of these systems to a myriad of existing stressors as well as their capacity to provide valuable ecosystem goods and services to humans.

Effects of the Invasive Pacific Red Lionfish *Pterois volitans* on Native Atlantic Coral-reef Fish Communities

by
Mark A. Albins

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APPROVED:

Major Professor, representing the Department of Zoology

Chair of the Department of Zoology

Dean of the Graduate School

I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Mark A. Albins, Author

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First and foremost, I thank my advisor, Mark A. Hixon for his sincere and enduring dedication to excellence in research and teaching. Mark has a deep relationship with coral reefs and the fishes that inhabit them, and an understanding of these beautiful and diverse systems that can only come from spending innumerable hours literally immersed in their world. His insatiable curiosity about the workings of these systems, and his passion for their conservation are contagious. He has been a mentor, colleague and friend throughout the process leading to this dissertation, and has consistently provided guidance, encouragement, advice, financial support, assistance in the field, and thorough and thoughtful feedback on proposals, papers and talks. He has been approachable, available, and engaged when I needed it most, and has also given me the room to make my own mistakes.

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CONTRIBUTION OF AUTHORS

While none of the chapters presented here would have been possible without the extensive support and involvement of my advisor, Mark Hixon, he is a co-author on Chapters 2 and 3, for which his contributions were particularly extensive. Mark contributed substantially to all phases of the experiment described in Chapter 2, from the planning and implementation to the analysis and writing. He also shaped the overall approach, and wrote significant portions of Chapter 3.

Chapter 5 was co-authored with Patrick J. Lyons, a PhD candidate in the Department of Ecology and Evolution at SUNY Stony Brook, who led the in-lab observations of lionfish, and came-up with a creative way to visualize and record their behavior on video. Patrick also contributed substantially to the literature research, writing, and editing of the manuscript.

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DEDICATION

In memory of my cousin, Martin Apolinar, and all the young men and women whose bravery, service, and sacrifice have made it possible for me to do what I do.

Effects of the Invasive Pacific Red Lionfish *Pterois volitans* on Native Atlantic Coral-reef Fish Communities

Chapter 1 — General Introduction

Biological invasions resulting from human transport of non-indigenous species can reduce biodiversity, interfere with evolutionary processes, and impair ecosystem function (Carlton & Geller 1993, Vitousek et al. 1997, Wilcove et al. 1998, Chapin et al. 2000, Mack et al. 2000). Invasive species can negatively affect the distribution and abundance of natives through predation, competition, and habitat alteration, and are a major contributor to both local and global extinctions (Vitousek et al. 1997, Mack et al. 2000). The economic costs associated with invasive species have been estimated to exceed 120 billion dollars annually in the United States alone (Pimentel et al. 2005). While most invasions have occurred in terrestrial or aquatic systems, marine invasions are increasing at an alarming rate and can have substantial impacts on the stability of ocean ecosystems and the goods and services that they provide (Carlton & Geller 1993, Cohen & Carlton 1998, Ruiz et al. 1999, Rilov & Crooks 2009). Unfortunately, rigorous experimental studies establishing and measuring the causal relationships between invasive species and their effects on native ecosystems — essential for prioritizing management and conservation efforts — are often lacking, particularly in marine systems.

Some of the most damaging biological invasions, in terms of biodiversity loss and ecosystem disruption, have resulted from the introduction of predatory freshwater fishes (e.g. Ogutu-Ohwayo 1990, Ross 1991, Witte et al. 1992, Lever 1996, Fuller et al. 1999, Marchetti 1999, Lowe et al. 2000, reviewed in Helfman 2007). Non-native diadromous and estuarine fishes have also become invasive, causing negative effects in native communities and ecosystems (Baltz 1991, Courtenay 1993, Lever 1996, Fuller et al. 1999).

In contrast, while many strictly marine fishes have been intentionally and unintentionally introduced into new ecosystems by humans, relatively few of these introductions have resulted in self-sustaining reproductive populations (Randall 1987, Baltz 1991, Semmens et al. 2004, Helfman 2007). Of those that have become established, few have been studied. Of those that have been studied, investigations of their effects on native populations and communities have occurred decades after the initial introductions, and have been limited to observational rather than experimental approaches (Friedlander et al. 2002, Bariche et al. 2004, Goren & Galil 2005, Schumacher & Parrish 2005).

Two closely related species of predatory lionfish (*Pterois volitans* and *P. miles*) were introduced to Florida waters sometime during the mid to late 1980s (Schofield 2009). While southern Florida is a “hotspot” for non-native marine fishes, primarily due to releases from aquaria (Courtenay 1995, Semmens et al. 2004), lionfishes appear to be the only non-native marine fishes to have established self-sustaining breeding populations in the tropical western Atlantic. Lionfish sightings in the Atlantic were sparse until the early 2000s when reports began to increase substantially. By 2007, the year in which my dissertation research was initiated, lionfish had become established continuously along the eastern seaboard of the United States from Miami to Cape Hatteras, and had spread to Bermuda and the Bahamas (details in Schofield 2009). Genetic evidence suggested that *P. miles* remained restricted to the northern end of the invaded range, while *P. volitans* was responsible for the southward expansion (Freshwater et al. 2009). At the time, every indication was that *P. volitans* would continue this rapid range expansion across the Caribbean and into the Gulf of Mexico, which it subsequently has done.

Not only had lionfish begun to spread rapidly across the tropical and subtropical western Atlantic over a handful of years, they had also reached extremely high abundances in some regions. By 2007, lionfish densities as high as 20 ha^{-1} had been reported for sites off the coast of North Carolina, densities that were similar to, or higher than those of most native grouper species (Whitfield et al. 2007). Lionfish sightings at our regularly visited long-term study sites in the Bahamas had increased from two individuals in 2006 to over 100 individuals in 2007 (Chapter 2: Albins & Hixon 2008), and by 2008 lionfish densities exceeding 390 ha^{-1} had been reported from sites in the Bahamas (Green & Côté 2008). Invasive lionfish also appeared to reach larger maximum sizes in the invaded range (Whitfield et al. 2007) than had been reported from their native Pacific (Randall et al. 1990).

Unfortunately, prior to the onset of this invasion, very little was known about lionfish ecology or life-history characteristics. A thorough literature review on lionfish conducted in 2007 revealed the following (Whitfield et al. 2007): Lionfish are native to the sub-tropical and tropical regions of the South Pacific (*P. volitans*), Indian Ocean and Red Sea (*P. miles*), where they are found on coral and rocky reefs to a depth of at least 50 meters (Schultz 1986). They are known predators of small fishes and crustaceans (Fishelson 1975), with high consumption rates (Fishelson 1997), and are reported to grow to a maximum size of 38 cm total length (Randall et al. 1990). Lionfish are well defended by venomous fin spines (Allen & Eschmeyer 1973), and have few natural predators (Fishelson 1975, but see Bernadsky & Goulet 1991). Females release a mucous balloon of eggs that is fertilized externally (Thresher 1984), and an estimated pelagic larval duration (PLD) of between 25 and 40 days suggests that lionfish are capable of long-range dispersal via ocean currents (Whitfield et al. 2007). Lionfish are highly prized aquarium fish, representing a significant component of aquarium fisheries in the Indo-Pacific, especially in the Philippines. They also represent a small portion of subsistence and small-scale commercial food fisheries within their native range (Carpenter & Niem 1999).

In combination with what was known of lionfish ecology and life history, the rapid range expansion and high population growth of these non-native marine predators was cause for substantial concern (Whitfield et al. 2007). Speculation about their potential effects on native communities included reductions in prey-sized native fishes via predation, competition for prey resources with native predators (including important fisheries species such as groupers), and competition for other limited resources (including refuge space) with a variety of native fishes (Whitfield et al. 2007). In particular, the threat of invasive lionfish was seen to have the potential to act in concert with a myriad of existing stressors, including pollution, overfishing and climate change, to cause substantial and potentially irreversible consequences to native ecosystems and economically valuable fisheries.

At the time, all of these potential effects of invasive lionfish, while based on a fairly robust set of assumptions, remained speculative. The primary goal of my dissertation research was to conduct a set of controlled field experiments to examine the effects of lionfish on native coral-reef fish communities, thereby determining whether, and to what extent, these concerns were justified.

This dissertation research represents the first effort to determine experimentally the effects of invasive lionfish on native reef-fish communities. This work is particularly novel because previous studies examining the effects of invasive marine fishes have occurred decades after the invasions, and have been limited to observational and correlative approaches. This dissertation consists of five stand-alone manuscripts that are published, in review, or in the final stages of preparation for submission to peer-reviewed scientific journals.

Chapter 2, "Invasive Indo-Pacific lionfish *Pterois volitans* reduce recruitment of Atlantic coral-reef fishes," published in *Marine Ecology Progress Series* in 2008, describes a controlled field experiment using a matrix of small translocated coral and artificial patch reefs to examine the short-term effects of lionfish on the recruitment of native fishes in the Bahamas. After baseline censuses were conducted, single small lionfish were transplanted onto 10 of 20 experimental reefs. Following transplants, fish recruitment censuses were conducted at ca. 1 wk intervals for 5 wk during the summer 2007 recruitment period (July to September). Net recruitment (all species combined) to experimental reefs was compared between treatments, and species-specific contributions to this overall effect were examined. We also examined gut contents of lionfish, and conducted captive feeding trials to determine the types of native prey consumed by invasive lionfish.

Chapter 3, "Worst case scenario: potential long-term effects of invasive predatory lionfish *Pterois volitans* on Atlantic and Caribbean coral-reef communities" was written as an invited contribution, and is currently published *Online First* as part of a special issue of *Environmental Biology of Fishes* scheduled to appear late in 2011. This chapter is based on a presentation given in a special session on fish conservation at the 2009 meeting of the American Association for the Advancement of Science, and provides a brief review of the current state of knowledge about the lionfish invasion, speculates about the long-term effects of that invasion on coral-reef communities, and discusses potential mitigation measures.

Chapter 4, “Effects of invasive Pacific red lionfish *Pterois volitans* vs. a native predator on Bahamian coral-reef fish communities,” currently in review by *Biological Invasions*, describes a controlled field experiment conducted on small patch reefs in the Bahamas to examine the effects of invasive lionfish on native coral-reef fish communities relative to, and in combination with, those of a similarly sized native predator, the coney grouper (*Cephalopholis fulva*). Twenty small experimental patch-reefs were censused and grouped into blocks based on similarity of the preexisting communities. Four predator treatments were then established on reefs in each block. Treatments included a single native grouper, a single invasive lionfish, one native grouper and one lionfish together, and a predator-free control. Subsequent reef censuses were conducted at ca. 1 wk intervals for 8 wk. I compared the relative effects of native grouper and invasive lionfish, and the relative effects of the pre-invasion (grouper only) and post-invasion (grouper + lionfish) predator treatments on the changes in abundance and species richness, evenness, and diversity of small native fishes. I also examined overall community change under the four predator treatments using a multivariate approach. Weights and lengths of both invasive lionfish and native grouper were also measured at the beginning and again at the end of the experiment to compare predator growth rates.

Chapter 5, "Jet assisted predatory behavior by the invasive red lionfish *Pterois volitans*," currently in review by *Marine Ecology Progress Series*, is a short note describing field and aquarium observations of a previously undocumented piscivorous behavior by invasive lionfish: blowing jets of water at prey fish. This behavior may confer a high degree of predation efficiency, thus contributing to the dramatic success of invasive lionfish.

Chapter 6, "Effects of the Pacific lionfish *Pterois volitans* on Bahamian coral-reef fish communities: a large-scale, long-term experiment," currently in preparation for submission to *Ecological Applications*, describes a controlled field experiment designed to examine the effects of lionfish on native reef fish communities at spatial and temporal scales approximating those at which conservation and management efforts are typically applied. Ten large (1400 to 4000 m^2) isolated coral reefs were paired based on habitat similarities. Baseline surveys of the reef-fish communities were conducted. Subsequently, quarterly removals of lionfish were conducted on one reef in each pair, while the densities of lionfish on the other reefs were standardized at a typical post-invasion level via transplants. After initiation of these treatments, quarterly surveys of the native reef-fish community were completed for approximately 14 months. I compared the changes in density, biomass, and species richness, evenness, and diversity of small and medium sized native fishes (all species combined) between the two treatments. I also compared the changes in density and biomass of two ecologically important groups of native fishes (herbivores and piscivores), and examined species-specific contributions to differences in density and biomass between the two treatments. In addition, I used a multivariate approach to examine differences in the overall change in the small reef-fish community through time for the two treatments.

This dissertation presents a comprehensive evaluation of a marine fish invader. I have used a set of rigorous experimental studies conducted over a range of spatial and temporal scales to establish and measure the causal relationships between invasive lionfish and their effects on native coral-reef fish communities. This research provides essential information for prioritizing management and conservation efforts.

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Chapter 2 — Invasive Indo-Pacific lionfish *Pterois volitans* reduce recruitment of Atlantic coral-reef fishes

Mark A. Albins and Mark A. Hixon

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ABSTRACT

The Indo-Pacific lionfish *Pterois volitans*, introduced to Florida waters in the early 1990s, is currently spreading rapidly throughout the Caribbean region. This invasive carnivore may cause deleterious changes in coral-reef ecosystems via predation on native fishes and invertebrates as well as competition with native predators. We conducted a controlled field experiment using a matrix of translocated coral and artificial patch reefs to examine the short-term effects of lionfish on the recruitment of native reef fishes in the Bahamas. Lionfish caused significant reductions in the recruitment of native fishes by an average of 79 % over the 5 wk duration of the experiment. This strong effect on a key life stage of coral-reef fishes suggests that invasive lionfish are already having substantial negative impacts on Atlantic coral reefs. While complete eradication of lionfish in the Atlantic is likely impossible, it would be prudent to initiate focused lionfish control efforts in strategic locations.

2.1 INTRODUCTION

Biological invasions are a leading cause of biodiversity loss and represent a substantial contribution to human-caused global change (Carlton & Geller 1993, Wilcove et al. 1998). While invasions by marine fishes are relatively uncommon and their ecological effects are largely unknown, introductions of predatory freshwater fishes have often proven to be devastating to native communities (Helfman 2007).

Two closely related species of predatory lionfish (*Pterois volitans* and *P. miles*) were recently introduced from their native range in the Indo-Pacific to the Western Atlantic (Hamner et al. 2007). Genetic evidence of a strong founder effect suggests either a single introduction of a small founding population or multiple introductions of individuals with the same haplotype (Hamner et al. 2007). Lionfish may have been introduced into the Atlantic at Biscayne Bay, Florida, when several individuals were released from an aquarium during Hurricane Andrew in 1992 (Courtenay 1995, Hamner et al. 2007). Whether the introduction of lionfish to the Atlantic occurred as a single event or multiple events, it is likely that the source of the introduction was intentional or unintentional release from aquaria off the coast of Florida (Whitfield et al. 2002, Hare & Whitfield 2003, Semmens et al. 2004, Ruiz-Carus et al. 2006).

Between 1992 and 2006, lionfish spread rapidly northward along the eastern seaboard of the U.S. and southward into the Caribbean. They have now been sighted as far east as Bermuda, as far north as Rhode Island, and as far south as Jamaica (Whitfield et al. 2002, Hare & Whitfield 2003, Whitfield et al. 2007), with unconfirmed reports from the Yucatan Peninsula, Puerto Rico, and the Lesser Antilles (L. Akins, REEF, pers. comm.), and they are now fairly common in the Bahamian archipelago off Florida. While *P. volitans* and *P. miles* are difficult to distinguish morphologically due to some overlap in meristic values, genetic evidence indicates that *P. volitans* is the only introduced lionfish currently found in the Bahamas (D.W. Freshwater et al., UNCW, pers. comm.).

Our lab has studied coral reefs in the 200 × 70 km Exuma Sound of the Bahamas since the early 1990s. In the summer of 2005, we found our first lionfish near Lee Stocking Island (LSI), one of our primary study sites. In 2006, we collected another lionfish at LSI and one near Eleuthera. During this same year, other researchers documented sightings of several individuals in the Abacos on Little Bahama Bank (Snyder & Burgess 2007).

Between the fall of 2006 and the summer of 2007, the lionfish population in the Bahamas increased substantially. During the summer of 2007, we sighted over 100 individual lionfish in the vicinity of LSI, 3 in the Exuma Cays Land and Sea Park, and 2 at Cat Island. The clear increase in lionfish numbers at these regularly visited study sites indicated an extremely rapid expansion within the Bahamas.

Between June and September of 2007, we documented recruitment of newly settled lionfish to a matrix of 48 experimental patch reefs near LSI. We observed recruitment of 24 lionfish to these ca. 3 m^2 experimental reefs over a 70 d period. Extrapolated, this pattern would be equivalent to a recruitment rate of ca. 24 fish ha^{-1} of hard substrate per day, although settlement may be greater, per unit area, to patch reefs than to continuous reefs.

The lionfish represents a potential major threat to coral-reef ecosystems in the Caribbean region by decreasing survival of a wide range of native reef animals via both predation and competition. Adults (300 to 400 g) in the Indo-Pacific are reported to consume approximately 8.5 g of prey d^{-1}, which translates to ca. 230 kg yr^{-1} for 80 adult fish on a 1 km reef (Fishelson 1997). Lionfish herd and corner prey using ornate oversized pectoral fins and attack with a rapid strike (Allen & Eschmeyer 1973, Fishelson 1997). Naivety of Atlantic prey to this novel predation strategy may result in high predation efficiency of lionfish relative to its native range, as well as compared to similarly-sized native predators in the invaded system. High predation efficiency may translate into a large ecological effect of lionfish, both on native prey species and on potential competitors.

Lionfish may be cannibalistic, but otherwise have few documented natural predators in their native range (but see Bernadsky & Goulet 1991). While it is important to mention that extensive studies of predation on lionfish have not been reported, the apparent paucity of natural predators may be due, in part, to the defensive dorsal, anal, and pelvic spines of lionfish, which deliver potent venom that may be fatal to fishes (Allen & Eschmeyer 1973). It is likely that few native Atlantic (including Caribbean) species represent significant potential predators of lionfish. Despite recent evidence that native groupers may prey on lionfish (Maljković et al. 2008), such large-bodied predators have been systematically overfished throughout the region (Sadovy & Eklund 1999), and thus are not likely to substantially reduce the effects of invasive lionfish on Atlantic coral-reef communities.

Predation on post-settlement reef fishes represents an important and disproportionately large component of overall mortality and may have a strong effect on population densities as well as the structure of reef fish communities (Carr & Hixon 1995, Almany & Webster 2006). Because lionfish may be particularly effective predators on small post-settlement reef fishes, they may potentially have large effects on native coral-reef fish populations and communities. Here we report the results of a field experiment designed to determine whether and to what extent lionfish affect recruitment of native coral-reef fishes.

2.2 MATERIALS AND METHODS

We conducted a controlled field experiment to examine the effects of lionfish on coral-reef fish recruitment at LSI in the Bahamas. We used an existing matrix of 3 m^2 translocated live-coral patch reefs and 1 m^2 artificial concrete-block reefs, all of which were constructed and deployed in the early 1990s and are now essentially natural features (Carr & Hixon 1995, 1997, Hixon & Carr 1997). These experimental reefs are separated from the nearest natural reefs by at least 1 km and from each other by 200 m (Fig. 2.1a). An initial survey of all experimental reefs confirmed that no lionfish were present at the outset of the experiment. During this initial survey we also counted all strongly interacting fish species, including territorial damselfishes and resident piscivores, which are known to have negative effects on the recruitment of reef fishes in the Bahamas (Carr et al. 2002). Twenty reefs (10 translocated and 10 artificial) were paired based on spatial proximity (Fig. 2.1b), and similarity of the pre-existing communities, as determined by the number of fish in major groups of known strong interactors (Table 2.1). Reef pairings were used to account for potential spatial variability in recruitment and the potential effects of members of the pre-existing community on post-settlement survival of reef fishes. One reef in each pair was designated as a control reef (lionfish absent) and the other as a treatment reef (lionfish present). Single lionfish were then transplanted from nearby reefs to each of the lionfish-present reefs. Transplanted lionfish ranged in size from 11.8 to 28.5 cm total length (TL) (mean = 16.5 cm TL). Following lionfish transplants, fish recruitment censuses were conducted at ca. 1 wk intervals for 5 wk during the summer 2007 recruitment period (July to August). Recruitment censuses were conducted by 2 divers using SCUBA, who counted all recruits <5 cm TL on each reef.

Because this experiment ran during the larval recruitment season, we expected to see overall increases in the number of small reef fish on all reefs over the course of the study period (i.e. positive net recruitment). However, we also predicted that net recruitment would be lower on lionfish treatment reefs than on control reefs.

We used a multi-way analysis of variance model, with *treatment* and *reef type* as explanatory factors and *reef pair* as an error term, to draw inferences regarding the effect of lionfish on net recruitment. Visual examination of standardized residuals vs. fitted values, as well as stratum-three residuals vs. normal quantiles, indicated that the data conformed to the assumptions of homogeneity of variances and normality.

2.3 RESULTS

Net recruitment was significantly lower on lionfish reefs than on control reefs at the end of the 5 wk experiment (F = 6.182, p = 0.038, Fig. 2.2). Lionfish reduced net recruitment by a mean of 28.1 fish reef^{-1} (95 % CI of 2.2 to 54.0 fish reef^{-1}), representing an average reduction in net recruitment of 79 %. There was no evidence of a difference in net recruitment between translocated and artificial reefs, although the power of the test was low (F = 0.084, p = 0.779, power = 0.364), and there was no evidence of an interaction between reef type and treatment (F = 1.263, p = 0.294, power = 0.887). There was also no evidence of a difference between control and lionfish reefs in the number of small fishes present at the beginning of the experiment (F = 1.77 , p = 0.221, power = 0.931).

During the experiment, 49 species of reef fish from 16 families recruited to the study reefs, with 38 species from 14 families recruiting to both lionfish and control reefs. Of these 38 species, 23 suffered reduced recruitment in the presence of lionfish. Four of the five species of parrotfish (Family Scaridae) recruiting to both lionfish and control reefs suffered reduced recruitment in the presence of lionfish (Table 2.2).

Stomach content analyses and observations of feeding behavior showed that reductions in recruitment were almost certainly due to predation. Stomach contents were examined from all 10 fish used in the field experiment (9 of which had consumed fish) as well as from 42 additional lionfish collected from various sites around Exuma Sound. Of the 52 stomachs examined, 48 contained identifiable food items, including whole fish, fish parts, and small crustacean parts. In 14 cases, prey items were identifiable to the species level, including fairy basslet *Gramma loreto*, bridled cardinalfish *Apogon aurolineatus*, white grunt *Haemulon plumierii*, bicolor damselfish *Stegastes partitus*, several wrasses *Halichoeres bivittatus*, *H. garnoti*, *Thalassoma bifasciatum*, striped parrotfish *Scarus iserti*, and dusky blenny *Malacoctenus gilli*. Stomach content examination also confirmed that individual lionfish ate both large quantities of prey (max. = 53, mean = 5.7) and large prey relative to their body size. Fish prey ranged in size from 1 to 12 cm TL. One 11.9 cm TL lionfish contained a 5.4 cm TL white grunt for a maximum observed prey:predator size ratio of 0.44. Initial examination of crustacean prey suggested that lionfish may also eat juvenile spiny lobster *Panulirus argus*, an important subsistence and commercial fishery species.

In the field, we observed lionfish stalking and feeding on several different reef fish species throughout the daylight hours, with no indication that lionfish behaved in a way consistent with interference competition (e.g. aggression). On one occasion, we observed a large adult lionfish consume over 20 small wrasses *Halichoeres bivittatus* (1 to 3 cm TL) during a 30 min period.

Lionfish removed from nearby reefs and held in aquaria ate a wide variety of native reef fishes, including six different species from five families (Table 2.3). Consistent with our field observations, captive lionfish ate both large volumes of small fish as well as large fish in relation to their body size. It was not unusual to observe lionfish consuming prey up to ⅔ of their own length. This pattern was especially apparent in smaller lionfish, including newly settled individuals. For example, one 3.1 cm TL lionfish recruit cornered and consumed a 2.0 cm TL cottonwick grunt *Haemulon melanurum*.

2.4 DISCUSSION

The present study represents the first experimental evidence that the invasive Indo-Pacific lionfish has a direct negative effect on Atlantic coral-reef fish populations. The documented reduction in net recruitment due to lionfish predation is an important component, but likely represents an underestimation, of the overall effects of lionfish on native reef-fish communities. The large reduction in recruitment suggests the possibility that lionfish may compete with native piscivores by monopolizing this important food resource. Also, by decreasing recruitment of fishes, lionfish have the potential to decrease the abundance of ecologically important species, such as parrotfishes and other herbivorous reef fishes, which are crucial for preventing seaweeds from over-growing corals (Williams & Polunin 2001, Mumby et al. 2006). Considering the sizes of lionfish currently found in the Atlantic (up to 45 cm TL, Whitfield et al. 2007), and the size of prey fish found in stomach contents, the effects of lionfish predation on adult fish is also likely to represent a significant impact of this invasive species on native communities. It is also important to note that lionfish have the potential to act synergistically with other existing stressors, such as climate change, overfishing and pollution, making this invasion of particular concern for the future of Atlantic coral reefs.

The current geographic extent and rapid population growth of lionfish in the Atlantic makes complete eradication of this invasive species untenable. Nonetheless, it would be prudent for affected nations to initiate targeted lionfish control efforts as soon as possible. Concerted and sustained efforts to reduce densities of lionfish at key locations, including potential “choke” or dispersal points (Hare & Whitfield 2003), as well as particularly vulnerable or valuable reef areas, may help to mitigate their ecological impacts. Recovering and maintaining healthy populations of potential native predators of lionfish, such as large grouper and sharks, may also help reduce the deleterious effects of these voracious invasive predators.

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Table 2.1 Numbers of native strong-interactor fishes on experimental reefs. Treatments — L: lionfish present; C: lionfish absent (control). Large piscivores included >30 cm total length (TL) Nassau grouper *Epinephelus striatus* and moray eels *Gymnothorax* spp. Small piscivores include coney grouper *Cephalopholis fulva* and graysby grouper *C. cruentata*. Aggressive damselfish included >3 cm TL beaugregory, cocoa, and dusky damselfishes (*Stegastes leucostictus*, *S. variabilis*, and *S. adustus*, respectively).

Reef Pair	Treatment	Large Piscivores	Small Piscivores	Aggressive Damselfish	Total
Translocated Reefs					
1	L	0	0	0	0
	C	0	0	5	5
2	L	0	0	5	5
	C	0	0	5	5
3	L	0	0	5	5
	C	0	1	7	8
4	L	2	0	1	3
	C	0	1	6	7
5	L	1	1	2	4
	C	1	1	7	9
Total	**L**	**3**	**1**	**13**	**17**
	C	**1**	**3**	**30**	**34**
Artificial Reefs					
6	L	2	1	0	3
	C	3	0	3	6
7	L	1	0	1	2
	C	2	0	1	3
8	L	2	0	3	5
	C	2	1	3	6
9	L	0	0	0	0
	C	1	0	0	1
10	L	0	1	0	1
	C	2	0	0	2
Total	**L**	**5**	**2**	**4**	**11**
	C	**10**	**1**	**7**	**18**
Totals for all reefs combined					
	L	**8**	**3**	**17**	**28**
	C	**11**	**4**	**37**	**52**

Table 2.2 Mean net recruitment of fishes on experimental reefs. Mean net recruitment is the mean difference between the number of fish <5 cm total length (TL) present on experimental reefs at the final (week 5) census and the number present at the initial (week 1) census (dnr indicates that the species did not recruit to any of the reefs of that type). The lionfish effect was calculated as the mean net recruitment to lionfish reefs minus mean net recruitment to control reefs for each species (a negative effect indicates that lionfish reduced recruitment). The lionfish effect was only calculated for species that recruited to both lionfish and control reefs. Table continued on next page.

Family	Species	Mean net recruitment		Lionfish effect
		Control n=10	Lionfish n=10	
Holocentridae	*Myripristis jacobus*	0	0	0
	Sargocentron coruscum	0	-0.6	-0.6
Serranidae	*Cephalopholis fulva*	0	0	0
	Serranus tigrinus	0.2	0.1	-0.1
Apogonidae	*Apogon aurolineatus*	0	dnr	
	Apogon binotatus	0.1	dnr	
	Apogon maculatus	0.6	-0.1	-0.7
	Apogon townsendi	dnr	0	
Lutjanidae	*Ocyurus chrysurus*	0	-0.1	-0.1
Haemulidae	*Haemulon melanurum*	4.3	0.3	-4
	Haemulon plumierii	-0.7	-0.7	0
	Haemulon sp. (juvenile)	-0.8	0	0.8
Mullidae	*Pseudupeneus maculatus*	0	0	0
Chaetodontidae	*Chaetodon capistratus*	-0.1	dnr	
	Chaetodon ocellatus	0	0	0
	Chaetodon sedentarius	-0.1	-0.1	0
	Chaetodon striatus	0	dnr	
Pomacanthidae	*Holacanthus ciliaris*	0.2	dnr	
Pomacentridae	*Stegastes diencaeus*	0.1	dnr	
	Stegastes leucostictus	0.5	1.2	0.7
	Stegastes partitus	-0.4	-0.6	-0.2
	Stegastes variabilis	0.2	0.1	-0.1
Labridae	*Bodianus rufus*	-0.3	-0.2	0.1
	Halichoeres garnoti	0.1	-0.3	-0.4
	Halichoeres maculipinna	-0.3	-0.7	-0.4
	Halichoeres pictus	2.5	-0.4	-2.9
	Halichoeres poeyi	0.7	0	-0.7
	Halichoeres radiatus	-0.2	0	0.2
	Thalassoma bifasciatum	-0.9	-0.5	0.4

Table 2.2 (Continued).

Family	Species	Mean net recruitment		Lionfish effect
		Control n=10	Lionfish n=10	
Scaridae	*Cryptotomus roseus*	0.3	0.1	-0.2
	Scarus taeniopterus	-0.1	0	0.1
	Sparisoma atomarium	0.3	0.2	-0.1
	Sparisoma aurofrenatum	2.4	-0.2	-2.6
	Sparisoma viride	2	1.5	-0.5
	Unknown parrotfish	dnr	0	
Labrisomidae	*Malacoctenus gilli*	1.9	-0.6	-2.5
	Malacoctenus macropus	0.3	0.1	-0.2
	Malacoctenus triangulatus	-0.2	-0.1	0.1
Callionymidae	*Callionymus bairdi*	0.1	dnr	
Gobiidae	*Coryphopterus dicrus*	0.2	0	-0.2
	Coryphopterus glaucofraenum	11.9	4.4	-7.5
	Gnatholepis thompsoni	10.4	3.4	-7
	Gobiosoma genie	-0.1	0	0.1
	Unknown goby	dnr	0	
	Unknown sponge goby	0.1	dnr	
	Priolepis hipoliti	0.5	0.4	-0.1
Acanthuridae	*Acanthurus chirurgus*	-0.2	0	0.2
	Acanthurus coeruleus	0.2	-0.1	-0.3
Tetraodontidae	*Canthigaster rostrata*	0	-0.1	-0.1
	TOTAL	**35.5**	**6.9**	**-28.1**

Table 2.3 List of species eaten by lionfish in aquaria.

Family	Species
Haemulidae	*Haemulon melanurum*
Pomacentridae	*Stegastes leucostictus*
Labridae	*Halichoeres pictus*
Opistognathidae	*Opistognathus aurifrons*
Gobiidae	*Gnatholepis thompsoni*
	Coryphopterus glaucofraenum

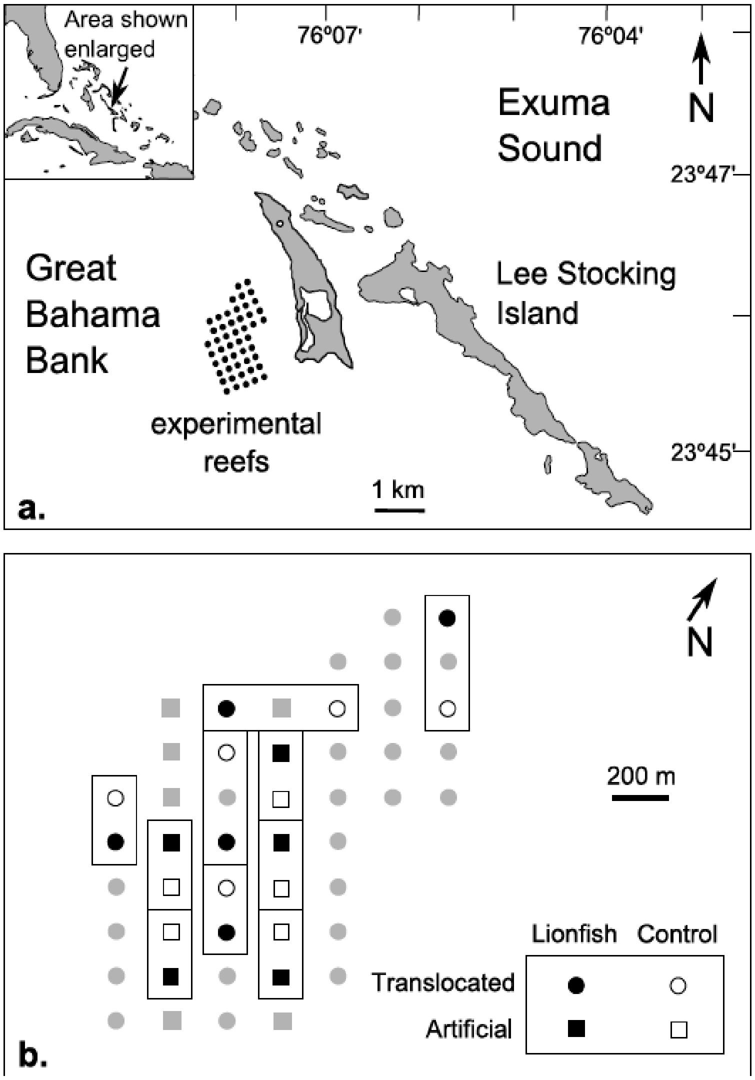

Figure 2.1 Matrix of experimental patch reefs near Lee Stocking Island, Bahamas (a) and experimental design, showing treatment assignments of pairs of reefs surrounded by boxes (b). Grey symbols represent unused reefs. Map redrawn from Almany (2003).

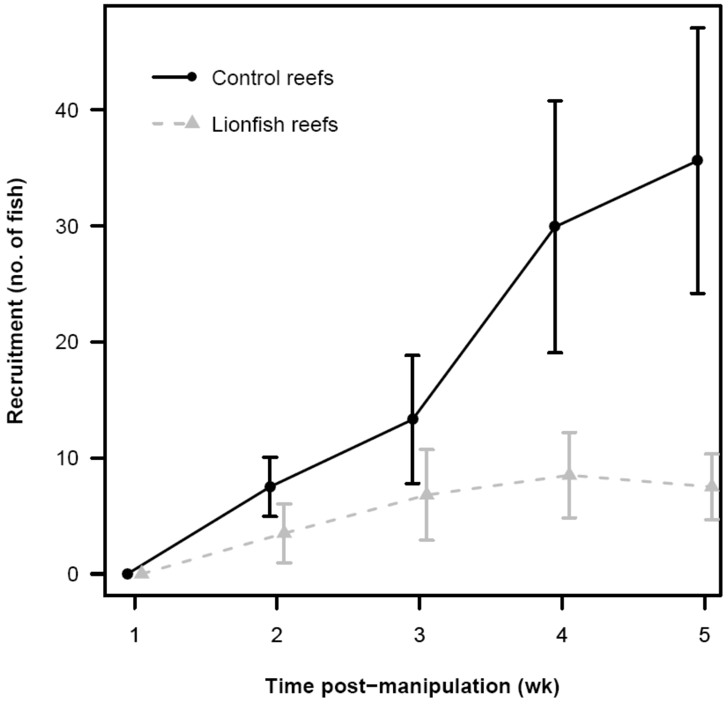

Figure 2.2 Recruitment (mean ± SEM) of juvenile fish to experimental patch reefs after lionfish were transplanted onto 10 reefs, with 10 other reefs serving as lionfish-free controls. Recruitment was measured as the number of small fish present on each reef at the beginning of the experimental period, subtracted from the number of small fish present on each reef during subsequent censuses (i.e., net accumulation of new recruits). Recruitment at week 5 represents net recruitment over the experimental period because daily settlement and mortality were not monitored.

Chapter 3 — Worst case scenario: potential long-term effects of invasive predatory lionfish *Pterois volitans* on Atlantic and Caribbean coral-reef communities

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ABSTRACT

The Pacific red lionfish has recently invaded Western Atlantic and Caribbean coral reefs, and may become one of the most ecologically harmful marine fish introductions to date. Lionfish possess a broad suite of traits that makes them particularly successful invaders and strong negative interactors with native fauna, including defensive venomous spines, cryptic form, color and behavior, habitat generality, high competitive ability, low parasite load, efficient predation, rapid growth, and high reproductive rates. With an eye on the future, we describe a possible “worst case scenario” in which the direct and indirect effects of lionfish could combine with the impacts of preexisting stressors -- especially overfishing -- and cause substantial deleterious changes in coral-reef communities. We also discuss management actions that could be taken to minimize these potential effects by, first, developing targeted lionfish fisheries and local removals, and second, enhancing native biotic resistance, particularly via marine reserves that could conserve and foster potential natural enemies of this invader. Ultimately, the lionfish invasion will be limited either by the lionfish starving -- the worst end to the worst case scenario -- or by some combination of native pathogens, parasites, predators, and competitors controlling the abundance of lionfish.

3.1 INTRODUCTION

Biological invasions are a major cause of ecosystem disruption and biodiversity loss, and are a major source of human-caused global change (Elton 1958, Vitousek et al. 1997, Mack et al. 2000). Invasive species are estimated to result in environmental and economic costs exceeding 120 billion dollars annually in the United States alone (Pimentel et al. 2005). While the majority of invasions have occurred in terrestrial and freshwater systems, marine invasions are increasing at an alarming rate and may have substantial impacts on the stability of ocean ecosystems and the multitude of goods and services they provide (Ruiz et al. 1997). However, until recently there have been no documented cases in which an introduced marine fish has become a major invasive threat. This situation has now changed with the invasion of Atlantic and Caribbean coral reefs by the Indo-Pacific red lionfish *Pterois volitans*, an event that has recently been recognized as one of the world's top conservation issues (Sutherland et al. 2010).

Two species of Indo-Pacific lionfish (*Pterois volitans* and *P. miles*) were apparently introduced to Florida coastal waters during the mid 1980s (Morris and Whitfield 2009), and have become the first truly invasive marine fishes in the Atlantic. The most likely vectors for the introduction were releases or escapes from marine aquaria (Hare & Whitfield 2003, Semmens et al. 2004, Ruiz-Carus et al. 2006). Over the past two decades and especially since 2005, the range of *P. volitans* has expanded rapidly across a substantial portion of the tropical and sub-tropical Western Atlantic and Caribbean (Schofield 2009), with the highest densities currently reported from coral reefs in the Bahamas (Green & Côté 2009). *P. volitans* occurs throughout the invaded range, whereas sibling species *P. miles* appears to be restricted to the U.S. mainland (Freshwater et al. 2009). A recent detailed review of the lionfish invasion is provided by Morris and Whitfield (2009).

Here, we briefly examine the potential for lionfish to cause one of the most devastating marine invasions to date. We summarize possible long-term direct and indirect effects of the invasion based on current knowledge of coral-reef ecology, and discuss potential mitigation measures.

3.2 CONSUMMATE INVADER AND STRONG NEGATIVE INTERACTOR

Invasive lionfish exhibit high individual growth and reproductive rates, apparently spawning throughout the year and several times per month, with an estimated annual fecundity of over two-million eggs female^{-1} (Morris & Whitfield 2009). Consequently, population growth rates have been phenomenal in some invaded regions (Fig. 3.1). Lionfish at certain locations in the Bahamas have reached densities greater than 390 fish ha^{-1} (Green & Côté 2009), far exceeding the highest densities reported from their native Pacific range of ca. 80 fish ha^{-1} (Schiel et al. 1986, Fishelson 1997, Kulbicki et al. in review). Lionfish densities at sites along the eastern seaboard of the United States exceed those of all but one species of native grouper (Whitfield et al. 2007). Though mostly found on coral reefs, invasive lionfish are also somewhat generalized among warm shallow marine habitats, including seagrass beds (authors, pers. obs.) and mangroves (Barbour et al. 2010), as well as artificial structures, such as shipwrecks (authors, pers. obs.). In the Bahamas, they have been observed from submersibles at a depth of 300 m (R. G. Gilmore, pers. comm.).

Growing rapidly (Chapter 4: Albins in review) and measuring up to nearly 50 cm in total length (L. Akins, REEF, pers. comm.), invasive lionfish are both unique and effective predators of small fishes and crustaceans. They are unique predators in two ways. First, their slow movements, cryptic coloration, and elongated fin rays give them the appearance of a tuft of seaweed, a crinoid, or a tube-worm, perhaps a case of masquerade mimicry as well as camouflage (general reviews by Endler 1981, Skelhorn et al. 2010). Second, while stalking prey, lionfish flare their large, fan-like pectoral fins and slowly herd small fish, which are typically cornered then rapidly consumed. Atlantic prey fishes have not encountered such a predator in their evolutionary history, and native prey seem to take no evasive action. These patterns help to explain why invasive lionfish exhibit higher consumption rates than similarly sized native predators occupying the same habitats (Chapter 4: Albins in review). Divers in the Bahamas have observed a single lionfish consume over 20 juvenile reef fish in just 30 min (Chapter 2: Albins & Hixon 2008), and average consumption rates throughout the day are on the order of 1 to 2 prey hr^{-1} (Côté & Maljković 2010). Prey include a broad diversity of small reef fishes, as well as shrimps and other small mobile invertebrates (Morris & Akins 2009). Prey reef fishes include over 40 species from over 20 families, making lionfish a highly generalized predator of both small species and juveniles of large species.

As well as being efficient predators, invasive lionfish themselves appear to be largely impervious to predation, although available data are sparse and contradictory. Perhaps due to the slow movements and crypsis/mimicry of the invader, native predators seldom appear to recognize lionfish as potential prey (Morris 2009, authors, pers. obs.). Lionfish are also defended by long venomous fin spines, such that, even when sharks or large grouper do attack, they almost always immediately retreat without obvious injury to the lionfish (authors, pers. obs.). Nonetheless, there is a published report of fishermen in the Bahamas capturing one tiger grouper *Mycteroperca tigris* and two Nassau grouper *Epinephelus striatus*, each with a lionfish in its stomach (Maljković et al. 2008). Additionally, divers in the Cayman Islands have trained wild Nassau grouper to consume lionfish, without the grouper showing ill effects (authors, pers. obs.). However, one large Nassau grouper that ate a large lionfish tail first appeared to be literally stunned (authors, pers. obs.). Additionally, large and clearly hungry Nassau grouper held in tanks will not eat small lionfish (M. Cook and W. Raymond, unpubl. data). In controlled field experiments, Nassau grouper have no effect on the growth and survival of small lionfish (T. J. Pusack, unpubl. data). Thus, it is presently uncertain whether or not large Atlantic grouper are effective predators of invasive lionfish.

Additionally, invasive lionfish appear to be effective competitors and resistant to parasitism. A field experiment in the Bahamas demonstrated that lionfish have 2.4 times the negative effect on native reef-fish populations as do ecologically similar native coney grouper *Cephalopholis fulva*, and grow about 4 times as rapidly (Chapter 4: Albins in review). Lionfish in the Bahamas are also infected by very low levels of endo- and ecto-parasites that commonly infect native fishes inhabiting the same reefs (Morris et al. 2009, Sikkel et. al. in prep.), and parasite loads appear to be greater in their native Pacific habitats (Sikkel et al. in prep.). Lower parasite loads in invaded Atlantic habitats could translate to higher growth rates and greater fecundity.

Overall, it appears that a broad combination of traits make lionfish consummate invaders and particularly strong negative interactors with native fishes (review by Morris & Whitfield 2009). In contrast, lionfish are relatively rare throughout most of their native Pacific range (Kulbicki et al. in review). While rarity alone does not necessarily indicate low ecological importance, and while conclusive data comparing the ecological impact of lionfish in their native range to that in the invaded range are not yet available, lionfish tentatively appear to play a relatively minor ecological role on Pacific coral reefs. This contrast indicates that, upon invading the relatively species-poor Atlantic from the relatively diverse Pacific, lionfish have undergone substantial “ecological release” from natural controls (sensu Elton 1958). In other words, Atlantic coral reefs thus far exhibit little “biotic resistance” to the lionfish invasion.

3.3 WORST CASE SCENARIO: DEPAUPERATE REEF-FISH COMMUNITIES AND DEGRADED CORAL REEFS

To date there have been few studies of the ecological impacts of the lionfish invasion. Albins and Hixon (Chapter 2: 2008) compared the net recruitment of fishes to 10 coral patch reefs with lionfish vs. 10 reefs without lionfish in the Bahamas. Over 5 wk during the height of the summer recruitment season, single lionfish reduced recruitment significantly, by an average of 79 % relative to controls, including 23 of 38 species (14 families) that settled on both sets of reefs. A subsequent field experiment in the same location and season showed that, after two months, native coney grouper alone had reduced the abundance of small fish on the reefs by an average of 35 %, whereas invasive lionfish alone had reduced prey fish by 90 % (Chapter 4: Albins in review). Such rates of reduction in fish abundances cannot be sustained (Green et al., unpubl. data). Clearly, lionfish pose a potential threat to native reef fishes as both a predator and a competitor. Yet, given the scarcity of data, we can only speculate on the future.

Sampling over 1,000 lionfish stomachs from the Bahamas, Morris and Akins (2009) documented that the invaders consumed a broad variety of small reef fishes, especially gobies (Gobiidae), wrasses (Labridae), and basslets (Grammatidae). Other reef fishes affected by lionfish predation include important food species, such as groupers, snappers, and goatfishes (Chapter 2: Albins & Hixon 2008, Morris & Akins 2009). If populations of preferred prey are depleted through time, then it is possible that lionfish will eventually concentrate on juveniles of these economically important fisheries species. In any case, the possibility that lionfish could substantially divert the biomass of small fishes otherwise destined to grow and feed higher trophic levels, including humans, is certainly conceivable. The Caribbean coral-reef aquarium fish trade would also likely suffer. Of the top 20 ornamental species collected from the Western Atlantic (Bruckner 2005), seven are members of the top ten families that comprise lionfish diets in the Bahamas (Morris & Akins 2009).

Indirect effects of lionfish predation may be even more severe, given that their prey include parrotfishes (Chapter 2: Albins & Hixon 2008, Morris & Akins 2009). It is well-documented that overfishing parrotfishes and other herbivores contributes to the demise of reef corals by reducing the herbivory that normally helps to prevent seaweeds from outcompeting corals and/or interfering with coral recruitment (Mumby et al. 2006, Mumby & Steneck 2008). Lionfish can thus be viewed as potentially effective at “overfishing” juvenile parrotfishes and other small herbivorous fishes, with possibly devastating indirect effects on reef-building corals. This impact could be exacerbated in food webs that exhibit trophic cascades where top predators are already overfished (Stallings 2009). In such circumstances, top predators (such as large groupers) no longer reduce the abundance of native mesopredators (such as small groupers), thereby freeing the smaller predators to reduce the abundance of small herbivorous fishes (Stallings 2008). This phenomenon has been called “mesopredator release,” and in general is capable of destabilizing communities and causing local extinctions (Prugh et al. 2009). Given that lionfish may be naturally “released” mesopredators simply because they may be impervious to predation, they may also have free reign to reduce the abundance of herbivores, thereby indirectly negatively affecting reef corals by fostering seaweed growth. In this case, a combination of ecological release of an invasive mesopredator and release of native mesopredators due to overfishing could conspire to deal a substantial double blow to already threatened reef-building corals. More extreme fishing that targets all trophic levels yet ignores lionfish because of their venomous spines could eliminate release of native mesopredators, yet still trap native reef fishes between “the devil” of lionfish eating juveniles and “the deep blue sea” of humans overfishing adults.

These potential direct and indirect effects are illustrated in Figure 3.2, which shows greatly simplified interaction webs on undisturbed reefs vs. reefs with both human and lionfish impacts, typical of the Caribbean region. The left-hand web shows the normal trophic cascade that indirectly benefits corals. The right-hand web — the worst case scenario — shows how fishing can reduce the abundance of all larger fishes of all trophic levels. Such overfishing is now exacerbated by over-consumption of the juveniles of many of these same species by lionfish, further worsening the phase shift toward seaweeds replacing corals as the dominant benthos.

Besides possible indirect effects of invasive lionfish on corals and other benthos, the decline of other mid-sized predators via predation by or competition with lionfish could destabilize populations of still other reef fishes. Such native predators, including mid-sized grouper, have been documented to be important sources of density-dependent mortality that may regulate local populations of reef fishes [review by Hixon and Jones (2005), see Hixon and Carr (1997) and Carr et al. (2002) for examples from the Bahamas].

Overall, one can imagine a worst case scenario in which most reef-fish biomass is converted to lionfish biomass, leaving invaded reefs depauperate of native fishes, except for those species that are not susceptible to (or perhaps indirectly benefit from) lionfish predation. Such survivors could include sharks and rays (whose new-born pups are too large to be eaten by lionfish), tunas and other transient predators (which do not visit reefs until reaching invulnerable sizes), puffers and relatives (which are morphologically and chemically defended), and scattered survivors of species that live and spawn in areas inaccessible to lionfish (perhaps reefs with strong prevailing currents). Unfortunately, sharks and other large predators are already overfished by humans in many regions (Stallings 2009), which produces a double jeopardy for reefs: (1) human-caused decline of species that may be naturally resistant to lionfish predation, and (2) human-caused decline of species that could possibly learn to consume and thereby control lionfish abundance. In the worst case scenario, the geographic range of invasive lionfish would eventually be limited only by water temperature and associated physiological constraints, with gradual expansion due to ocean warming. Their abundance would be controlled only by within-species competition as living space and/or food became limited, perhaps resulting in extensive cannibalism. Based on sea surface temperature constraints, Morris and Whitfield (2009) predicted the potential invasive range of adult lionfish as extending from Cape Hatteras, North Carolina, in the Northern Hemisphere, to the southern border of Brazil in the Southern Hemisphere. Combined with the accelerated demise of corals due to overfishing herbivores, coral bleaching, and local environmental degradation, the resulting reef ecosystems could become vastly different from even the present despoiled state of Atlantic reefs (Jackson 2010).

3.4 AVOIDING THE WORST CASE SCENARIO

Efforts to stem the lionfish invasion have thus far focused on local control via periodic collections by divers on specific reefs. Fortunately, slow swimming lionfish are usually easy to locate and capture by divers using hand nets (authors, pers. obs.). Successful “lionfish derbies” have been held in the Bahamas and Florida that result in hundreds to thousands of fish being removed in a single day, typically followed by a lionfish cookout. Such efforts are promoted by the Reef Environmental Education Foundation (REEF, www.reef.org), the Bahamas Reef Environment Educational Foundation (BREEF, www.breef.org), and similar volunteer organizations. The Bahamas and other nations are encouraging lionfish fisheries, given that the venom of the fish spines denatures when cooked and that lionfish flesh is tasty, much like other scorpionfishes, although the fillets are small. Bounties would foster such fisheries. Some restaurants in the United States are offering invasive lionfish as a conservation dish, which could further encourage lionfish fisheries. If such fisheries are successful, it will be important to ensure that they are restricted to the Atlantic Ocean, given that lionfish are relatively rare in their native Pacific range (Kulbicki et al. in review).

Unfortunately, there are far more reefs to patrol than there are divers in most areas, and in any case, invasive lionfish have been reported to several hundred meters depth, providing an effective deepwater refuge unless effective traps can be developed. Therefore, the ultimate hope is regional control via natural agents of biotic resistance. These agents are presently unknown, but may eventually include some combination of native pathogens, parasites, predators, and competitors. Although there is presently no evidence for Atlantic diseases or parasites attacking lionfish in any substantial way, it is certainly conceivable that native sharks, groupers, and other top predators will eventually learn to target lionfish (review by Csányi & Dóka 1993). Besides anecdotal information that Atlantic grouper occasionally eat lionfish (Maljković et al. 2008), there are scattered reports from the Pacific that cornetfish (Bernadsky & Goulet 1991) and other predatory fishes also attack lionfish. Such predation could be fostered by divers training such piscivores to consume lionfish at particular reefs.

Ultimately, fishing restrictions and marine reserves that protect species capable of controlling lionfish abundance may be the most effective management action to address the invasion. Marine reserves on coral reefs are well-documented to effectively protect predatory fishes and otherwise foster larger body sizes (Halpern 2003). While it is unknown whether native piscivores, even under the best circumstances, will be capable of reducing lionfish numbers sufficiently or quickly enough to mitigate their negative effects, preserving the integrity of native apex predator populations via fishing restrictions and marine reserves remains a precautionary and foresighted management approach to the lionfish invasion. In any case, the ongoing spread of invasive lionfish throughout the greater Caribbean region will eventually be controlled either by starvation of lionfish, which would be the most extreme ending of the worst case scenario, or by native species (competitors, predators, parasites, and/or pathogens) finally providing biotic resistance to the invasion. Only time will tell whether local and regional control efforts, or simply nature running its course, will limit the potentially disastrous invasion of Atlantic and Caribbean coral reefs by Pacific lionfish.

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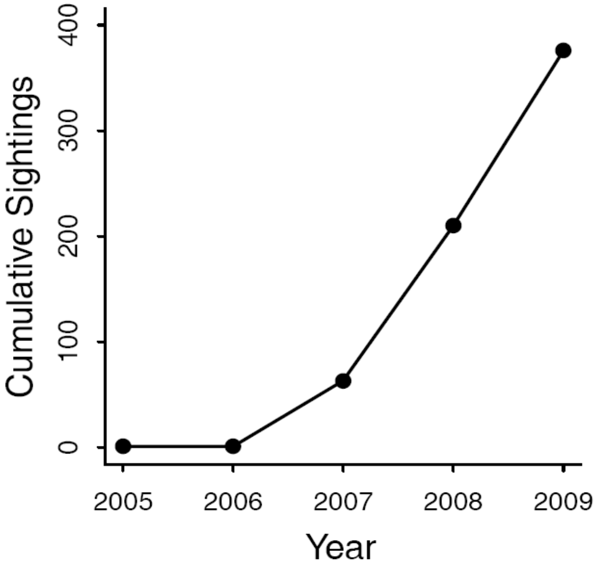

Figure 3.1 Cumulative number of lionfish sightings at 7 coral reefs annually surveyed by the authors and their colleagues in the vicinity of Lee Stocking Island, Bahamas, from 2005, when the first juvenile was observed, through 2009 (observations began in the early 1990s). New sightings were calculated as the number of fish observed at a site during a given survey year minus the number observed at that site during the previous survey year.

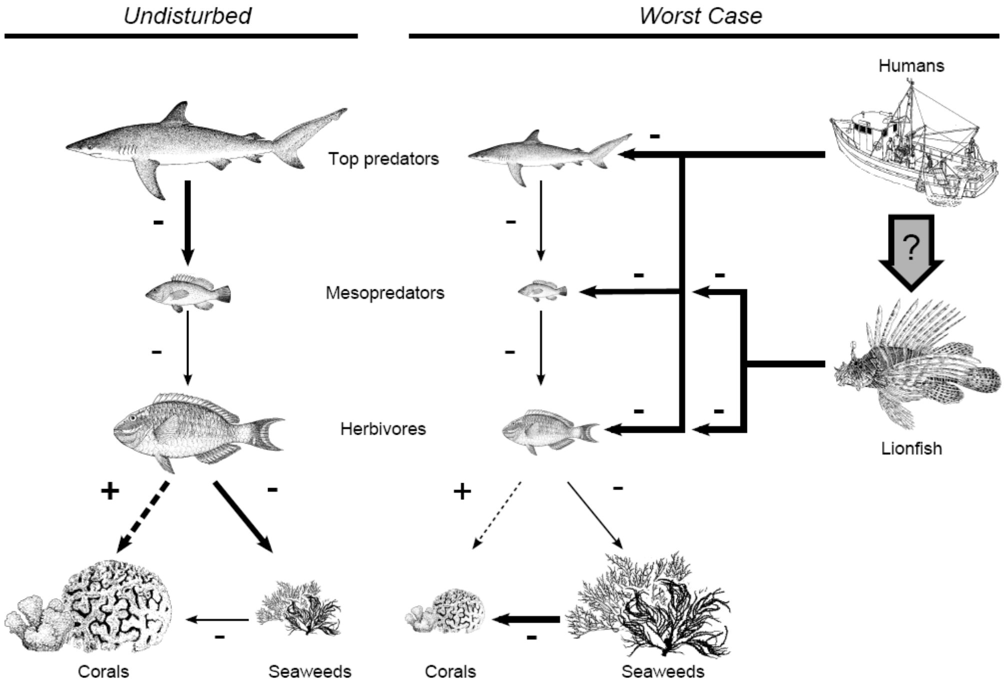

Figure 3.2 Worst case scenario for future Atlantic and Caribbean coral-reef ecosystems caused by a combination of human overfishing of larger fishes of all trophic levels and invasive lionfish consuming small fishes and competing with other mesopredators (right), compared to an undisturbed system (left). The size of each kind of organism represents its relative abundance comparing the two interaction webs, and the thickness of each arrow represents the relative interaction strength between organisms. Solid arrows are direct effects representing predation (including fishing), except in two cases: competitive effects of (1) seaweeds on corals and (2) lionfish on other mesopredators and juveniles of some top predators (such as juveniles of large grouper species). The dashed arrow is the indirect positive effect of herbivores on reef-building corals. The unknown future effect of humans on lionfish is indicated by a question mark, and will be the focus of control efforts. Images courtesy of FAO.

Chapter 4 — Comparing the effects of invasive Pacific red lionfish *Pterois volitans* and a native predator on coral-reef fish communities

Mark A. Albins

Biological Invasions
In Review

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 of a broad diversity of native coral-reef fishes. Otherwise, little is known about how lionfish affect native coral-reef communities. A controlled field experiment conducted on small patch-reefs in the Bahamas demonstrated that (1) compared to predator-free control reefs, invasive lionfish caused significant reductions in the abundance (93.4 % reduction) and richness (loss of 4.6 ± 1.6 species) of small native coral-reef fishes over short time scales; (2) the effect of lionfish on the change in abundance of native reef-fishes was 2.6 ± 0.5 times stronger (mean ± SEM) than the effect of a similarly sized native predator (the coney grouper *Cephalopholis fulva*); (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 are not ecologically equivalent to similarly sized native piscivores, and may represent a substantial threat to native coral-reef fishes.

4.1 INTRODUCTION

Some of the most notorious and destructive biological invasions, in terms of loss of native species and disruption of ecosystems, have resulted from the introduction of non-native predatory freshwater fishes (Ogutu-Ohwayo 1990, Ross 1991, Witte et al. 1992, Lever 1996, Fuller et al. 1999, Marchetti 1999, Lowe et al. 2000, reviewed in Helfman 2007). Introductions of non-native predatory estuarine and diadromous fishes have also resulted in invasions that have negatively affected native communities and ecosystems (Baltz 1991, Courtenay 1995, Lever 1996, Fuller et al. 1999).

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 (Randall 1987, Baltz 1991). Examples of marine fishes which have become established after introduction include the peacock grouper *Cephalopholis argus* and the bluelined 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). The few that have were conducted decades after the introductions occurred, and have been restricted to observational rather than experimental approaches (Friedlander et al. 2002, Bariche et al. 2004, Goren & Galil 2005, Schumacher & Parrish 2005, Dierking et al. 2009). In contrast, the effects of invasive lionfish on native coral-reef fishes have been examined in a prior experimental study (Chapter 2: Albins & 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. Since the early 2000s, their range has expanded rapidly throughout the tropical and sub-tropical Western Atlantic Ocean and Caribbean Sea (Schofield 2009). In addition to their rapid range expansion, invasive lionfish are of particular concern for several reasons (reviews by Morris & Whitfield 2009, Chapter 3: Albins & Hixon 2011). Lionfish in the Atlantic demonstrate high individual growth and reproductive rates (Morris & Whitfield 2009) and high population growth rates (Chapter 3: Albins & Hixon 2011). They are reaching higher densities (nearly 5 times greater) in the invaded range (Green & Côté 2009) than have been reported from their native Pacific range (Schiel et al. 1986, Fishelson 1997). As generalist piscivores, lionfish have great potential to cause substantial harm to native reef-fish communities.

The success of lionfish in the invaded range, as compared to their native Pacific where they are typically found in relatively low densities, suggests some form of ecological release or a lack of biotic resistance in the Atlantic (sensu Elton 1958). While it is likely that a number of mechanisms are contributing to the success of invasive lionfish, potential factors include resistance to native predators and/or parasites, and a lack of effective resistance to lionfish by native prey. Lionfish are well defended by venomous fin spines, which may confer some degree of protection from Atlantic predators (Morris 2009), but see Maljković et al. (2008). Lionfish also have reduced parasite loads as compared to similarly sized native fishes (P. Sikkel pers. comm.). In addition, 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 (Chapter 3: Albins & Hixon 2011). A combination of slow 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 (Chapter 3: Albins & Hixon 2011). When hunting, lionfish slowly approach prey with their large fan-like pectoral fins flared and held perpendicular to their body. Prey are often herded into a corner and consumed with a rapid strike (Chapter 3: Albins &

Hixon 2011). The fact that Atlantic prey species are naïve to this particular set of characteristics and behaviors may make them particularly susceptible to predation by lionfish.

Invasive lionfish consume a broad diversity of native coral-reef fishes (Chapter 2: Albins & Hixon 2008, Morris & Akins 2009). 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 (Chapter 2: Albins & Hixon 2008). Such drastic reductions in populations of small fishes will likely have a detrimental effect on native coral-reef communities (Chapter 3: Albins & Hixon 2011).

It is also likely that lionfish will have indirect negative effects on native piscivores by reducing prey availability. While native piscivore populations are already substantially 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. Invasive lionfish have reached some of the most remote reefs and readily cross reserve boundaries. Therefore, potential competitive interactions between lionfish and native piscivores could inhibit conservation and stock rebuilding efforts for these species.

Reductions in the survival of juvenile herbivorous fish could additionally 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). This potential for lionfish to cause indirect destabilizing effects on native coral reefs is of particular concern due to the fact that these ecosystems have already been substantially degraded by a suite of human caused disturbances, including overfishing, pollution, and climate change (Mora 2008). In short, what is currently known of the ecology of invasive lionfish suggests that this predator could manifest one of the most damaging marine-fish invasions to date (Sutherland et al. 2010, Chapter 3: Albins & Hixon 2011).

While a previous experiment has shown that lionfish reduce the abundance of small native coral-reef fishes (Chapter 2: Albins & Hixon 2008), many questions about the effects of this invasion on native communities remain unanswered. This study explores the effects of lionfish on native reef-fish communities relative to a common, similarly sized, native predator, the coney grouper *Cephalopholis fulva*, and addresses the following questions: (1) What are the effects of invasive lionfish on the community composition of small native coral-reef fishes? (2) How do the effects of lionfish on native reef-fish communities compare to those of a similarly sized native predator? (3) What are the combined effects of invasive lionfish and native predators on native reef-fish communities? (4) Does the presence of invasive lionfish affect the growth rates of the native predator (and vice versa)? (5) How do growth rates compare between the invasive and native predators under identical conditions?

4.2 METHODS

4.2.1 Study site and experimental design

The study system consisted of 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 ca. 3 m^2, which were translocated in the early 1990s and are now essentially natural features (Carr & Hixon 1995, Hixon & 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. 4.1). The degree of spatial isolation among reefs, coupled with relatively featureless intervening habitat (flat, sandy, seagrass beds), means that the resident reef-fish communities can be treated as independent replicates (i.e., negligible juvenile and adult movement among reefs, Almany 2003).

I conducted an initial 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 based on the number of territorial damselfishes, as these species are known to have strong effects on the recruitment of fishes (Almany 2003). I also removed all resident adult piscivores from the experimental reefs (after removals, no adult piscivores were observed on experimental reefs during the study). I then randomly assigned four different resident-predator treatments to the four reefs in each of the five blocks. The treatments included a single native grouper, a single invasive lionfish, one native grouper and one invasive lionfish together, and a predator-free control. The first treatment corresponded to the pre-invasion community, whereas the second and third represented the post-invasion community in the absence and presence (respectively) of native predators. A comparison of univariate and multivariate responses indicated that communities of small native reef-fishes were essentially similar among experimental reefs assigned to the four treatments at the beginning of the experiment (see methods and results sections for details).

Because of the randomized-block design of the experiment, I assumed that visitations by highly mobile predators, such as jacks and barracuda, would be distributed among experimental reefs with negligible bias. If mobile predator visitations were biased among experimental treatments, it seems reasonable to assume that they would be highest on reefs with the highest densities of prey (control reefs) due to an aggregative response, and would thus result in conservative estimates of resident predator effects.

Predator treatments were established by transplanting live lionfish and coney grouper onto the experimental reefs. Predators were captured using small hand nets, and were 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 mean (±SEM) length of transplanted lionfish was 7.1 ± 0.4 cm TL, and the mean mass was 4.0 ± 0.5 g, while the mean length of transplanted grouper was 7.0 ± 0.3 cm TL, and the mean mass was 4.7 ± 0.7 g. At the end of the experiment, all native coney grouper were released, and all invasive 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 established the coney as being an effective predator of small reef fishes in the study system (Almany 2003, 2004a, 2004b, Stallings 2008).

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

2 divers using SCUBA, who counted and sized all fishes ≤5 cm TL on each reef following methods described by Hixon & Beets (1989, 1993).

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. Therefore, 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 native species and on post-settlement juveniles of both small-bodied and large-bodied species.

4.2.2 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} is the change in abundance for reef i at census t, and n_{tij} is the abundance of species j on reef i at census t. Therefore, ΔN represents 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 juvenile 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', which combines richness and evenness (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 modeling it as 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 & Molenberghs 2000) indicated that inclusion of the random *reef* term resulted in significantly better fits for each of the response variables (Table A.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 variance and correlation structures. I compared the resulting models using Akaike's Information Criterion (AIC) and used the optimal models for hypothesis testing (Table A.1). Visual examination of standardized residuals from the final optimal models indicated that all 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 potential competitor), 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 LRTs for length growth, but inclusion of a random term for *reef* provided the best fit for mass growth (Table A.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 (Table A.1). Examination of the residuals from the optimal models suggested that all assumptions including homogeneity, independence, and normality, were met. Once the best fitting baseline response models, in terms of random effects and variance structures were selected, I refit each model using Maximum Likelihood estimation, and used LRTs to test for significance of 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 & Wish 1978, McCune & Grace 2002), and a permutation-based Multivariate Analysis of Variance (perMANOVA, McArdle & Anderson 2001), with 1000 permutations constrained within experimental blocks. This analysis was run 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 (wk 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 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 & 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 to 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 & 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 and used the associated packages *MASS*, *nlme* and *vegan* (Venables & Ripley 2002, Pinheiro et al. 2009, R Development Core Team 2009, Oksanen et al. 2010). Evaluation of LMMs and selection of appropriate random structures followed the guidelines and procedures described in Zuur et al. (2009).

4.3 RESULTS

4.3.1 Native reef-fish abundance

During the summer recruitment period of study, the overall abundance of small native reef fish (≤5 cm TL) on predator-free control reefs increased by 66.6 ± 10.4 fish reef^{-1}(mean ± SEM) over the course of the 8 wk experiment ($t = 6.43$, $p < 0.001$; Fig. 4.2). Compared to predator-free controls, single lionfish reduced the change-in-abundance (ΔN) by 62.4 ± 11.9 fish reef^{-1} ($t = 5.25$, $p < 0.001$), representing an average reduction of 93.7 %. While ΔN on native-grouper-only reefs was 24.2 ± 12.0 fish reef^{-1} lower, on average, than ΔN on control reefs, this effect was only 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 reef^{-1} ($t = 5.26$, $p < 0.001$). The abundance of small fish did not differ among reefs assigned to the four predator treatments at the baseline census (i.e. prior to establishment of predator treatments, Table A.2).

Most of the overall change in abundance on predator-free control reefs (ΔN) was due to increases in the abundance of two common species, the bridled goby *Coryphopterus glaucofraenum* and the beaugregory damselfish *Stegastes leucostictus*. Fourteen other species in ten different families contributed to the increase, including three herbivorous species (Table A.3). Of these top sixteen contributors, the change in abundance of fifteen species (including all three herbivores) was lower on both lionfish-only reefs and reefs with both predators present than on control reefs. The exception was the goldspot goby *Gnatholepis thompsoni*, which increased slightly more on both 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, was also lower on grouper-only reefs than on control reefs. A notable exception included the stoplight parrotfish *Sparisoma viride*, which increased substantially more on grouper-only reefs than on control reefs.

4.3.2 Predator growth rates

Invasive lionfish did not affect the growth rates of native coney grouper, and native grouper had no 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). However, 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 d^{-1} and in mass by 0.26 ± 0.02 g d^{-1}, while coney increased in length by 0.13 ± 0.02 mm d^{-1} and in mass by 0.04 ± 0.01 g d^{-1} (means ± SEMs).

4.3.3 Native reef-fish richness, evenness and diversity

During the summer recruitment period of study, the species richness of small reef fish increased by 3.4 ± 1.15 species (mean ± SEM) on predator-free control reefs over the experimental period (t = 2.97, p = 0.004; Fig. 4.3a). Compared to controls, lionfish caused a reduction in the change in richness (ΔS) of 4.6 ± 1.6 species (t = 2.84, p = 0.011). While ΔS was reduced by 2.4 ± 1.6 species on grouper-only reefs compared to control reefs, this difference was not significant (t = 1.48, p = 0.157). The effect of invasive lionfish on ΔS was 1.9 ± 0.7 times larger than the effect of native grouper, although this difference also was not significant (t = 1.36, p = 0.193). The effect of lionfish and grouper together, however, 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 8.8 ± 1.6 species compared to predator-free controls. Richness did not differ among reefs assigned to the four predator treatments at the baseline census (Table A.2).

Over the course of the experiment, there was a negative change in species evenness (ΔJ) of 0.12 ± 0.03 (mean ± SEM) on the predator-free control reefs ($t = 4.23$, $p < 0.001$; Fig. 4.3b). 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, although the difference between the two treatments was not significant ($t = 1.76$, $p = 0.096$). While each of the predator species alone appeared to have a positive effect, if any, 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 reduction in ΔJ of 0.10 ± 0.05, although this difference was only marginally significant ($t = 2.07$, $p = 0.054$). At the beginning of the experiment, prior to the establishment of predator treatments, evenness was 0.10 ± 0.04 higher on reefs assigned to the combined predator treatment than on reefs assigned to the grouper only treatment ($t = 2.39$, $p = 0.030$). Otherwise, evenness did not differ among the predator treatments at the baseline census (Table A.2).

The Shannon-Wiener species diversity index (H') remained relatively constant over the course of the experiment on predator-free control reefs, showing a slight, but non-significant decrease of -0.06 ± 0.13 (mean ± SEM; t = 0.50, p = 0.621; Fig. 4.3c). Neither native grouper alone nor invasive lionfish alone caused differences in $\Delta H'$ compared to predator-free controls (t = 0.27 and 0.22, p = 0.791 and 0.826, respectively). 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). At the beginning of the experiment, before establishment of predator treatments, diversity was 0.48 ± 0.17 higher on reefs assigned to the combined predator treatment than on reefs assigned to the grouper only treatment (t = 4.02, p = 0.001), and 0.37 ± 0.17 higher on combined predator treatment reefs than on lionfish only reefs (t = 3.53, p = 0.003). Otherwise, diversity did not differ among reefs assigned to the four treatments at the baseline census (Table A.2).

4.3.4 Multivariate community response

An NMDS ordination of communities at the beginning of the experiment (final stress = 18.07, linear r^2 = 0.83, Monte-Carlo p = 0.02) illustrated a high degree of overlap among reefs across the four treatments (Fig. 4.4a). Results of a perMANOVA suggest 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 (final stress = 12.81, linear $r^2 = 0.92$, Monte-Carlo p = 0.02) illustrated clear differences among the four predator treatments in terms of species composition and relative abundances (Fig. 4.4b). 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 occupied a similar range to lionfish-only reefs along axis-1, but were distributed much more broadly across axis-2 than any of the other treatments.

4.4 DISCUSSION

4.4.1 Native reef-fish abundance and predator growth rates

The experiment clearly demonstrated that single small lionfish drastically reduced the abundance of small native fishes on patch reefs over short time periods, and that this effect of lionfish was much stronger than that of a similarly sized native predator. Native fish abundance was also substantially lower in the combined-predator treatment than in the native-grouper treatment.

The experimental design deliberately confounded number of predators with predator identity because that is the nature of an invasion: a new species is added to an existing native community. The treatments used were the best experimental approximations of comparisons between pre-lionfish-invasion systems and post-lionfish-invasion systems. In fact, the real-world implications of this invasion mirror these experimental treatments quite closely. Before the lionfish invasion, it would have been typical to find patch reefs with single small resident coney groupers; 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 can be viewed as a simplified pre-invasion food web, while the combined predator treatment represents 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 & Whitfield 2009, Schofield 2009). The lionfish-only treatment provided a possible future scenario where lionfish have excluded native predators.

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 (the bridled goby and beaugregory damselfish), with a broad diversity of fishes (including three herbivorous species) 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 was spread across a majority of the most commonly recruiting species (Table A.3).

Such a drastic reduction in the recruitment of a broad diversity of native reef fishes, if widespread in the system as a whole, could have serious direct demographic consequences for native fish populations. The 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 & Hixon 1995, Hixon & Jones 2005, Almany & Webster 2006). If the drastic 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 have far-reaching and destabilizing consequences for entire coral-reef ecosystems (Chapter 3: Albins & Hixon 2011).

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). Together this evidence suggests that lionfish may have both direct (via predation on juveniles) and indirect (via exploitation of food resources) negative impacts on ecologically and commercially important native predators like groupers. One highly speculative, yet nonetheless important, potential implication of the relatively rapid growth rates of lionfish documented in this study is the possibility that cohorts of lionfish may affect contemporaneous cohorts of native predators serially, first as juvenile competitors for limited prey resources, and later as adult intra-guild predators, preying on the now-smaller natives. Native predators are already severely overfished in many locations across the Caribbean, especially in areas with high human population densities (Stallings 2009). While 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.

4.4.2 Native reef-fish richness, evenness, and diversity

Richness of small native reef-fishes increased on control reefs and decreased on combined-predator reefs over the course of the experiment. The increase on control reefs was due to the addition of rare species via larval settlement that were not present at the beginning of the experiment. Compared to controls, lionfish caused a reduction in the number of native species over the course of the experiment, whereas native grouper did not. Lionfish and grouper together (post-invasion treatment) caused a substantial reduction in native fish species richness compared to grouper alone (pre-invasion treatment). It is important to note, however, that species richness may have been higher on the combined predator treatment reefs than on the grouper-only reefs at the beginning of the experiment (Table A.2). Despite this caveat, the results of this study suggest that one of the ultimate effects of the lionfish invasion may be a reduction in the local richness of native fishes.

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 could be explained by invoking a type III functional response (Holling 1959) in which lionfish consume more common species at higher per-capita rates than less common species. This would effectively reduce the differences in abundance between common and rare species. While the effect of native grouper on the change in evenness is not certain, the mean difference compared to controls was positive (similar to the lionfish effect). However, change in evenness for the combined-predator treatment was more similar to that for the control treatment than it was to either of the single-predator treatments. This non-additive effect of the two predators on evenness is difficult to explain. One highly speculative explanation is that in combination, the two predators reduced the abundance of common species so drastically that it became inefficient for one or both predators to target these species, thus causing a shift to less common prey species. This increased predation on rare species could have resulted in an increased difference in abundance between common and rare species, and a decrease in evenness (Almany & Webster 2004).

Species diversity (richness and evenness combined) did not change on control reefs or for either of the single-predator treatments (lionfish-only and coney-only) over the course of the experiment. However, diversity was reduced on the combined predator treatment reefs compared to the other treatments. Given that both richness and evenness declined in this treatment, it is not surprising that diversity would decline along with them. Diversity remained relatively constant on the other three treatments because losses of species were offset by increased evenness in all three cases.

4.4.3 Multivariate community response

The multivariate analysis of the baseline census data demonstrated that there were no pronounced differences among reefs in terms of community composition and relative abundance at the beginning of the experiment. Comparison of the ordination from the baseline census 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 the two ordination axes from the final ordination (Table A.4) indicated that the structure of the ordination along the first axis was driven by the abundances of the majority of species present, particularly the most common, whereas the structure along the second axis was primarily determined by a small subset of relatively rare species. The final pattern among the reefs in the four treatments along axis 1 can be explained by a moderate effect of native grouper on the abundance of common species (causing a small shift towards the negative end of axis 1), and a stronger effect of lionfish on those species (causing a larger shift to the negative end of the axis). The pattern along axis 2 is more difficult to explain. It is likely that the broad distribution of the combined-predator reefs along the second axis was primarily due to an increasing influence of rare species as the abundances of common species were drastically reduced by the combined effects of the two predators.

4.4.5 Conclusions

Lionfish are not ecologically equivalent to similarly sized native piscivores. They grow at substantially faster rates, and have stronger relative effects on the abundance of native reef fishes.

Invasive predators across a wide variety of systems tend to have stronger effects on native prey than do native predators (Salo et al. 2007). Novel characteristics and behaviors of introduced predators and naïveté of native prey are generally thought to be contributing factors to predator invasion success (Sih et al. 2010). 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 (Allen & Eschmeyer 1973, Chapter 3: Albins & Hixon 2011), may not recognize the invader as a threat, and may lack morphological or behavioral traits to reduce risk.

The strong effect of lionfish on small native coral reef fishes may alter community composition via both direct and indirect effects, and may have important and far-reaching consequences for coral-reef ecosystems. Coral-reefs and the fishes that occupy them are threatened by a wide range of human-caused disturbances including overfishing, climate change, and habitat destruction. Invasive species in general and lionfish in particular, represent an additional threat to these already over-stressed systems.

It should be emphasized that the effects reported here were caused by relatively small lionfish, and were measured over small spatial and temporal scales. Thus, the results of this study likely represent an underestimation of the overall impact of invasive lionfish on native coral-reef fish communities. 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 scales, and to determine whether, and to what extent, the short term effects of single small lionfish on patch reefs scale-up to long-term effects of high densities of adult lionfish on large contiguous reefs.

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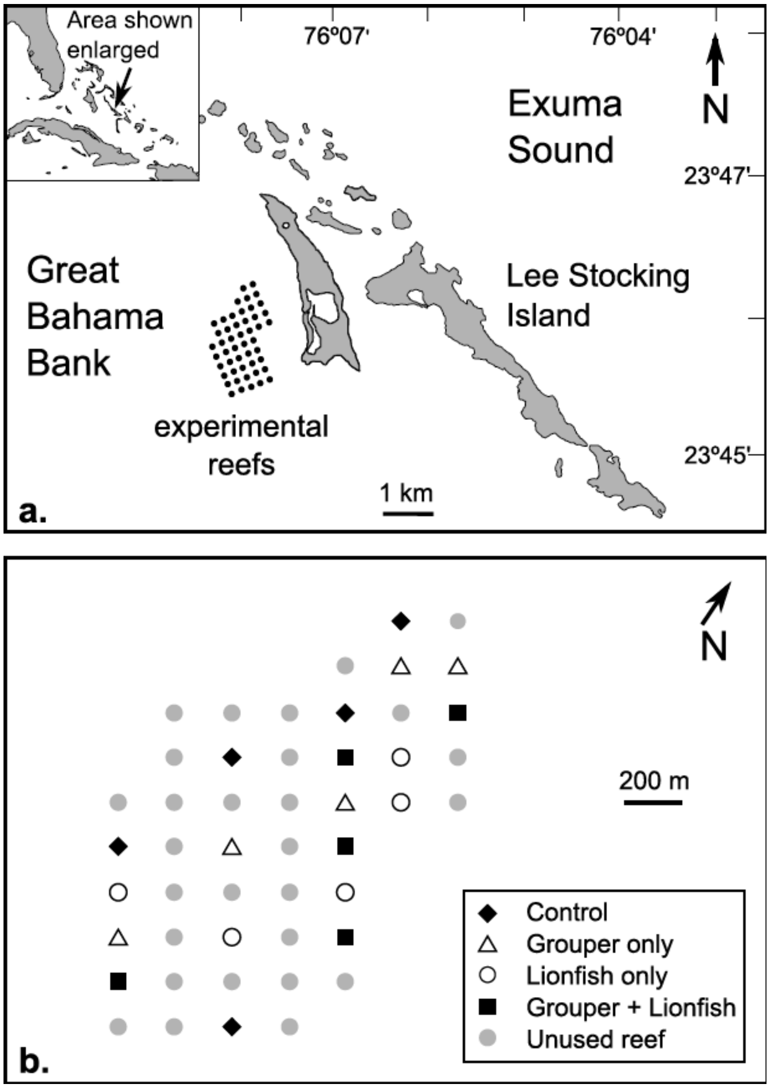

Figure 4.1 Matrix of patch reefs near Lee Stocking Island, Bahamas (a) and experimental design showing treatment assignments (b). Grey symbols represent unused reefs. Map redrawn from Almany (2003).

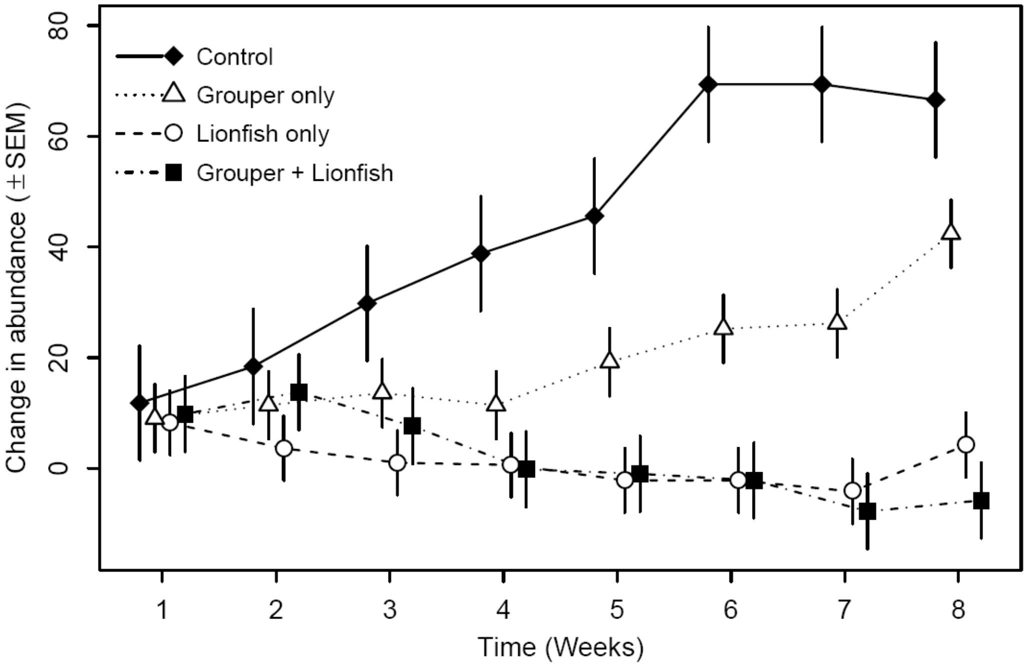

Figure 4.2 Change in abundance Δ*N* (mean ± SEM) of juvenile fish on experimental coral patch reefs under four different predator treatments: predator-free controls, native grouper only, invasive lionfish only, and combined grouper + lionfish. N = 5 patch reefs per treatment. Symbols are offset along the x-axis to facilitate viewing.

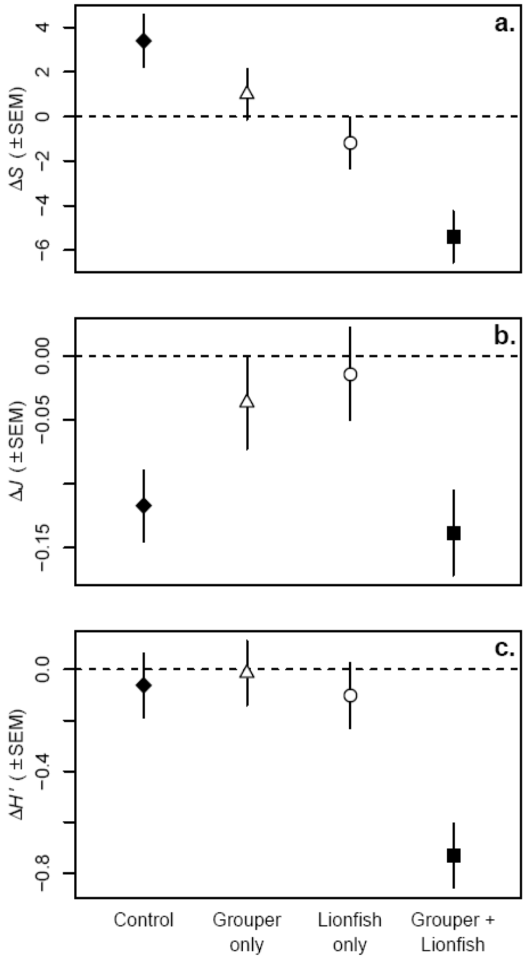

Figure 4.3 Changes (mean ± SEM) in (a) species richness Δ*S*, (b) species evenness Δ*J*, and (c) species diversity Δ*H′* of juvenile coral-reef fishes under four different predator treatments: predator-free controls (solid diamonds), native grouper only (open triangles), invasive lionfish only (open circles), and combined grouper + lionfish (solid squares). N = 5 reefs per treatment. The experiment ran for 8 weeks; values represent the change in each metric between the baseline survey (before establishment of predator treatments) and the final survey.

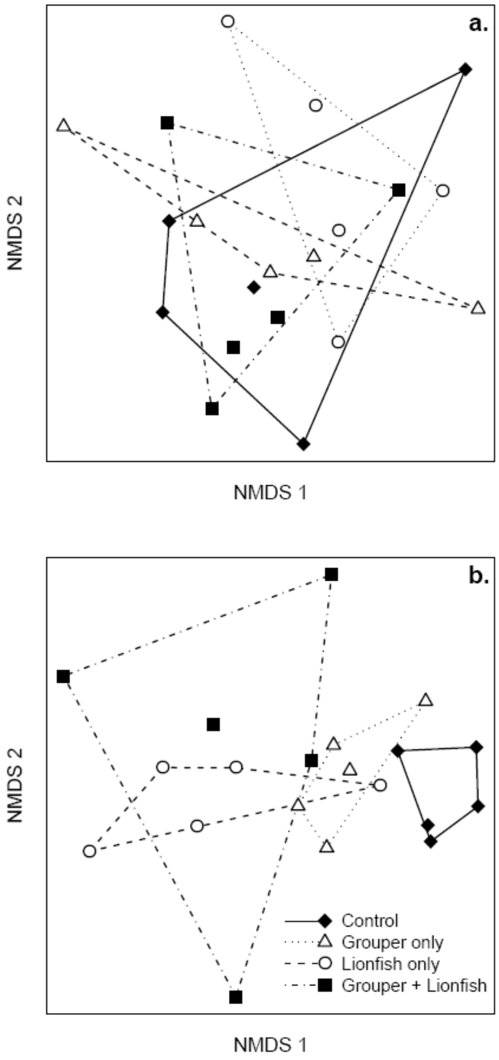

Figure 4.4 Non-metric multidimensional scaling ordinations of experimental reefs in species space (a) at the beginning of the experiment (baseline census) and (b) at the end of the experiment (final census) with minimum convex hull polygons for each predator treatment group: predator-free controls, native 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 Table A.4 for list of species-specific linear correlations with each NMDS axis.

Chapter 5 — Jet assisted predatory behavior by the invasive red lionfish *Pterois volitans*

Mark A. Albins and Patrick J. Lyons

Marine Ecology Progress Series
In Review

ABSTRACT

Field and lab observations of feeding by invasive Pacific red lionfish *Pterois volitans* were conducted during June through August of 2008, 2009 and 2010 near Lee Stocking Island, Bahamas. Observations of this invasive marine predator revealed a previously undocumented piscivorous behavior. While slowly approaching prey fish, lionfish produce jets of water via buccal compression that are directed toward their prey. These jets may confuse or distract prey, and often result in prey fish facing the attacking lionfish, increasing the probability of headfirst capture and swallowing. While a variety of fishes create directed water jets, lionfish appear to be the only species to do so when consuming other fish. This behavior may confer a high degree of predatory efficiency, and thus contribute to the dramatic success of this Pacific invader of tropical Western Atlantic and Caribbean coral reefs.

5.1 INTRODUCTION

One of the primary goals of invasion biology is to understand how the physiological, ecological and behavioral characteristics of non-native species interact with the characteristics of native communities to determine the degree of invasion success. Often biotic invasions are facilitated by specific traits or behaviors that allow invasive species to avoid predators or parasites, out-compete native species, or be particularly efficient predators (Holway & Suarez 1991). Here we describe a unique feeding behavior in a particularly successful invasive marine predator. The novelty of this behavior in the invaded community may confer a high degree of predatory efficiency, and thus may contribute to the dramatic success of this invasion.

The Pacific red lionfish *Pterois volitans*, introduced to the Atlantic near Florida during the 1990s, has rapidly spread across much of the Western Atlantic and Caribbean (Schofield 2009, 2010), where they have reached substantially higher densities than reported in their native Pacific range (Green & Côté 2009). Lionfish feed on a wide diversity of native Atlantic reef fishes and crustaceans (Morris & Akins 2009), and can reduce the abundance of small native coral-reef fishes on patch reefs by nearly 80 % (Chapter 2: Albins & Hixon 2008). Lionfish appear to be a particularly successful invader with strong effects on native communities, and may comprise one of the most damaging marine invasions to date (Chapter 3: Albins & Hixon 2011).

The success of lionfish in the invaded range is likely augmented by a set of physiological, morphological, and behavioral characteristics that confer protection from native predators, and allow lionfish to be highly efficient predators (Chapter 3: Albins & Hixon 2011). Lionfish are well defended by a set of venomous dorsal, pelvic and anal fin spines, which likely confer some degree of protection from native predators (Morris 2009, Morris & Whitfield 2009). They also display a combination of slow movement, disruptive barred light-dark color pattern, numerous elongated fin rays, and a variety of fleshy and bony projections, which, in concert, may reduce the detectability of lionfish by both predators and prey (Chapter 3: Albins & Hixon 2011).

Lionfish herd and corner prey fishes with oversized fanlike pectoral fins, and have been observed hunting in conspecific groups (authors, pers. obs.). Here we describe a newly discovered behavior of invasive lionfish which has not, to our knowledge, been described for any other piscivore, and which may contribute to their dramatic success as an invader of Atlantic and Caribbean coral reefs.

5.2 METHODS

Behavioral observations described here were made by SCUBA divers on shallow coral reefs of the Exuma Cays near Lee Stocking Island, Bahamas, where we have been conducting long-term studies of the lionfish invasion. Field observations were supplemented by a variety of ad-hoc feeding trials and observations in aquaria. Several lionfish and native gobies (*Coryphopterus glaucofraenum* and *Gnatholepis thompsoni*) were captured using hand-nets from coral-reefs and seagrass beds. These gobies were readily eaten by lionfish in the wild and in captivity. Lionfish and gobies were acclimated to 190 liter flow-through aquaria. After lionfish were acclimated to aquaria (i.e., would accept meals), observations of predation events and unsuccessful strikes were filmed using digital video cameras. Lionfish were first presented gobies in an aquarium lacking shelter. We then presented lionfish with gobies in transparent containers within the aquaria so that the lionfish could see the prey, but could not consume it. This also provided control over the location of the goby within the aquarium. We then conducted trials in which lionfish were presented with prey in transparent containers, during which a glass pipette was used to release food-grade dye in front of the mouth of the lionfish to better visualize the speed, direction, and flow of the water jets.

5.3 RESULTS

While approaching prey fish, lionfish typically faced the prey, flared their pectoral fins perpendicular to their longitudinal axis, undulated their dorsal spines, and moved within striking distance very slowly using short, small caudal-fin thrusts. During this approach, lionfish often produced a strong, pulsed, jet of water via buccal compression, directed towards the target fish (Fig. 5.1, Movie 5.1).

The pulsed water jet increased in frequency and intensity as the lionfish approached the prey, and was matched closely to the frequency and intensity of the caudal-fin thrusts. The opposing forces of the forward thrust created by the caudal fin and the backwards thrust created by the water jet were thus balanced in such a way that the lionfish maintained position or moved slightly forward with each pulse. Lionfish across a range of body sizes (5 to 25 cm total length) produced these water jets while hunting a variety of prey fishes. However, the use of water jets appears to be more predominant in smaller lionfish (5 to 15 cm total length), and when targeting prey fish that sit on the seafloor, such as gobies and blennies.

5.4 DISCUSSION

Water jets could increase the predation efficiency of lionfish in two potentially complementary ways. First, water jets may disorient prey, making them more vulnerable during a strike. Second, jets may increase the incidence of head-first capturing and swallowing. Fish typically orient facing into currents, thereby reducing drag and the energy required in maintaining position. Thus, a water jet may result in prey fish facing the approaching lionfish. Headfirst capture is advantageous for several reasons. During a headfirst strike, posteriorly pointing fin spines of the prey fish reduce the chance of escape, and thrusts of the struggling prey's caudal fin push it further into the predator's esophagus. For many piscivores, the time elapsed between strike and complete swallowing is shorter for headfirst strikes than for tailfirst strikes, especially when prey are large relative to the size of the predator (Reimchen 1991, Nilsson & Brönmark 1999). Additionally, esophageal abrasion of the predator is less likely to occur during headfirst swallowing (Reimchen 1991).

Most, if not all, teleost fishes display coughing behavior in which water is expelled through the open mouth by buccal compression, thereby expelling indigestible or unpalatable items (Wainwright & Turingan 1997). Several teleosts also display blowing behavior, a modification of coughing in which the expelled water is forced through a partially closed mouth, creating a strong, directed jet of water. Blowing behavior is exhibited by a number of predatory teleosts when uncovering, manipulating, and capturing marine (Frazer et al. 1991) and even terrestrial (Elshoud & Koomen 1985) invertebrates. However, lionfish appear to be the only predator known to display blowing behavior when capturing other fish. The cranial muscle activities involved in coughing and blowing are very similar in tetraodontiform fishes and analyses suggest that blowing involves a simple evolutionary adaptation of the coughing mechanism (Wainwright & Turingan 1997).

Traits of invasive predators not previously encountered by native prey may contribute to the success of predator invasions in a number of systems (Sih et al. 2010). If water-jet facilitated piscivory is indeed unique to the genus *Pterois*, it is unlikely that Atlantic coral-reef fish prey have encountered this predatory behavior during their evolutionary history, and therefore have not evolved effective behavioral or physiological antipredator responses. This lack of effective defensive responses in native prey has likely contributed to the unprecedented success of invasive lionfish, and may exacerbate the direct negative effects of lionfish on native prey populations as well as the indirect negative effects of lionfish on competing native piscivores.

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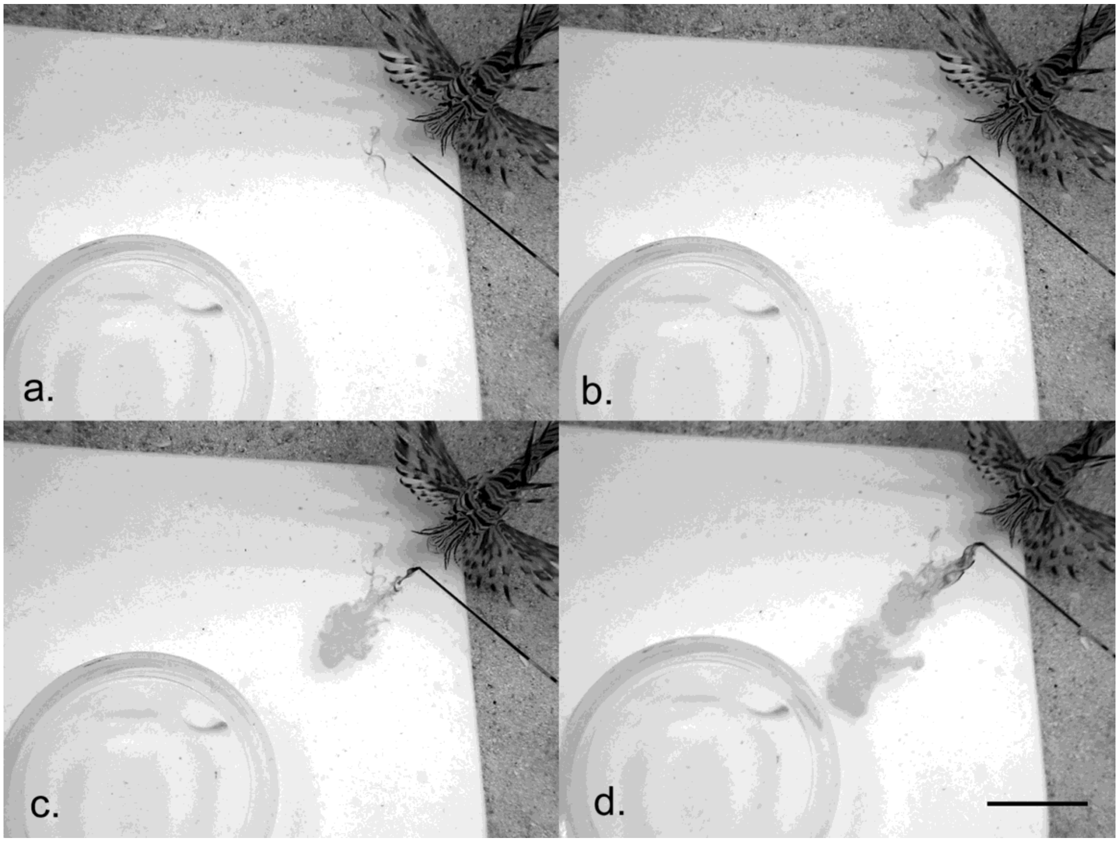

Figure 5.1 Sequence (a, b, c, and d) of still images captured from a video (Movie 5.1) of a predatory lionfish producing a water jet directed toward a goby under a glass dish. Blue food-grade dye (grey in photo) was released from the end of a glass pipette in front of the lionfish to help visualize the water jet. Scale bar is ca. 4 cm.

Chapter 6 — Effects of the Pacific lionfish *Pterois volitans* on Bahamian coral-reef fish communities: a large-scale, long-term experiment

Mark A. Albins

Ecological Applications
In Preparation

ABSTRACT

Previous experiments examining the effects of invasive lionfish on native coral-reef fish communities have been conducted on small patch reefs (several square meters) over short time periods (two months or less). While these experiments have shown that lionfish cause substantial reductions in the net recruitment and species richness of native reef fishes, their effects on native reef-fish communities over larger spatial scales and longer temporal scales — scales at which conservation and management efforts are typically applied — have not been examined. I conducted such a large-scale, long-term field experiment, initiated in June 2009, near Lee Stocking Island, Bahamas. Ten large, isolated coral reefs were paired based on location and similarity of habitat, and baseline surveys of their fish communities were conducted by observers on SCUBA. Subsequent to baseline surveys, quarterly removals of lionfish were completed on one reef in each pair, while the densities of lionfish on the other reefs were standardized at typical post-invasion levels via transplants. Through August 2010, quarterly surveys showed that lionfish caused significant changes in native reef-fish communities, including reductions in the total density (-3.22 ± 0.95 fish m^{-2}), biomass (-3.26 ± 1.10 g m^{-2}), and species richness (-4.9 ± 2.09 species) of small (<10 cm total length) native fishes (means ± SEMs). Lionfish also caused reductions in the biomass of small native herbivorous fishes (-0.36 ± 0.17 g m^{-2}) and piscivores (-0.10 ± 0.04 g m^{-2}), and induced

overall shifts in the community structure of prey-sized native fishes. However, these negative effects on small fish did not translate to observable declines in larger size classes over the 14-month study period. These results corroborate and extend those of earlier small-scale, short-term experiments and show that the effects of lionfish on small native coral-reef fishes scale-up both spatially and temporally.

6.1 INTRODUCTION

The Pacific red lionfish *Pterois volitans*, the first non-native marine fish to become an established invasive in the western Atlantic, has undergone a broad and rapid range expansion over the last ten years, spreading along the southeastern seaboard of the US (from Miami to Cape Hatteras), across the Bahamas, Caribbean, and Gulf of Mexico, and as far south as the northern coast of Venezuela (Schofield 2009, 2010). In addition to this rapid range expansion, lionfish in some invaded areas have reached densities exceeding those of all but the most common native mesopredators (Whitfield et al. 2007), and far exceeding those reported from their native Pacific (Schiel et al. 1986, Fishelson 1997, Green & Côté 2009, Darling et al. 2011, Kulbicki et al. in review). Reports suggest that both individual somatic growth rates and population growth rates of invasive lionfish are both extremely high in the invaded range (Claydon et al. 2008, Chapter 3: Albins & Hixon 2011, Chapter 4: Albins in review). Additionally, the maximum lionfish size reported from the invaded

Atlantic, 45 cm TL (L. Akins, pers. comm.), exceeds the Pacific record of 38 cm TL (Randall et al. 1990).

Invasive lionfish are generalist predators, feeding on at least 25 different families of native fishes, including the juveniles of economically and ecologically important species such as groupers and parrotfishes (Albins & Hixon 2008, Morris & Akins 2009, Muñoz et al. 2011). They are also highly efficient consumers. With a mean kill rate of over 1 fish hour^{-1} (Côté & Maljković 2010), an average sized lionfish is estimated to consume between 12 and 15 g of prey day^{-1} (Green et al. 2011). As many as 21 individual fish prey have been found in a single lionfish gut (Morris & Akins 2009), and we have seen a single adult lionfish consume more than 20 small wrasse (1 to 3 cm TL) in a 30 min time period (Chapter 2: Albins & Hixon 2008).

The dramatic success of Pacific lionfish in the invaded Western Atlantic is likely due to a combination of ecological release from natural enemies and a lack of native biotic resistance (sensu Elton 1958). It is clear that some biotic interactions, whether related to predation, parasitism, competition, or some combination of these, keeps lionfish populations at relatively low levels in their native range (Kulbicki et al. in review). Current evidence suggests that invasive lionfish have escaped those controlling mechanisms, and that native Atlantic communities have thus far not provided sufficient compensation via biotic resistance to keep lionfish populations in check. Lionfish appear to be resistant to native predators and piscivores, and due to a lack of effective resistance from prey species, may be particularly effective predators in the invaded system.

There have been some indications that native apex predators may prey on lionfish and may even have the potential, under certain circumstances, to limit their populations. For example, invasive lionfish have been found in the stomachs of native grouper (Maljković et al. 2008) and observations conducted in and around the Exuma Cays Land and Sea Park (ECLSP) — a particularly successful marine reserve in the Bahamas — have detected a negative correlation between native grouper biomass and invasive lionfish biomass (Mumby et al. 2011). However, several lines of evidence indicate that substantial control of lionfish populations by native apex predators is not likely under current conditions. First, lionfish are well defended by an array of venomous fin spines. Not surprisingly, multiple captive feeding trials have found that native grouper do not readily feed on lionfish of any size (Morris 2009, Pusack et al. unpubl. data). Second, the correlative study by Mumby et al. (2011) was confounded by the fact that extensive lionfish removal efforts have been in place in the ECLSP for several years (Bahamas National Trust, pers. comm.). Additionally, even if native apex predators do provide some level of biotic resistance to the lionfish invasion, these species have been severely overfished across a majority of the tropical Western Atlantic (Sadovy 1994, Sadovy & Eklund 1999), particularly in areas with high human populations (Stallings 2009). Lionfish also appear to be resistant to infection by parasites, having reduced parasite loads compared to similarly sized Atlantic fishes as well as lionfish in the Pacific (P. Sikkel et al. unpubl. data).

In addition to being resistant to native predators and parasites, lionfish themselves may be particularly effective predators of native Atlantic prey. Lionfish demonstrate a suite of predatory characteristics and behaviors that native prey have not encountered in their evolutionary history (Chapter 3: Albins & Hixon 2011). Unlike many other mesopredators, which are themselves susceptible to predation by larger apex predators and so must maintain a high level of vigilance while hunting, lionfish are well defended by venomous spines and are thus free to hover above the reef, stalking their prey with apparent impunity. Their appearance — with a combination of spiny and fleshy projections on the head and face, a zebra-like barred coloration pattern, and elongated feather-like fin rays — may provide crypsis or mimicry, causing the invasive predator to appear to be a harmless invertebrate or plant. When hunting, lionfish flare their large fan-like pectoral fins, typically approaching prey slowly, and herding the prey into a corner of the reef or against the seafloor. During this process, lionfish often create a jet of water directed towards the prey, which may serve to confuse the prey or to increase the probability of head-first capture (Chapter 5: Albins & Lyons in review). While some native mesopredators possess one or another of these traits or behaviors, none possess all the attributes of invasive lionfish. Their particular suite of morphological characteristics and behaviors is unique in the invaded community, and naiveté of native prey to lionfish may reduce prey vigilance and the effectiveness of prey avoidance behaviors, conferring a high degree of predatory efficiency and contributing to the remarkable success of the lionfish invasion.

To date, experimental studies examining the effects of lionfish on native coral-reef fishes have been limited to the effects of single small lionfish on small patch reef communities (several square meters) over short time periods (two months or less). These experiments have shown that lionfish reduce the net recruitment (by up to 93 %) and species richness (by up to 32 %) of native fishes (Chapter 2: Albins & Hixon 2008, Chapter 4: Albins in review). These experiments have also demonstrated that lionfish have stronger effects on native fish communities and grow more than six times faster than a similarly sized native predator, the coney grouper, *Cephalopholis fulva* (Chapter 4: Albins in review).

Such strong effects on the recruitment of native fishes, if widespread, could have important implications for the resilience of coral-reef ecosystems as a whole, including the capacity for reefs to provide ecosystem goods and services to humans (Chapter 3: Albins & Hixon 2011, Chapter 4: Albins in review). Reductions in the numbers of small post-settlement juveniles of larger-bodied species, especially those of ecological and/or economic importance, could translate into reduced adult abundances. If lionfish reduce the abundance of ecologically important species such as herbivores, which prevent fleshy macroalgae from outcompeting or otherwise inhibiting reef building corals (Mumby et al. 2006), they could have indirect negative effects on corals themselves. For fisheries species such as snappers and groupers, lionfish may have negative effects in two ways. First, reductions in juvenile abundance of these species could translate directly into reduced adult abundances. Second, reductions in the abundance of small fish in general will reduce the prey base available to these native predators. Combined, these effects could have serious negative consequences for the ability of stocks to continue to support fishing rates which, in many cases, are already too high to be sustainable.

Given that ecological processes are often temporally and spatially scale dependent (Levin 1992), the question remains whether and how the effects of lionfish on small patch-reefs over several weeks scale-up to larger contiguous reef areas over years, scales at which management and conservation decisions and actions are typically applied. This study was designed to determine how typical post-invasion densities of lionfish on large reefs affect native reef-fish communities over more than a year.

6.2 MATERIALS AND METHODS

6.2.1 Study site

Ten isolated large reefs (ca. 1400 to 4000 m^2), located on the Great Bahama Bank near Lee Stocking Island, Bahamas, were selected as experimental units. These reefs, ranging in depth from ca. 2 to 11 m, represented a diversity of habitat types and experienced a range of exposures to predominant weather patterns and tidal currents. Baseline surveys of the reef-fish communities on all ten reefs were conducted in July 2009 (see detailed survey methods below). Reefs were paired based on similar characteristics including depth, area, proximity to other reefs, proximity to major tidal channels, proximity to the Exuma Sound (an adjacent basin of oceanic depths), and the predominant substrate type (Figs. 6.1, B.1, Table B.1). Reefs in each pair were then haphazardly assigned to either a low-lionfish-density (LLD) or a high-lionfish-density (HLD) treatment group. Reef-fish communities did not differ between treatment assignments at the beginning of the experiment (see statistical methods and results sections for details). A team of divers thoroughly searched each LLD reef and removed all lionfish using hand nets. Because lionfish densities varied considerably among reefs at the baseline survey, lionfish removed from LLD reefs were tagged, measured, and transplanted onto certain HLD reefs in order to standardize lionfish densities among the high-density treatment reefs. Artificially augmented lionfish densities on HLD reefs were never increased beyond the highest "natural" densities observed on similar reefs in the area. Reefs were resurveyed and treatments were maintained at 3 to 4 month intervals for 14 months.

6.2.2 Reef surveys

Survey areas comprised a total of 400 m^2 at each experimental reef, and consisted of six sub-sample areas including two permanent square plots (10 × 10 m) and four permanent strip transects (2 × 25 m) placed to provide representative coverage of each reef. During each survey, pairs of SCUBA divers conducted complete censuses of each plot and strip transect, identifying and estimating the total length (TL) of all fish within each area, extending from small holes in the reef upward into the water column above. Total length was estimated to the nearest cm for fish ≤5 cm TL, and to the nearest 5 cm for fish >5 cm TL. Prior to conducting censuses, all observers participated in training dives to calibrate visual fish length estimates. Trained observers were able to accurately estimate total length of a variety of fishes, with typical errors much smaller than the size bins used.

Censuses employed temporally stratified observations (Samoilys & Carlos 2000), designed to accurately sample large mobile species as well as small cryptic fishes. During each square-plot census, the primary observer first swam quickly around the outside of the plot counting and sizing all large, mobile fish while a secondary observer laid a guideline delineating the borders of the plot. Both observers then slowly swam in a concentric path from the outer edge of the plot to the center of the plot, maintaining positions on opposite sides of the plot, and counting and sizing all small, cryptic and site-attached fish. During each strip-transect census, the primary observer first swam the length of the transect quickly, using a compass and known landmarks for navigation, maintaining a vertical position 1 to 2 m above the seafloor, and counting and sizing all large, mobile fish. The secondary observer followed behind the primary observer, deploying a guideline. Both divers then slowly swam back along the guideline, just above the seafloor, counting and sizing all small, cryptic, site-attached fish. For both types of surveys, observations were compared and averaged after each dive, with substantially more weight given to those of the primary observer, particularly for large mobile fish. Paired reefs (one from each treatment group) were always surveyed by the same set of divers within 24 hours of one another, and the primary observer (the author) was the same for all surveys.

6.2.3 Response variables

The primary response variables included change in density and change in biomass of small (<10 cm TL) and medium (10 to 20 cm TL) sized fishes in three categories: all species combined, all herbivores combined, and all piscivores combined. Biomass was calculated using published species-specific length-weight conversions when available, and by using parameters for closely related or similarly shaped species when not available (Table B.2). When lionfish affected density or biomass of all species combined, I calculated the contribution of individual species to these overall effects. I also examined the effect of lionfish on the change in species richness (number of species per sample unit), evenness measured as Pielou's *J* (Pielou 1966), and diversity measured as Shannon-Wiener's *H'* (Pielou 1966) separately for the two size categories.

Changes in density and biomass within each size class were calculated separately for each species by subtracting the baseline value for each sub-sample from the value measured during subsequent surveys of that sub-sample. Similarly, the changes in richness, evenness and diversity within each size class were calculated as the difference in each metric between the baseline survey and each subsequent survey for each sub-sample.

The size bins used for this analysis (small: <10 cm TL, medium: 10 to 20 cm TL) were based on existing information about typical lionfish prey sizes. A previous lionfish gut-content study estimated that the average size of prey consumed by invasive lionfish in the Bahamas varied between 1.5 and 3.0 cm TL depending on lionfish size, and that while capable of consuming prey up to half their own length, the average ratio between prey TL and lionfish TL was approximately 0.14 (Morris & Akins 2009). A more recent lionfish gut-content study conducted off the Southeast coast of the US, and including lionfish ranging in size from 14.5 to 45 cm TL reported a mean fish prey size of ca. 4.4 cm TL and a maximum of 10 cm TL (Muñoz et al. 2011). Lionfish on our experimental HLD reefs ranged in size from new recruits (ca. 2

cm TL) to large adults (ca. 35 cm TL), with the majority measuring from 15 to 25 cm TL. Therefore, I assumed that fish in the small size class included the vast majority of prey items of lionfish, while fish in the medium size class were rarely, if ever, consumed. I expected that any effects of lionfish on small fish would be primarily due to direct predation and would occur relatively quickly, whereas any effects on medium fish would be a combined result of rare predation events, potential competition, and any carryover effect, in which reductions in juveniles would translate over time into reductions in adults as fish grew.

I also expected the responses associated with the small size class to be strongly affected by seasonal patterns of recruitment (increases in the abundance of juvenile fish as a result of larval settlement). During the relatively benign summer months in this region, large numbers of coral-reef fish settle (making the transition from pelagic larvae to reef-dwelling juveniles), while the relatively harsh winter months typically see drastic reductions in the abundance and diversity of small coral-reef fish due to mortality exceeding recruitment.

6.2.4 Univariate analyses

To assess the effects of lionfish on the primary response variables, I used linear mixed effects models (LMMs) with *sub-sample* (six sub-samples per reef) nested within *reef* (ten reefs) as random effects, and with *time* (five levels: Aug.

2009, Nov. 2009, Jan. 2010, Jun. 2010, and Aug. 2010) and lionfish *treatment* (two levels: HLD and LLD) as categorical fixed effects (Pinheiro & Bates 2000, Bolker et al. 2009, Zuur et al. 2009). I used *time* as a categorical rather than continuous predictor because there was no a priori reason to assume linear relationships between response variables and time. I fitted models with and without random effects using Restricted Maximum Likelihood Estimation, and compared them using Akaike's Information Criterion (AIC) and likelihood ratio tests (LRTs) with an adjustment for testing-on-the-boundary (Verbeke & Molenberghs 2000, Zuur et al. 2009). Models including random effects always resulted in better fits than did models without them (Table B.3).

Visual examination of the residuals from these models indicated departures from the assumptions of homogenous variance among reefs and independence with respect to time. Therefore, I allowed variance to differ among reefs by including weighted terms in the models, and allowed for temporal autocorrelation within sub-samples using AR1 structures (Zuur et al. 2009). For all response variables, allowing variance to differ among reefs improved the model fits based on both AIC and LRTs (Table B.3). Inclusion of autocorrelation was found to improve several, but not all, of the model fits. However, I included an AR1 structure in all of the models to allow for a more direct comparison of results (e.g. between density and biomass models). Re-examination of the residuals from the final models indicated that all assumptions, including homogeneity, independence, and normality were met.

Once the best fitting models in terms of random structure, variance structure, and temporal correlation were selected, I refit each using Maximum Likelihood Estimation and used LRTs to assess the significance of the fixed effects (Zuur et al. 2009). When LRT results suggested that the *treatment* × *time* interaction was significant, I used the methods described by Hothorn et al. (2008) to make simultaneous inferences about the marginal effects of the lionfish treatment at each survey period by adjusting the p-values associated with these specific linear combinations to maintain an approximately 95 % family-wise error rate. When the *treatment* × *time* interaction was not found to be significant based on LRT results, it was dropped from the model and each of the main effects were tested using LRTs. Whether or not the *treatment* × *time* interaction was found to be significant, I used models with the full set of fixed effects (interaction term included) to estimate expected values and uncertainties (SEMs) for each of the response variables in each treatment at each survey period. To determine whether response variables differed between the groups reefs assigned to each lionfish treatment at the baseline survey, I also fit models similar to those described above, but with density, biomass, richness, evenness, and diversity (rather than the *change* in each of these) as response variables.

6.2.5 Multivariate analyses

To gain a more comprehensive understanding of the effect of lionfish on the community of small native reef fishes (<10 cm TL), I used a multivariate approach combining non-metric multidimensional scaling (NMDS, Kruskal & Wish 1978, McCune & Grace 2002) with permutation-based Multivariate Analysis of Variance analogue tests (perMANOVA, McArdle & Anderson 2001). The community matrix was constructed using observations of each sub-sample at each survey period; so the entire time series was used in a single ordination. This approach allowed an assessment of community change trajectories through time. I used a square-root transformation of the community matrix and chose not to relativize by species. This approach moderated the influence of the most common species, without overemphasizing the influence of rare species in the ordination results. I did not relativize by sample units because I wanted the ordination to reflect differences in total abundance. Bray-Curtis distances were used for both the ordination and the perMANOVA hypothesis testing (Bray & Curtis 1957). NMDS ordination routines included multiple random starts (up to 50, with up to 200 iterations each) at a variety of levels of dimensionality (1 to 5 axes) to ensure that global solutions were reached and that the choice of dimensionality for the final ordination was appropriate. I also used Monte-Carlo tests based on 50 random permutations of the community matrix to assure that the ordination was extracting stronger axes than would be expected by chance. The final ordination was rotated for maximum correlation between the total change in density of small fish and the first NMDS axis for ease of interpretation. To test whether reef sub-sample communities differed between the two treatments, perMANOVA tests were run separately for each time step, each with 1000 permutations constrained within reef pairs.

All statistical analyses were conducted in the *R* language and software environment (*R* Development Core Team 2009) using add-on packages *nlme* (Pinheiro et al. 2009) and *multcomp* (Hothorn et al. 2008) for the univariate analyses, and *vegan* (Oksanen et al. 2010) for the multivariate ordination and analysis.

6.3 RESULTS

6.3.1 Treatment effectiveness

Due to low levels of recruitment and/or immigration of lionfish onto low-lionfish-density (LLD) reefs between surveys (ca. every 3 months), removals were not 100 % effective (i.e. there were no reefs without lionfish). However, removals maintained lionfish density on LLD reefs at a consistent mean (± SEM) of 0.003 ± 0.001 fish m^{-2} over the course of the experiment. In comparison, lionfish density on high-lionfish-density (HLD) reefs was consistently an order of magnitude higher, at 0.030 ± 0.004 fish m^{-2} and was maintained through translocation as necessary. This is well within the range, but considerably below the maximum, of densities reported on un-manipulated invaded reefs in the Bahamas (mean ± SD: 0.039 ± 0.014 fish m^{-2}, Green & Côté 2009).

6.3.2 Density and biomass of native fishes

There were substantial fluctuations in the mean density of small (<10 cm TL) native reef fishes (all species combined) through time, with large increases during the Aug. 2009, Nov. 2009, and Aug. 2010 surveys and a decrease during the Jan. 2010 survey (Fig. 6.2a). The effect of lionfish on the change in density of small fish changed over the course of the experiment (*treatment* × *time* interaction: LRT p = 0.015), so this effect was evaluated separately for each survey period. Lionfish caused reductions of 2.20 ± 0.95 fish m^{-2} (mean ± SEM) during the Aug. 2009 survey (p_{cor} = 0.049) and 3.22 ± 0.95 fish m^{-2} during the Aug. 2010 survey (p_{cor} = 0.010). The mean change in density was always lower on HLD reefs than on LLD reefs, but not significantly so for other survey periods (Table B.4).

Similarly, the biomass of small native fishes fluctuated over the course of the experiment with peaks during the Nov. 2009 and Aug. 2010 surveys (Fig. 6.2c). Lionfish reduced the biomass of small fishes by 3.26 ± 1.10 g m^{-2} (LRT p = 0.007), and this effect did not vary over time (Table B.4). With the exception of an initial increase on all reefs, both the density and biomass of medium sized (10 to 20 cm TL) native fishes remained relatively constant across time (Fig. 6.2b, d), with no effects of lionfish treatment (Table B.4).

Lionfish had no effect on the density of small herbivores (Fig. 6.3a, Table B.4), but did reduce small-herbivore biomass by 0.36 ± 0.18 g m^{-2} (LRT $p = 0.044$, Fig. 6.3c). Lionfish had no effect on the density or biomass of medium sized herbivores (Fig. 6.3b, d, Table B.4). Herbivorous species observed on experimental reefs included three surgeonfishes (Acanthuridae), one chub (Kyphosidae), and ten parrotfishes (Scaridae), most of which appeared in both size classes (Table B.5).

Lionfish had no effect on the density of small piscivores (Fig. 6.4a, Table B.4), but did reduce small-piscivore biomass (Fig. 6.4c). For each of these response variables, the effect of lionfish varied through time (*treatment × time* interaction: density LRT $p < 0.001$, biomass LRT $p < 0.001$). In the case of density, none of the marginal effects of treatment were significant (Table B.4), but by the final survey, lionfish had reduced the biomass of small piscivores by 0.10 ± 0.04 g m^{-2} ($p_{cor} = 0.047$). As with herbivores, lionfish had no effect on density or biomass of piscivores in the medium size class (Fig. 6.4b, d, Table B.4). Piscivorous species observed on experimental reefs included a hawkfish (Cirrhitidae), a trumpetfish (Aulostomidae), a flounder (Bothidae), several groupers (Serranidae), a snapper (Lutjanidae), two scorpionfishes (Scorpaenidae), and lizardfishes (Synodontidae), with most of these species appearing in both size categories (Table B.5).

Of the 144 species of fish in the small size class (<10 cm TL) observed on experimental reefs, lionfish reduced the density of 84 species (averaged over the two late summer survey periods) and reduced the biomass of 83 species (averaged over all post-baseline time steps). Of these, two species combined — the bridled goby (*Coryphopterus glaucofraenum*), and the bluehead wrasse (*Thalassoma bifasciatum*) — contributed 52.9 % of the total lionfish effect on density and 54.8 % of the total lionfish effect on biomass, with the remaining top 20 species contributing an additional 37.4 % of the total density effect and 37.8 % of the total biomass effect (Fig. 6.5). The top twenty contributors to the effects of lionfish on overall density and biomass each included three herbivores, but did not include any piscivores (Fig. 6.5).

The top two contributors, the bridled goby and the bluehead wrasse, were also the most abundant species on experimental reefs overall. While these species made up the bulk of the overall lionfish effects on density and biomass of small reef fishes, their shares of these effects were not in proportion to their density. In fact, species with the highest ratios between the mean lionfish effects on density and biomass (difference between LLD reefs and HLD reefs) and density and biomass on LLD reefs were very different from those described above, and were dominated by rare species rather than common ones (Table B.6). The species with the top twenty highest effect-to-density ratios included two herbivores (*Acanthurus bahianus* and

Scarus vetula), two piscivores (*Scorpaenodes caribbaeus* and *Cephalopholis cruentatus*), several cardinalfishes (*Apogon maculatus*, *A. binotatus*, and *A. townsendi*), and several rare cryptic species, among others (Table B.6). The species with the top twenty highest effect-to-biomass ratios did not include any herbivores, but did include two piscivores (*Scorpaenodes caribbaeus* and *Mycteroperca tigris*), several grunts (*Haemulon album, H. melanurum, and H. parra*), and several other relatively rare species (Table B.6).

6.3.3 Community indices

Species richness of small (<10 cm TL) fish fluctuated somewhat across time (Fig. 6.2e) with slight increases during the summer and fall survey periods (Aug. 2009, Nov. 2009, Jun. 2010, and Aug. 2010) and a decline during the winter survey period (Jan. 2010). Lionfish reduced species richness by an average (± SEM) of 4.92 ± 2.09 species (LRT $p = 0.022$), and this effect was consistent through time (Table B.4). This effect was due in part to a loss of richness on HLD reefs, but primarily due to a gain in richness on LLD reefs (Fig. 6.2e).

The pattern seen in the change in richness at the sub-plot scale was also reflected in richness measured at the whole-reef scale. During the baseline survey 72 species were observed on HLD reefs, and 60 were observed on LLD reefs. By the final survey the average number of species lost on HLD reefs was 9.8 ± 2.9 (mean ± SEM), and the number of species gained was 6.6 ± 1.5, while the number of species lost on LLD reefs was only 4.0 ± 1.0, and the number of species gained was 10.6 ± 0.9 species (see Tables B.7 and B.8 for a list of species losses and gains).

The species richness of medium-sized fish did not differ between treatments (Table B.4). There was no effect of lionfish treatment on the evenness (J) or diversity (H') of either small or medium sized fish (Table B.4, Fig. B.2). Additionally, none of the response variables discussed above — including density, biomass, richness, evenness, and diversity in each size class, as well as density and biomass of herbivores and piscivores in each size class — differed between reefs assigned to the two treatments at the baseline survey before the lionfish manipulations (Table B.9).

6.3.4 Multivariate responses

An NMDS ordination of the communities of small fish (<10 cm TL) on reef sub-samples across the entire experimental time series (final stress = 15.79, non-metric $r^2 = 0.98$, linear $r^2 = 0.90$, Monte-Carlo $p = 0.02$) illustrated several community-level effects of lionfish. The communities on the experimental reefs differed substantially among experimental pairs at the baseline survey, with the two deepest reefs (Pair 2), and the two most isolated reefs (Pair 1) supporting distinctly different communities than those of the six reefs located in the shallow waters nearest the Exuma archipelago (Pairs 3, 4, and 5) (Figs. 6.1, 6.6a). There was substantial overlap of communities between lionfish treatments at the beginning of the experiment (perMANOVA $p = 0.070$). However, the communities shifted over time, with increasing segregation based on lionfish treatment (perMANOVA $p < 0.001$ for all post-baseline time steps). This segregation consisted of a shift in HLD reef sub-samples towards the negative ends of both NMDS axes, and a shift in LLD reef sub-samples towards the positive ends of both axes (Fig. 6.6b). This shift was most evident at both of the late summer surveys (Aug. 2009 and Aug. 2010) with communities subjected to the two treatments becoming slightly more similar during the intervening fall, winter, and spring surveys (Nov. 2009, Jan. 2010, Jun. 2010) (Fig. B.3). By the final survey, HLD communities became completely segregated from LLD communities for three of the five reef pairs (Pairs 3, 4, and 5).

Eleven reef fish species had strong linear correlations (>0.3 or <-0.3) with NMDS axis 1 — all of them positive — and included three herbivorous species (Table B.10). Sixteen species were strongly correlated with axis 2 — all but one positive — and included two herbivorous species (Table B.10).

6.4 DISCUSSION

6.4.1 Density and biomass

I had assumed that differences in density or biomass of small fish (<10 cm TL) between the HLD and LLD reefs would primarily be the direct result of lionfish predation, and that any differences in density or biomass of large fish would be indirectly caused by one or both of two potential mechanisms: reductions in the numbers of juveniles surviving to grow into larger size classes, or competition between lionfish and native piscivores for limited prey. There were clear effects of lionfish on density and biomass in the small size class, but no effect on the larger size class was detected over the period of the study.

Evidence suggests that many, if not most, coral-reef fish populations are regulated, at least in part, by early post-settlement mortality due to predation (reviews by Hixon & Webster 2002, Osenberg et al. 2002, Hixon & Jones 2005, Hixon et al. in review). Based on the results of this study, and those of earlier small-scale experiments (Chapter 2: Albins & Hixon 2008, Chapter 4: Albins in review), it is clear that lionfish cause a substantial increase in mortality of small fish. The density of small fish on LLD reefs varied seasonally as expected, with high levels of summer recruitment resulting in increased density during the summer months, and mortality exceeding recruitment during the winter months. The peaks in these seasonal fluctuations were greatly attenuated on the HLD reefs compared to the LLD reefs, presumably due to lionfish predation on small native fish. The difference in density between HLD and LLD treatments largely disappeared during the winter months, although biomass remained consistently higher on LLD reefs, indicating a larger average size of native fish (within the <10 cm size class) on reefs with low densities of lionfish. This difference in biomass, despite a lack of evidence for a difference in density during the winter surveys, could be indicative of a non-lethal effect of lionfish resulting in higher growth rates in the absence of the constant threat of predation by lionfish (Lima 1998).

The small-size category included both juveniles and adults of small-bodied fishes, as well as juveniles of larger species. The effect of lionfish on the density and biomass of small-bodied species (those with maximum sizes <10 cm TL) could have substantial ecological implications for the coral-reef community. Many of these small-bodied species have important roles in the ecosystem, including participation in cleaning mutualisms (reviews by Losey et al. 1999, Côté 2000). For example, the bluehead wrasse — the second most important species in terms of its share of the overall effects of lionfish on density and biomass — is a known facultative cleaner (Limbaugh 1961). Many of the small-bodied species negatively affected by lionfish also represent important forage fish for native piscivores. Reductions in this prey base are likely to lower prey availability to important commercial and subsistence fisheries species, such as snapper and grouper. While lionfish evidently had no effect on medium-sized piscivores, such competitive effects could emerge over longer time scales and broader spatial scales than those examined here. Competition with native piscivores would likely result in reduced vital rates, such as growth and reproduction, rather than immediate reductions in density. In fact, if by reducing the available prey base lionfish cause reductions in the fecundity of native piscivores, such an effect would likely only be detectable at the metapopulation scale, as offspring are not retained locally in most coral reef fishes.

The negative effect of lionfish on juveniles of large-bodied species could result in reductions in the number of juveniles surviving to grow into larger size classes. However, lionfish had no effect on the medium size class of fishes, at least over the time horizon of the current study. There are at least three possible explanations for this result. First, increased predation on juveniles of large-bodied species caused by lionfish may not be additive with other sources of mortality. In other words, lionfish predation may only affect the “doomed surplus” (sensu Errington 1956) or those individuals that would otherwise have died due to some other mechanism, and will therefore not have an effect on the realized adult population sizes of large-bodied fishes. Second, increased mortality due to the lionfish invasion may be additive with other sources of mortality, and may translate into reduced adult population densities, but this effect might not be detectable at the local habitat-patch scale due to compensatory ontogenetic movement of adult fishes among patches. While many coral-reef fishes are relatively site-attached, others demonstrate movement patterns beyond the scale examined here and well beyond the scale at which manipulative experiments are logistically feasible. For example, three species of parrotfish that were negatively affected by lionfish, *Scarus iserti, Sparisoma aurofrenatum*, and *S. viride*, have been reported to move over relatively long distances (Munro 2000).

Third, mortality due to lionfish predation may be additive with other sources of mortality, and may translate into reduced adult population densities, but my experiment has not run long enough to detect this effect. Species in this system have a wide range of generation times and ontogenetic growth patterns, making it difficult to estimate the time required for such effects to appear. However, based on a selection of available von Bertalanffy growth parameters for some of the large-bodied herbivorous species common in the system (Choat & Robertson 2002), estimates of the time expected for individuals to attain standard lengths of 10 cm (putting their total lengths well into the 10 to 20 cm TL size class of this study) ranges between 5 and 16 months. Since this experiment ran for only 14 months, and the initial recruitment pulse occurred three months into the study, it is quite possible that a longer time series, ideally one including several seasonal recruitment pulses (i.e. multiple years), would eventually detect effects on large-bodied species.

6.4.2 Community structure

In addition to reductions in density and biomass, lionfish caused substantial reductions in native species richness in the small size class. This was the case whether richness was measured at the sub-sample level or at the whole-reef level. While lionfish had large effects on the two most common species on the experimental reefs (*Coryphopterus glaucofraenum* and *Thalassoma bifasciatum*), these effects were not proportional to their densities. In fact, species with the highest effect-to-density and effect-to-biomass ratios were among the rarest species, 18 of which were extirpated from all of the HLD reefs on which they were originally found. In addition to a mean loss of species on HLD reefs, the difference between the treatments was largely due to gains in species on the LLD reefs. Species were also gained on the HLD reefs, but the list of species gained was much smaller. It is possible that HLD reefs also gained other species, but if so, they were extirpated by lionfish before they were detected by diver surveys.

Predatory fishes can have a range of effects on the species richness and evenness of prey communities (reviewed by Hixon 1986). If predators disproportionately consume the most abundant prey species, as might be expected based on predator foraging theory and the preponderance of density-dependent prey mortality in coral-reef fishes, the effect of predation would tend to increase the evenness of a community, and would not typically result in extirpations of rare species. Alternatively, predation can target all potential prey species in proportion to their densities, thereby having no effect on the equitability among species in the prey community, and causing extirpations only occasionally, when the last of a rare species happens to be consumed by chance. A third possibility, in which rare species are targeted at rates disproportionately large compared to their densities, has been documented in coral-reef fishes in two geographically distinct systems (see Hixon

1986, Almany & Webster 2004), and results in strong negative effects on species richness. The strong negative effect of lionfish on the richness of small native reef-fish, along with the disproportionately large effect-to-response ratios for both density and biomass of rare species, suggest that lionfish may fall into this third category. This result suggests that, in addition to causing substantial reductions in the abundance of common species, the lionfish invasion may represent a serious threat to native reef-fish biodiversity and the continued existence of globally rare species on Atlantic and Caribbean coral reefs.

The NMDS ordination, when viewed for each survey date individually, illustrated a clear trajectory of lionfish effects on communities of small fishes. Before initiation of lionfish treatments, communities within each pair of experimental reefs were similar. However the HLD communities began to diverge from those on LLD reefs as early as the first post-baseline survey, less than three months after lionfish treatments were established. This rapid community response was likely driven by high levels of larval settlement over the summer months. On LLD reefs, settlement resulted in relatively high net recruitment, whereas predation by invasive lionfish on HLD reefs increased early post-settlement mortality, severely attenuating the recruitment pulse. While communities in the two treatments became slightly more similar to one another during intervening winter surveys (when natural mortality exceeded recruitment), they never reached the same degree of community overlap observed at the baseline survey, suggesting a long-term lionfish effect on community structure that may have been caused by local extirpations of rare species. The final survey, occurring at the end of the second summer recruitment period, clearly showed the highest degree of community segregation due to the lionfish treatment. This increased effect during the second summer may simply have been caused by higher levels of settlement on all reefs during 2010, or could suggest an underlying long-term trend in the effect of lionfish on communities of small reef fishes. With the exception of one species — the slippery dick *Halichoeres bivittatus*, which had a strong negative correlation with axis 2 — all strong species-specific linear correlations with NMDS axes were positive, indicating that the negative effects of lionfish were community-wide.

6.4.4 Conclusions

This large-scale, long-term, controlled field experiment demonstrated that lionfish at typical invasion densities had negative effects on the density, biomass, species richness, and community composition of small (<10 cm TL) native coral reef fishes. However, after 14 months, these patterns were still not detectable on larger (10 to 20 cm TL) fish. While it is possible that this result is due to the fact that the experiment had not run long enough, it is also possible that lionfish were merely consuming the “doomed surplus” of juveniles of large-bodied species, or that the effects of lionfish on larger-bodied species manifest at spatial scales beyond those amenable to manipulative experiments.

The results of this experiment corroborate and greatly extend those of earlier small-scale, short-term experiments by showing that the effects of lionfish on small native coral-reef fishes scale-up both spatially and temporally. Lionfish may therefore represent a substantial threat to coral-reef ecosystems via a variety of mechanisms, including drastic reductions in the abundance of small-bodied, but ecologically important species, such as herbivores and cleaners, substantial loss of native reef-fish biodiversity, and declines in the prey base available to native piscivores, including important fisheries species.

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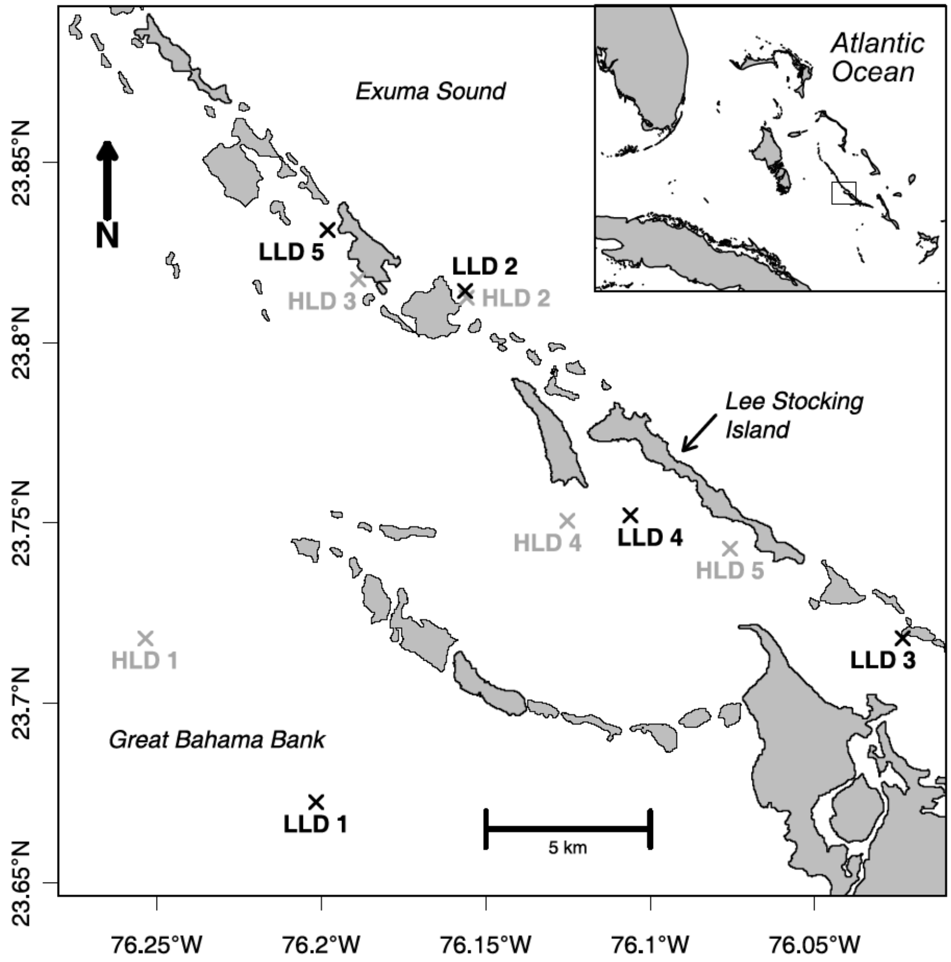

Figure 6.1 Map of the study site locations with low-lionfish-density (LLD) reefs marked by black ×'s and high-lionfish-density (HLD) reefs marked by grey ×'s. The numbers correspond to reef treatment pairs (see Table B.1 for reef characteristics, and Fig. B.1 for satellite photos of reefs). Note that reef pair 2 is in relatively deep water on the fore-reef of Exuma Sound, a semi-enclosed oceanic basin, and that reef pair 1 is in the relatively shallow waters of the extensive Great Bahama Bank. The remaining reefs are typical of moderate-depth habitats in the Bahamas.

Figure 6.2 Plots of total change in density (a, b), biomass (c, d), and species richness (e, f) in the two size classes (<10 cm TL and 10 to 20 cm TL) of all reef-fish species combined. The estimated values and SEMs around those estimates are from the full random- and fixed-effects models. Estimates for low-lionfish-diensity (LLD) treatment reefs (n = 5) are depicted by black squares connected by solid lines, and for high-lionfish-density (HLD) reefs (n = 5) by grey circles connected by dashed lines. Results of likelihood-ratio tests for the fixed effects are shown at the top left of each panel (ns: $p > 0.05$, *$p < 0.05$, **$p < 0.001$, ***$p < 0.0001$). When *treatment × time* interactions were significant, the marginal effects of *treatment* were examined individually for each survey date. In this case, significant p-values were adjusted to obtain an approximate family-wise error rate of 95 % and are displayed for each survey date. Note that y-axis scales for the two size classes are different, but the units are the same.

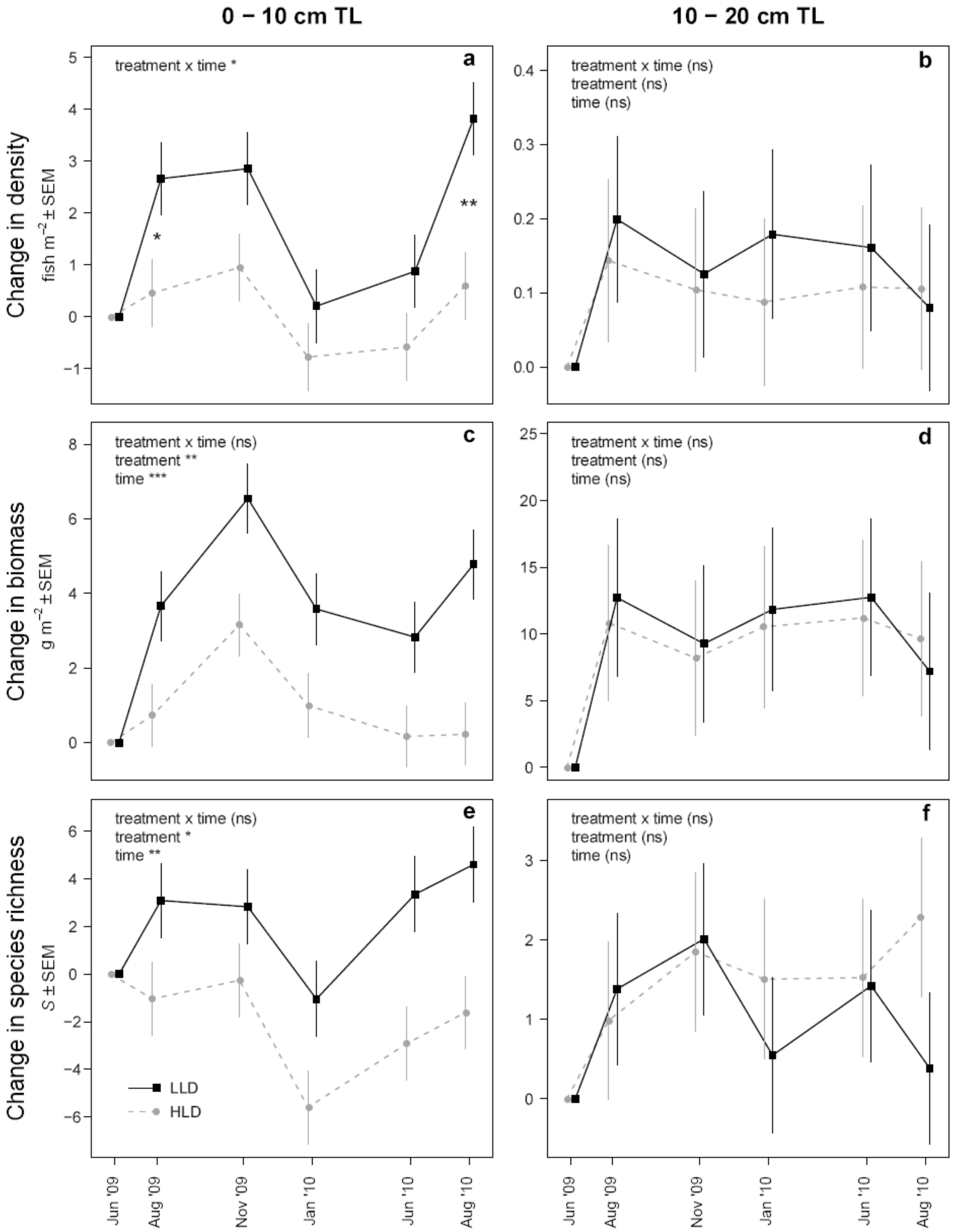
0 − 10 cm TL
10 − 20 cm TL
a
treatment x time *
*
**
b
treatment x time (ns)
treatment (ns)
time (ns)
c
treatment x time (ns)
treatment **
time ***
d
treatment x time (ns)
treatment (ns)
time (ns)
e
treatment x time (ns)
treatment *
time **
f
treatment x time (ns)
treatment (ns)
time (ns)
Change in density
fish m^{-2} ± SEM
Change in biomass
g m^{-2} ± SEM
Change in species richness
S ± SEM
LLD
HLD
Jun '09
Aug '09
Nov '09
Jan '10
Jun '10
Aug '10

Figure 6.2

Figure 6.3 Plots of total change in density (a, b) and biomass (c, d) for two size classes (<10 cm TL and 10 to 20 cm TL) of herbivorous reef fishes. The estimated values and SEMs around those estimates are from the full random- and fixed-effects models. Estimates for low-lionfish-density (LLD) treatment reefs (n = 5) are depicted by black squares connected by solid lines, and for high-lionfish-density (HLD) reefs (n = 5) by grey circles connected by dashed lines. Results of likelihood-ratio tests for the fixed effects are shown at the top left of each panel (ns: $p > 0.05$, $*p < 0.05$, $**p < 0.001$, $***p < 0.0001$). When *treatment × time* interactions were significant, the marginal effects of *treatment* were examined individually for each survey date. In this case, significant p-values were adjusted to obtain an approximate family-wise error rate of 95 % and are displayed for each survey date. Note that y-axis scales for the two size classes are different, but the units are the same. See Table B.5 for a list of species included in these response variables.

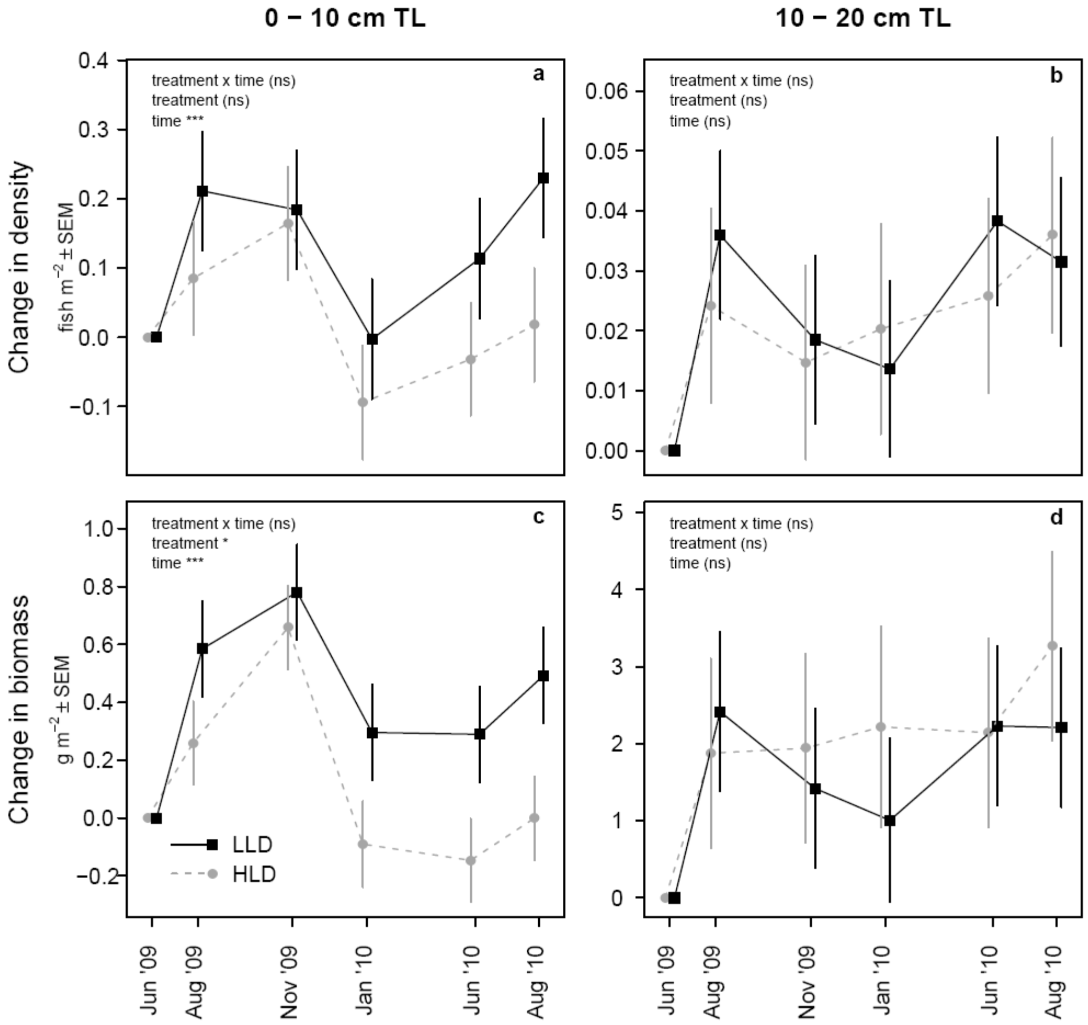
0 − 10 cm TL
10 − 20 cm TL
Change in density
fish m^{-2} ± SEM
Change in biomass
g m^{-2} ± SEM
a
treatment x time (ns)
treatment (ns)
time ***
b
treatment x time (ns)
treatment (ns)
time (ns)
c
treatment x time (ns)
treatment *
time ***
d
treatment x time (ns)
treatment (ns)
time (ns)
LLD
HLD
0.4
0.3
0.2
0.1
0.0
−0.1
0.06
0.05
0.04
0.03
0.02
0.01
0.00
1.0
0.8
0.6
0.4
0.2
0.0
−0.2
5
4
3
2
1
0
Jun '09
Aug '09
Nov '09
Jan '10
Jun '10
Aug '10

Figure 6.3

Figure 6.4 Plots of total change in density (a, b), and biomass (c, d) for two size classes (<10 cm TL and 10 to 20 cm TL) of piscivorous reef fishes. The estimated values and SEMs around those estimates are from the full random- and fixed-effects models. Estimates for low-lionfish-density (LLD) treatment reefs (n = 5) are depicted by black squares connected by solid lines, and for high-lionfish-density (HLD) reefs (n = 5) by grey circles connected by dashed lines. Results of likelihood-ratio tests for the fixed effects are shown at the top left of each panel (ns: $p > 0.05$, *$p < 0.05$, **$p < 0.001$, ***$p < 0.0001$). When *treatment × time* interactions were significant, the marginal effects of *treatment* were examined individually for each survey date. In this case, significant p-values were adjusted to obtain an approximate family-wise error rate of 95 %. Note that y-axis scales for the two size classes are different, but the units are the same. See Table B.5 for a list of species included in these response variables.

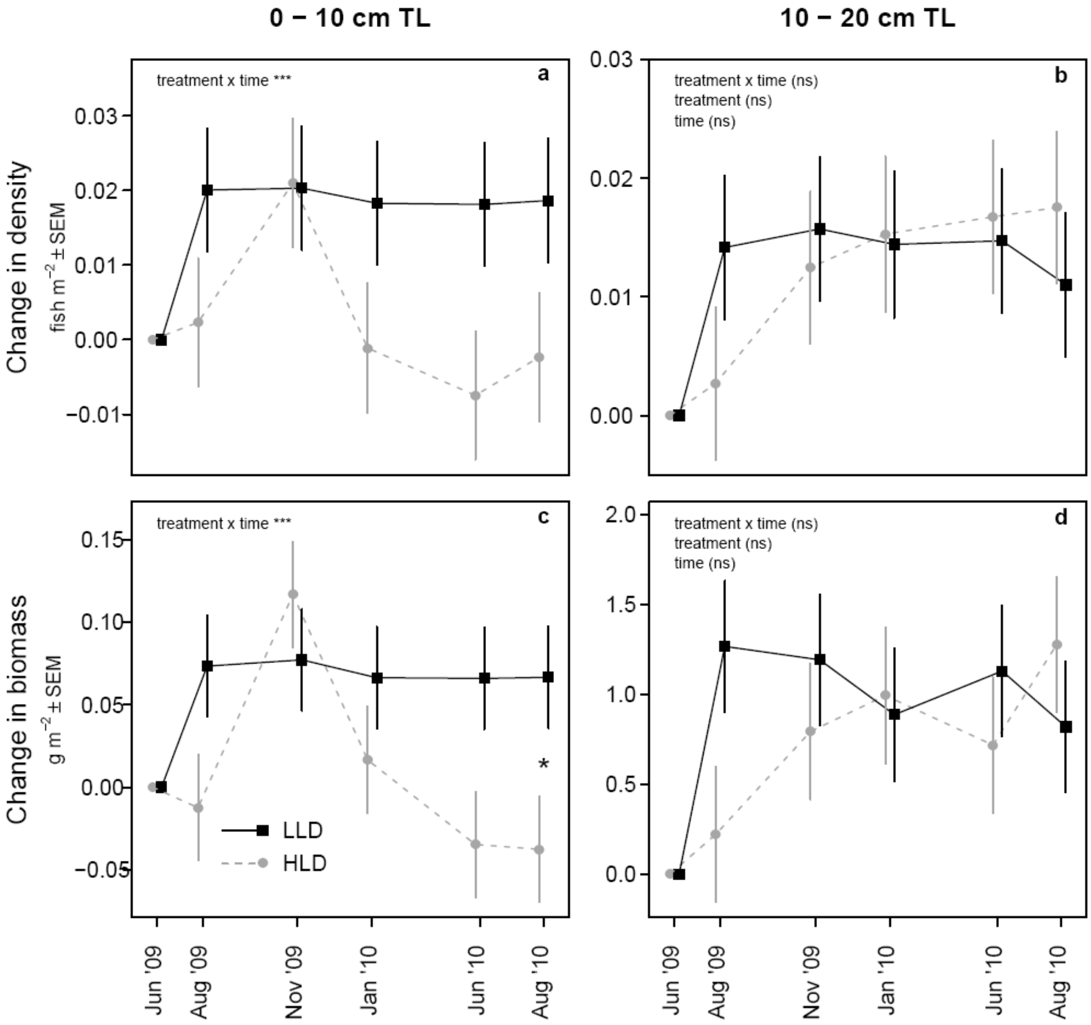
0 − 10 cm TL
10 − 20 cm TL
a
treatment x time ***
b
treatment x time (ns)
treatment (ns)
time (ns)
c
treatment x time ***
*
d
treatment x time (ns)
treatment (ns)
time (ns)
Change in density
fish m^{-2} ± SEM
Change in biomass
g m^{-2} ± SEM
0.03
0.02
0.01
0.00
−0.01
0.15
0.10
0.05
0.00
−0.05
2.0
1.5
1.0
0.5
0.0
LLD
HLD
Jun '09
Aug '09
Nov '09
Jan '10
Jun '10
Aug '10

Figure 6.4

Figure 6.5 Contributions of the top twenty species to the overall effect of lionfish on density (a) and biomass (b) of small (<10 cm TL) native reef fishes. The total contributions of all species sum to the overall lionfish effect on that response variable. Note that there are three herbivorous species in each list, and that there is a mix of small-bodied species and juveniles of medium to large bodied species represented in each list.

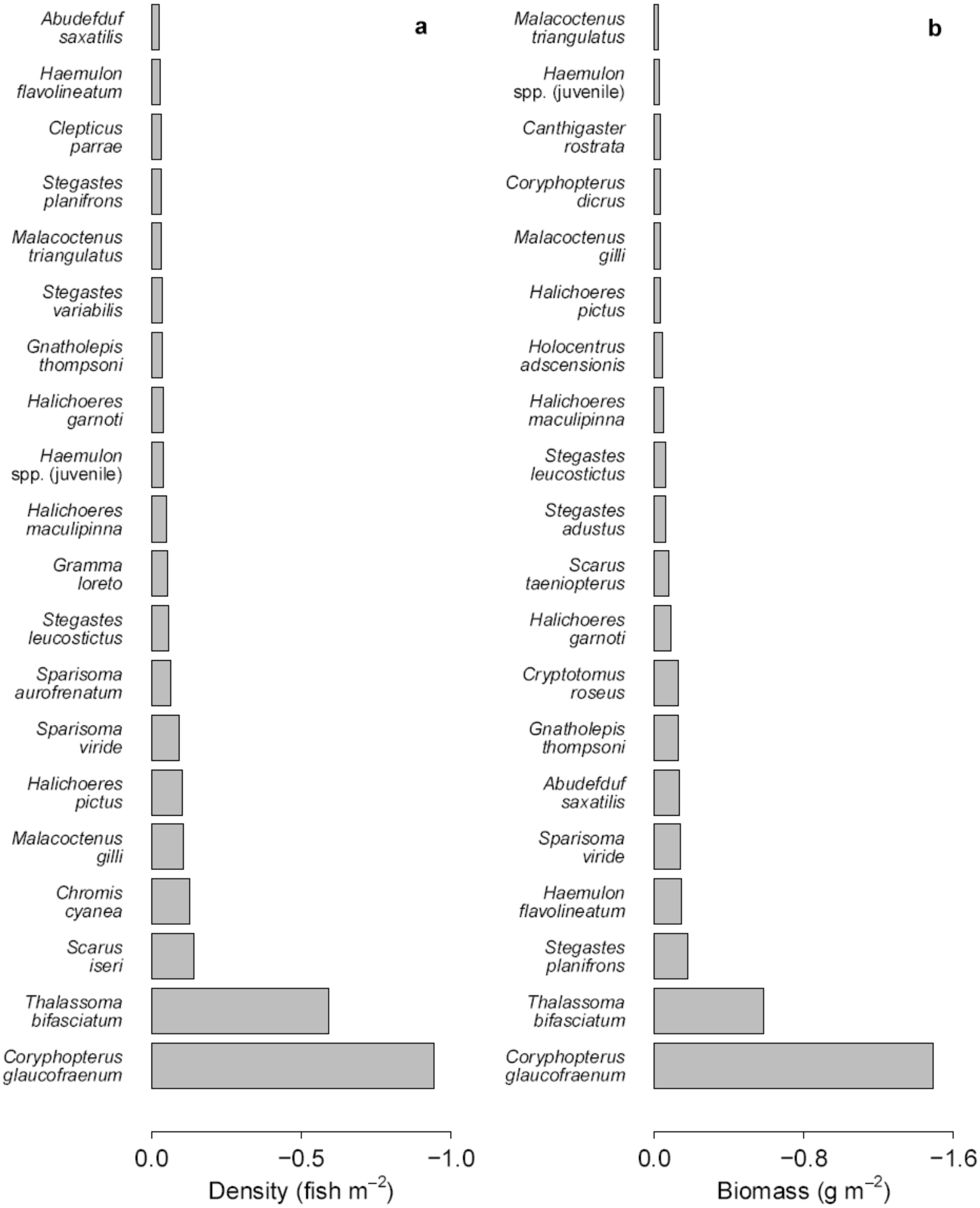
a
Abudefduf saxatilis
Haemulon flavolineatum
Clepticus parrae
Stegastes planifrons
Malacoctenus triangulatus
Stegastes variabilis
Gnatholepis thompsoni
Halichoeres garnoti
Haemulon spp. (juvenile)
Halichoeres maculipinna
Gramma loreto
Stegastes leucostictus
Sparisoma aurofrenatum
Sparisoma viride
Halichoeres pictus
Malacoctenus gilli
Chromis cyanea
Scarus iseri
Thalassoma bifasciatum
Coryphopterus glaucofraenum
0.0
−0.5
−1.0
Density (fish m−2)
b
Malacoctenus triangulatus
Haemulon spp. (juvenile)
Canthigaster rostrata
Coryphopterus dicrus
Malacoctenus gilli
Halichoeres pictus
Holocentrus adscensionis
Halichoeres maculipinna
Stegastes leucostictus
Stegastes adustus
Scarus taeniopterus
Halichoeres garnoti
Cryptotomus roseus
Gnatholepis thompsoni
Abudefduf saxatilis
Sparisoma viride
Haemulon flavolineatum
Stegastes planifrons
Thalassoma bifasciatum
Coryphopterus glaucofraenum
0.0
−0.8
−1.6
Biomass (g m−2)

Figure 6.5

Figure 6.6 Non-metric multidimensional scaling ordination of reef sub-samples in species space. The ordination was constructed using data from all survey periods, but the plots show only those points from (a) the baseline survey and (b) the final survey. Minimum convex polygons have been drawn around the sub-samples from each reef. Low-lionfish-density (LLD) reef sub-samples are indicated by black squares with solid lines, and high-lionfish-density (HLD) reef sub-samples are indicated by grey circles with dashed lines.

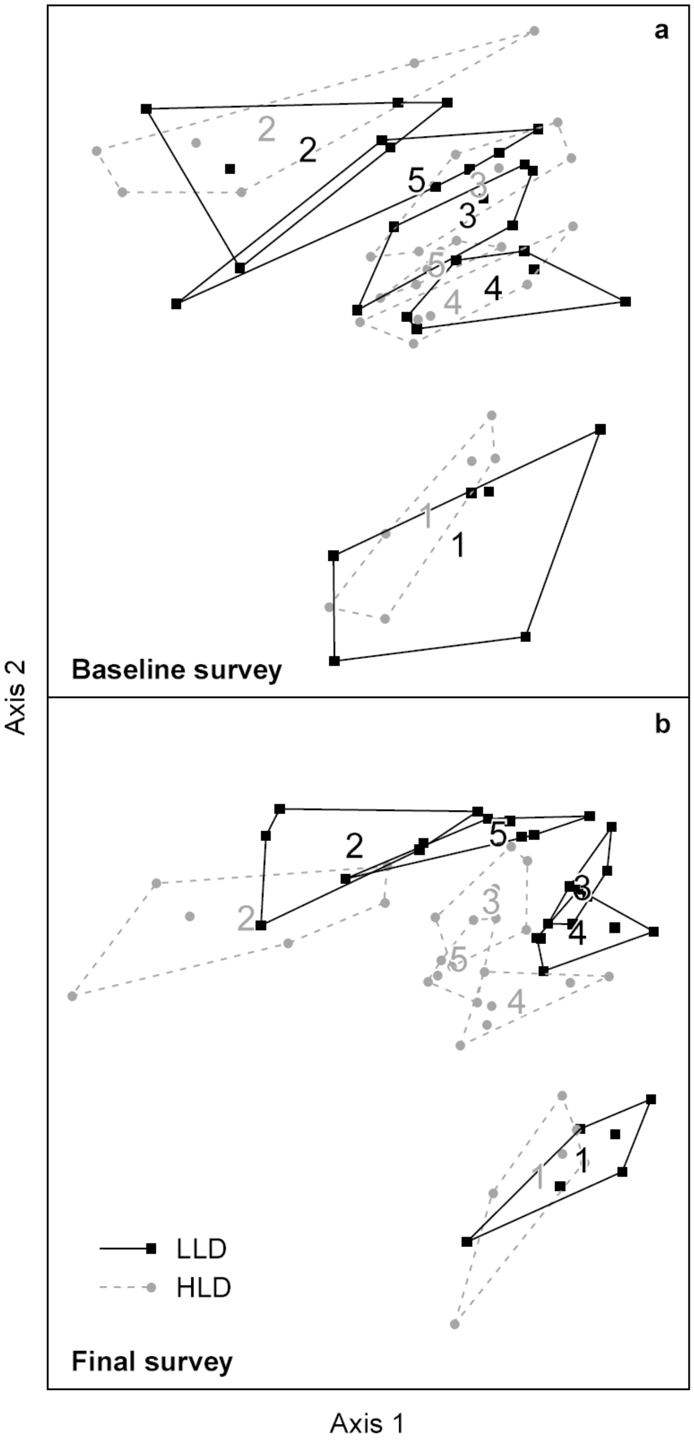
a
2
2
5
3
3
5
4
4
1
1
Baseline survey
b
2
5
2
3
3
4
5
4
1
1
LLD
HLD
Final survey
Axis 2
Axis 1

Figure 6.6

Chapter 7 — General Conclusions

The research described in this dissertation represents the first, and to this date only, experimental investigation of the effects of invasive lionfish on native Atlantic coral-reef fish communities. It is also the first time that the effects of an invasive marine fish have been examined immediately following the invasion, and the first time that such effects have been investigated experimentally. This work not only incorporated a quantitative experimental approach, but did so over a range of spatial and temporal scales, and provides confirmation that at least some of the initial concerns regarding the ecological effects of the lionfish invasion are justified. The information presented here is valuable not only for our basic understanding of invasion ecology, but also sheds light on the consequences of marine fish introductions, and in particular provides critical data necessary for an informed approach to managing the lionfish invasion.

The experiment described in Chapter 2 showed that single small lionfish on coral patch reefs reduced the recruitment of native fishes to these reefs by an average of 79 % over only 5 weeks. Of 38 species recruiting to both lionfish and control reefs, 23 suffered reduced recruitment in the presence of lionfish. Stomach-content analysis of fish on experimental and nearby reefs along with captive feeding trials suggested that lionfish consume a broad diversity of native fishes, including ecologically important species such as parrotfishes.

The information reviewed in Chapter 3, in combination with what is currently known of coral-reef ecology, suggests that lionfish may manifest one of the most damaging marine invasions to date. They possess a suite of behaviors and characteristics that make them particularly successful invaders and strong negative interactors with native fauna, including venomous spines, cryptic appearance, habitat generality, high competitive ability, low parasite load, efficient predation, rapid growth, and high reproductive rates. In the “worst case scenario” the direct and indirect effects of lionfish could combine with preexisting stressors — particularly overfishing — and cause substantial deleterious changes in coral-reef ecosystems. Management actions that have the potential to mitigate these effects include developing targeted lionfish fisheries and local removals, and enhancing potential native biotic resistance, particularly via marine reserves. The lionfish invasion will ultimately be limited either by lionfish starving — the worst end to the worst case scenario — or by some combination of native pathogens, parasites, predators, and competitors controlling their abundance.

The experiment described in Chapter 4 demonstrated that (1) single small lionfish caused significant reductions in the abundance and species richness of small native coral-reef fishes on patch reefs over short time scales, (2) the effect of lionfish on the change in abundance of native reef-fishes was stronger than that of a similarly sized native predator, (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 faster than the native predator under the same conditions. Invasive lionfish do not appear to be ecologically equivalent to similarly sized native piscivores, and may have both direct (via predation on juveniles) and indirect (via exploitation of food resources) negative impacts on ecologically and commercially important native predators like groupers.

The field and aquarium observations in Chapter 5 describe a previously undocumented piscivorous behavior by lionfish. While approaching prey, lionfish produce jets of water directed toward the prey. These jets may confuse or distract prey, and often result in prey-fish facing the attacking lionfish, increasing the probability of headfirst capture and swallowing. A number of fishes create water jets under various circumstances. However, lionfish appear to be the only species to do so when consuming other fishes. If water-jet piscivory is unique to the genus *Pterois*, it is unlikely that native prey species have encountered this predatory behavior during their evolutionary history, and may not have evolved effective antipredator responses. Therefore, this behavior may result in high levels of predation efficiency contributing to the remarkable success of invasive lionfish.

The experiment described in Chapter 6 demonstrated that the effects of lionfish on small native coral-reef fishes demonstrated by previous experiments scale-up both spatially and temporally. Quarterly surveys of the reef fish communities on these reefs over the 14 month period following initiation of lionfish treatments show that lionfish reduced the density, biomass, and species richness of small (<10 cm TL) native fishes. Lionfish also reduced the biomass of small native herbivores and piscivores, and generated overall shifts in the community structure of small prey-sized native fishes. However, after 14 months, effects on larger (10 to 20 cm TL) native fishes were not detected. While the effects of lionfish on common species are substantial, lionfish may target rare fishes disproportionately to their density, and may thus have substantial negative effects on both local and global native reef-fish biodiversity. The results of this experiment corroborate and greatly extend those of earlier small-scale, short-term experiments, and provide estimates of the effects of lionfish on a scale directly relevant to management and conservation efforts.

In sum, the research described in this dissertation demonstrates that invasive lionfish are having substantial negative effects on native communities of coral-reef fishes. In all cases, overall numerical reductions in small (prey-sized) native fishes caused by lionfish were considerable. Additionally it appears that lionfish may reduce the diversity of native reef-fishes via disproportionately high rates of predation on rare species. These findings indicate that the lionfish invasion may have long-term, broad-scale impacts on the structure and function of coral-reef ecosystems, potentially reducing the resilience of these systems to a myriad of existing stressors as well as their capacity to provide valuable goods and services to humans.

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APPENDICES

Appendix A Chapter 4 Supplementary Materials

Table A.1 Selection criteria for random effects, variance structure, and autocorrelation structure for candidate models for each response variable. LRT results: likelihood ratios, and associated p-values (corrected for testing-on-the-boundary) resulting from test between a model without random effects, and a model with *reef* as a random effect. Variance structure — equal: equal variance; treatment: separate variances for each treatment; species: separate variances for each species; species × treatment: separate variances for each species treatment combination. Autocorrelation structure — none: no autocorrelation; AR(1): AR(1) structure within reefs; n.a.: temporal correlation was not applicable. AIC — Akaike's Information Criterion for each model. The best fitting models have the lowest AIC values (indicated in bold-face type).

Response variable	*LRT* results		Variance structure	Autocorrelation structure	*AIC*
	L Ratio	p			
Change in abundance (ΔN)	47.3	< 0.001	equal	none	1145.6
			treatment	none	1129.1
			equal	AR(1)	1124.8
			treatment	**AR(1)**	**1107.6**
Change in richness (ΔS)	35.3	< 0.001	equal	none	678.6
			treatment	none	679.2
			equal	**AR(1)**	**648.4**
			treatment	AR(1)	652.8
Change in evenness (ΔJ)	62.4	< 0.001	equal	none	-236.9
			treatment	none	-244.3
			equal	AR(1)	-243.1
			treatment	**AR(1)**	**-248.4**
Change in diversity ($\Delta H'$)	58.8	< 0.001	equal	none	92.1
			treatment	none	98.0
			equal	**AR(1)**	**74.8**
			treatment	AR(1)	76.6
Rate of length growth	0.38	0.268	equal	n.a.	-65.4
			species	**n.a.**	**-73.6**
			treatment	n.a.	-64.6
			species × treatment	n.a.	-71.8
Rate of mass growth	5.26	0.022	equal	n.a.	-7.6
			species	n.a.	-22.0
			treatment	n.a.	-15.9
			species × treatment	**n.a.**	**-26.2**

Table A.2 Estimated coefficients from linear mixed effects models representing differences in four community response variables among reefs assigned to the four predator treatments at the baseline census (before predator treatments were established). Standard errors (SE), *t*-statistics (*t*), and p-values (p), are included for each coefficient estimate (degrees of freedom = 17 for all coefficient estimates and associated tests). Comparisons with significant (**) or marginally significant (*) p-values are denoted by bold face type.

Response variable	Hypothesis	Estimate	SE	*t*	p
Abundance (*N*)	control vs. grouper	-11.8	16.4	-0.72	0.481
	control vs. lionfish	-5.6	16.3	-0.34	0.735
	control vs. lionfish + grouper	2.2	16.7	0.13	0.900
	grouper vs. lionfish	6.2	13.7	0.45	0.656
	grouper vs. lionfish + grouper	14.0	14.1	0.99	0.336
	lionfish vs. lionfish + grouper	7.8	14.1	0.55	0.586
Richness (*S*)	control vs. grouper	-0.8	2.0	-0.41	0.688
	control vs. lionfish	-0.2	2.0	-0.1	0.920
	control vs. lionfish + grouper	2.8	2.0	1.43	0.171
	grouper vs. lionfish	0.6	2.0	0.31	0.763
	grouper vs. lionfish + grouper	**3.6**	**2.0**	**1.84**	***0.084**
	lionfish vs. lionfish + grouper	3.0	2.0	1.53	0.144
Evenness (*J*)	control vs. grouper	-0.05	0.04	-1.5	0.152
	control vs. lionfish	-0.01	0.03	-0.36	0.724
	control vs. lionfish + grouper	0.04	0.03	1.31	0.209
	grouper vs. lionfish	0.04	0.04	0.94	0.359
	grouper vs. lionfish + grouper	**0.10**	**0.04**	**2.39**	****0.030**
	lionfish vs. lionfish + grouper	0.06	0.04	1.38	0.187
Diversity (*H'*)	control vs. grouper	-0.18	0.17	-1.04	0.315
	control vs. lionfish	-0.06	0.17	-0.38	0.712
	control vs. lionfish + grouper	**0.30**	**0.17**	**1.77**	***0.094**
	grouper vs. lionfish	0.11	0.17	0.66	0.510
	grouper vs. lionfish + grouper	**0.48**	**0.17**	**2.81**	****0.012**
	lionfish vs. lionfish + grouper	**0.37**	**0.17**	**2.15**	****0.046**

Table A.3 Mean change in abundance (individuals reef^{-1}) of small native coral-reef fishes on predator-free control reefs over the course of the 8 wk experiment and the effect of each predator treatment on the mean change in abundance for each species. The treatment effects are calculated as the difference between mean change in abundance on control reefs at week 8 and mean change in abundance on grouper only, lionfish only, and grouper + lionfish treatment reefs at week 8, respectively. Table is sorted by increasing change in abundance on control reefs. Species with zeros in all columns were counted during reef censuses, but did not change in mean abundance over the course of the experiment on any of the four treatments. Table continued on next page.

Family	Species	Control	Grouper effect	Lionfish effect	Combined effect
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* spp. (juvenile)	0.2	-0.2	-0.2	-0.2
Scorpaenidae	*Scorpaena plumeiri*	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
Haemulidae	*Haemulon melanurum*	0.0	0.0	0.0	0.0
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
Labrisomidae	*Malacoctenus triangulatus*	0.0	0.0	0.0	0.0
Mullidae	*Pseudupeneus maculatus*	0.0	0.0	0.0	0.0
Paralichthyidae	*Paralichthys albigutta*	0.0	0.0	0.0	0.0
Apogonidae	*Apogon maculatus*	0.0	0.0	0.0	0.2
Serranidae	*Epinephelus guttatus*	0.0	0.0	0.0	-0.2

Table A.3 (Continued).

Family	Species	Control	Grouper effect	Lionfish effect	Combined effect
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**

Table A.4 List of families and species of juvenile coral reef fishes present on experimental reefs at the end of the experiment with associated linear correlations with each axis from the NMDS ordination (Fig. 4.3). List is sorted by correlation with axis 1. Correlations with absolute values greater than 0.3 are denoted by bold-face type.

Family	Species	Correlation	
		Axis 1	Axis 2
Gobiidae	***Coryphopterus glaucofraenum***	**0.685**	0.196
Labrisomidae	***Malacoctenus macropus***	**0.605**	-0.161
Pomacentridae	***Stegastes leucostictus***	**0.551**	-0.278
Labridae	***Halichoeres garnoti***	**0.489**	-0.172
Labridae	***Bodianus rufus***	**0.435**	0.024
Labridae	***Halichoeres maculipinna***	**0.427**	0.282
Labridae	***Halichoeres pictus***	**0.409**	0.169
Pomacentridae	***Stegastes partitus***	**0.381**	0.204
Labridae	***Thalassoma bifasciatum***	**0.378**	**0.495**
Scaridae	***Sparisoma viride***	**0.350**	-0.077
Acanthuridae	***Acanthurus chirurgus***	**0.322**	-0.250
Labridae	***Halichoeres radiatus***	**0.314**	-0.121
Pomacentridae	*Chromis cyanea*	0.283	0.150
Scaridae	*Sparisoma aurofrenatum*	0.273	-0.262
Haemulidae	*Haemulon* spp. (juvenile)	0.250	-0.216
Scorpaenidae	*Scorpaena plumieri*	0.250	-0.216
Scaridae	*Sparisoma atomarium*	0.250	-0.216
Gobiidae	***Gnatholepis thompsoni***	**0.244**	**0.407**
Gobiidae	*Priolepis hipoliti*	0.218	-0.266
Scaridae	*Scarus taeniopterus*	0.151	0.239
Serranidae	*Serranus tigrinus*	0.150	0.117
Gobiidae	*Coryphopterus dicrus*	0.117	-0.050
Tetraodontidae	***Canthigaster rostrata***	**0.100**	**-0.408**
Apogonidae	*Apogon townsendi*	0.024	-0.097
Labridae	*Halichoeres poeyi*	0.012	-0.155
Pomacanthidae	*Holacanthus tricolor*	0.000	0.073
Acanthuridae	*Acanthurus coeruleus*	-0.050	0.083
Apogonidae	***Apogon maculatus***	**-0.117**	**-0.316**
Scaridae	*Cryptotomus roseus*	-0.283	-0.283
Apogonidae	***Apogon binotatus***	**-0.314**	**-0.193**

Appendix B Chapter 6 Supplementary Materials

Table B.1 Reef pairs, treatment assignments, and general characteristics of experimental reefs.

Reef Pair	Reef Name	Treatment	Depth range (m)	Area (m^2)	Distance to			Predominant substrate type
					nearest reef (m)	tidal channel (m)	Exuma Sound (m)	
1	SE Barracuda Rocks	LLD	2-3	3600	5440	6200	15900	Pavement w/Bommies
	NW Barracuda Rocks	HLD	2-4	3500	5510	7000	15080	Pavement w/Bommies
2	Turtle Reef	LLD	7-11	1950	120	670	0	Pavement w/Gorgonians
	Coney Reef	HLD	7-11	1380	210	460	0	Pavement w/Gorgonians
3	Square Rock	LLD	2-7	2640	90	190	460	Pavement/Sand w/Bommies
	Woobie Rock	HLD	2-7	3180	215	0	1660	Pavement/Sand w/Bommies
4	Tug and Barge	LLD	2-3	3230	1550	1200	4650	Pavement/Sand w/Bommies
	Shark Rocks	HLD	2-3	3030	1050	1000	4590	Pavement/Sand w/Bommies
5	Goby Spot	LLD	3-4	3949	360	0	980	Sand w/Bommies
	Windsock Reef	HLD	3-4	3000	210	0	1050	Sand w/Bommies

Table B.2 L-W conversions used to calculate biomass for the study. Conversion equation used: $W = a \cdot L^b$ (weight in g, length in cm TL). When original L-W conversion parameters were reported by the reference in the $log(W) = log(a) + b \cdot log(L)$ format with lengths measured in mm, parameters were converted. When information for a particular species was not available, we used a closely related or similarly shaped substitute species. Additionally, if the source reported conversions from standard length or fork length we incorporated a length conversion multiplier in the *a* values based on length-length conversion factors from the FishBase database when available, or from our own analysis of species photographs, when not available. References are listed at the end of the table. Table continues on following pages.

Species	Substitute Species	a	b	Ref.
Ablennes hians		0.00034	3.33013	10
Abudefduf saxatilis		0.02003	3.14238	3
Acanthemblemaria aspera		0.00773	2.96248	3
Acanthostracion polygonia		0.00514	3.34702	3
Acanthostracion quadricornis		0.17830	2.25833	3
Acanthurus bahianus		0.03480	2.68940	4
Acanthurus chirurgus		0.02820	2.81370	4
Acanthurus coeruleus		0.03756	2.83271	3
Aluterus schoepfii		0.09448	2.33966	3
Aluterus scriptus		0.81391	1.81670	3
Amblycirrhitus pinos		0.00258	3.42575	3
Anisotremus virginicus		0.01328	3.16810	3
Apogon aurolineatus	*A. maculatus*	0.01518	3.07395	3
Apogon binotatus	*A. maculatus*	0.01530	3.07177	3
Apogon maculatus		0.01524	3.07300	3
Apogon pseudomaculatus		0.01913	2.94543	3
Apogon spp.	*A. maculatus*	0.01520	3.07357	3
Apogon townsendi	*A. maculatus*	0.01510	3.07533	3
Aulostomus maculatus		0.00384	2.87410	3
Balistes vetula		0.04054	2.87500	1
Bodianus rufus		0.01322	3.05580	3
Bothus lunatus		0.00985	3.18860	3
Calamus calamus		0.04129	2.79601	3
Cantherhines pullus		0.06821	2.56399	3
Canthigaster rostrata		0.06150	2.50000	15
Caranx bartholomaei		0.02254	2.90974	3
Caranx crysos		0.04522	2.68986	3
Caranx latus		0.01860	2.85630	4
Caranx ruber		0.02974	2.75223	3
Carcharhinus perezii	*C. amblyrhynchos*	0.00196	3.37300	11
Cephalopholis cruentatus		0.03902	2.80000	8
Cephalopholis fulva		0.01949	2.92862	3
Chaetodipterus faber		0.08662	2.68480	3
Chaetodon aculeatus		0.01868	3.14000	15
Chaetodon capistratus		0.01470	3.43010	4
Chaetodon ocellatus		0.03175	2.98381	3
Chaetodon sedentarius		0.02503	3.07759	3

Table B.2 (Continued)

Species	Substitute Species	a	b	Ref.
Chaetodon striatus		0.02223	3.13864	3
Chromis cyanea		0.01464	3.24000	15
Chromis multilineata		0.01489	3.24000	15
Clepticus parrae		0.01548	3.00000	15
Coryphopterus dicrus	*C. glaucofraenum*	0.01331	2.96402	3
Coryphopterus glaucofraenum		0.01281	2.97410	3
Coryphopterus personatus/hyalinus	*C. hyalinus*	0.02839	2.68000	15
Cosmocampus albirostris	*Aulostomus maculatus*	0.00421	2.85020	3
Cosmocampus spp.	*Aulostomus maculatus*	0.00429	2.84332	3
Cryptotomus roseus		0.05034	3.18177	3
Dasyatis americana		0.00070	2.86267	3
Diodon holocanthus		0.15985	2.39755	3
Diodon hystrix		0.53374	2.27588	3
Echeneis naucrates		0.12696	2.11256	3
Elacatinus evelynae	*E. digueti*	0.00708	3.35923	2
Elacatinus genie	*E. digueti*	0.00708	3.35923	2
Elacatinus horsti	*E. limbaughi*	0.00701	3.36107	2
Elacatinus louisae	*E. digueti*	0.00708	3.35923	2
Emblemaria pandionis	*Acanthemblemaria aspera*	0.00773	2.96226	3
Epinephelus adscensionis		0.01015	3.22400	5
Epinephelus guttatus		0.01108	3.11249	3
Epinephelus striatus		0.00635	3.23525	3
Equetus lanceolatus		0.00108	3.84677	3
Equetus punctatus		0.00737	3.20000	15
Eucinostomus jonesi		0.07852	2.65000	6
Gerres cinereus		0.01580	2.90920	4
Ginglymostoma cirratum		0.01032	2.89776	3
Gnatholepis thompsoni		0.00351	3.76758	3
Gobionellus saepepallens	*G. oceanicus*	0.00504	2.89200	9
Gramma loreto		0.01175	3.05000	15
Gymnothorax funebris		0.00404	2.88970	3
Gymnothorax moringa		0.00102	3.15555	3
Gymnothorax vicinus		0.00414	2.88321	3
Haemulon album		0.01296	3.07000	7
Haemulon aurolineatum		0.00009	3.09050	13
Haemulon flavolineatum		0.01300	3.03400	4
Haemulon melanurum		0.02062	2.95408	3
Haemulon parrai		0.01846	2.99594	3
Haemulon plumierii		0.01430	3.05020	4
Haemulon sciurus		0.01390	3.07420	4
Haemulon spp. (juvenile)	*H. plumierii*	0.01430	3.05020	4
Haemulon striatum		0.01548	3.09859	3
Halichoeres bivittatus		0.01343	2.93887	3
Halichoeres garnoti		0.00512	3.37837	3
Halichoeres maculipinna		0.00274	3.69289	3
Halichoeres pictus	*H. bivittatus*	0.01277	2.94267	3
Halichoeres poeyi		0.00950	3.13110	4
Halichoeres radiatus		0.01302	3.03927	3
Hemiemblemaria simulus	*Thalassoma bifasciatum*	0.01080	2.91368	3

Table B.2 (Continued)

Species	Substitute Species	a	b	Ref.
Heteropriacanthus cruentatus		1.22482	1.75112	3
Holacanthus ciliaris		0.03395	2.89815	3
Holocanthus tricolor		0.04311	2.85585	3
Holocentrus adscensionis		0.02130	2.77810	4
Holocentrus rufus		0.02560	2.63940	4
Hypleurochilus bermudensis		0.01208	3.03846	3
Hypoplectrus spp.	*H. unicolor*	0.01090	3.18317	3
Inermia vittata		0.00600	2.94000	15
Kyphosus sp.	*K. sectatrix*	0.01572	3.08169	3
Labrisomus spp.	*L. xanti*	0.00908	3.18060	2
Lachnolainus maximus		0.01893	2.98897	3
Lactophrys triqueter		0.31198	2.22854	3
Liopropoma rubre		0.01223	3.05000	15
Lutjanus analis		0.01479	3.01310	3
Lutjanus apodus		0.02110	2.92610	4
Lutjanus griseus		0.02020	2.89280	4
Lutjanus jocu		0.01586	2.99800	9
Lutjanus mahogoni		0.04056	2.72063	3
Lutjanus synagris		0.02494	3.00000	8
Malacoctenus boehlkei	*M. triangulatus*	0.00656	3.19236	3
Malacoctenus gilli	*M. macropus*	0.02877	2.17897	3
Malacoctenus macropus		0.02160	2.25711	3
Malacoctenus triangulatus		0.00682	3.18215	3
Malacoctenus versicolor	*M. macropus*	0.02732	2.19167	3
Micrognathus ensenadae	*Aulostomus maculatus*	0.00422	2.84881	3
Microspathodon chrysurus		0.02157	3.08279	3
Monacanthus tuckeri		0.00740	3.56130	4
Mulloidichthys martinicus		0.00190	3.66320	3
Mycteroperca bonaci		0.00822	3.14000	6
Mycteroperca tigris		0.01480	3.11000	6
Myripristis jacobus	*M. amaena*	0.01390	3.26100	11
Nes longus	*Gobionellus oceanicus*	0.00504	2.89200	9
Ocyurus chrysurus		0.01850	2.80150	4
Ophioblennius macclurei		0.03251	2.37894	3
Opistognathus aurifrons	*O. whitehursti*	0.00948	2.98434	3
Opistognathus macrognathus	*O. whitehursti*	0.00944	2.98535	3
Oxyurichthys stigmalophius	*O. papuensis*	0.01940	2.72700	12
Paradiplogrammus bairdi		0.02318	3.11970	3
Paralichthys albigutta		0.00779	3.13550	14
Paranthias furcifer		0.01170	3.04030	3
Platybelone argalus	*Tylosurus crocodilus*	0.00077	3.20500	12
Pomacanthus arcuatus		0.03420	2.96972	3
Pomacanthus paru		0.02042	3.12525	3
Priacanthus arenatus		0.01328	3.03398	3
Priolepis hipoliti		0.01348	3.03628	3
Pseudupeneus maculatus		0.00490	3.37340	4
Pterois volitans		0.00480	3.31630	16
Sargocentron coruscum		0.00760	3.25820	4
Scarus coeruleus	*S. iserti*	0.01580	3.05150	4

Table B.2 (Continued)

Species	Substitute Species	a	b	Ref.
Scarus iserti		0.01580	3.05150	4
Scarus taeniopterus		0.03351	2.70847	3
Scarus vetula	*S. taeniopterus*	0.03330	2.71018	3
Scomberomorus regalis		0.01806	2.80000	6
Scorpaena plumieri		0.02439	2.94787	3
Scorpaenodes caribbaeus	*S. guamensis*	0.01960	3.03800	11
Seriola spp.	*S. dumerili*	0.03096	2.80759	3
Serranus tigrinus		0.01385	3.04594	3
Sparisoma atomarium		0.01214	3.02654	3
Sparisoma aurofrenatum		0.00472	3.42689	3
Sparisoma chrysopterum		0.01540	3.04230	4
Sparisoma radians		0.01790	3.03480	4
Sparisoma rubripinne		0.01448	3.06236	3
Sparisoma viride		0.02237	2.92434	3
Sphoeroides spengleri		0.04200	2.61000	6
Sphyraena barracuda		0.00546	3.00000	6
Starksia hassi	*Malacoctenus macropus*	0.02536	2.21449	3
Stegastes adustus		0.03274	2.89605	3
Stegastes diencaeus	*S. adustus*	0.03231	2.89955	3
Stegastes leucostictus		0.02770	2.87110	4
Stegastes partitus		0.01606	3.15370	3
Stegastes planifrons		0.03275	2.85660	3
Stegastes variabilis		0.02886	2.83952	3
Synodus spp.	*S. intermedius*	0.00940	2.99449	3
Thalassoma bifasciatum		0.01069	2.91658	3
Tylosurus crocodilus		0.00077	3.20500	12
Urolophus jamaicensis		0.00717	3.08443	3
Xyrichtys splendens		0.01000	2.99834	3

Table B.2 References:

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15. *Sandin SA, Sampayo EM, Vermeji MJA (2008) Coral reef fish and benthic community structure of Bonaire and Curaçao, Netherlands Antilles. Caribbean Journal of Science 44:137-144 *NOTE: This paper refers to FishBase as the source for a number of L-W conversion estimates, but FishBase refers back to this paper as the original source of the estimates, therefore these conversions are of questionable origin.

16. Author's unpublished data. L-W curve based on 60 individuals ranging in size from 2.5 to 32.5 cm TL (R^2 = 0.992).

Table B.3 Akaike's Information Criterion (AIC) and p-values from likelihood-ratio tests (LRT p) used to determine whether including random effects, non-homogenous variance structures, and autocorrelation resulted in better models of the various response variables. Models compared — S: full fixed effects structure; R: random effect for *sub-sample* nested within *reef*; V: weighted term allowing variance to differ among *reef*; C: AR1 temporal autocorrelation structure. Likelihood-ratio tests comparing the full fixed effects model (S) to the model including a random effect for *sub-sample* within *reef* (S + R) incorporated an adjustment to the p-value to compensate for testing-on-the-boundary. The best fitting model is indicated by bold text, but analyses used the fullest model (S + R + V + C) for all response variables to facilitate comparison between models. Table continued on next page.

Table B.3

Group	Size class (cm TL)	Response variable (units)	Model components	AIC	LRT p
All species	<10	Density (fish m^{-2})	S	1309.6	
			S + R	1177.9	<0.001
			S + R + V	**1148.1**	**<0.001**
			S + R + V + C	1149.6	0.465
		Biomass (g m^{-2})	S	1642.0	
			S + R	1579.2	<0.001
			S + R + V	**1521.8**	**<0.001**
			S + R + V + C	1521.2	0.104
	10 to 20	Density (fish m^{-2})	S	598.9	
			S + R	546.1	<0.001
			S + R + V	404.8	<0.001
			S + R + V + C	**401.0**	**0.016**
		Biomass (g m^{-2})	S	2905.7	
			S + R	2865.7	<0.001
			S + R + V	**2742.3**	**<0.001**
			S + R + V + C	2742.3	0.156
	<10	Richness (# of spp.)	S	1774.8	
			S + R	1616.1	<0.001
			S + R + V	**1613.1**	**0.013**
			S + R + V + C	1613.6	0.224
		Evenness (*J*)	S	-405.7	
			S + R	-509.1	<0.001
			S + R + V	-554.3	<0.001
			S + R + V + C	**-557.4**	**0.023**
		Diversity (*H′*)	S	246.2	
			S + R	153.4	<0.001
			S + R + V	**123.6**	**<0.001**
			S + R + V + C	124.0	0.199
	10 to 20	Richness (# of spp.)	S	1658.7	
			S + R	1536.1	<0.001
			S + R + V	1532.3	0.009
			S + R + V + C	**1528.0**	**0.012**
		Evenness (*J*)	S	-252.3	
			S + R	-448.0	<0.001
			S + R + V	-484.8	<0.001
			S + R + V + C	**-496.6**	**<0.001**
		Diversity (*H′*)	S	504.6	
			S + R	339.7	<0.001
			S + R + V	330.3	0.001
			S + R + V + C	**324.9**	**0.007**

Table B.3 (Continued)

Group	Size class (cm TL)	Response variable (units)	Model Components	AIC	LRT p
Herbivores	<10	Density (fish m^{-2})	S	255.8	
			S + R	156.1	<0.001
			S + R + V	**78.4**	**<0.001**
			S + R + V + C	79.8	0.443
		Biomass (g m^{-2})	S	847.8	
			S + R	815.3	<0.001
			S + R + V	**741.4**	**<0.001**
			S + R + V + C	742.9	0.492
	10 to 20	Density (fish m^{-2})	S	-479.5	
			S + R	-530.1	<0.001
			S + R + V	**-569.0**	**<0.001**
			S + R + V + C	-567.1	0.751
		Biomass (g m^{-2})	S	1964.6	
			S + R	1909.4	<0.001
			S + R + V	**1866.3**	**<0.001**
			S + R + V + C	1868.0	0.608
Piscivores	<10	Density (fish m^{-2})	S	-1078.7	
			S + R	-1156.7	<0.001
			S + R + V	**-1252.8**	**<0.001**
			S + R + V + C	-1250.9	0.742
		Biomass (g m^{-2})	S	-258.2	
			S + R	-304.3	<0.001
			S + R + V	**-405.5**	**<0.001**
			S + R + V + C	-403.8	0.620
	10 to 20	Density (fish m^{-2})	S	-1010.0	
			S + R	-1090.0	<0.001
			S + R + V	**-1096.1**	**0.004**
			S + R + V + C	-1096.3	0.136
		Biomass (g m^{-2})	S	1354.4	
			S + R	1266.1	<0.001
			S + R + V	1246.5	<0.001
			S + R + V + C	**1241.4**	**0.008**

Table B.4 Results of hypothesis tests for the effect of lionfish treatment on response variables. The significance of fixed effects were tested by comparing nested models (fit by Maximum Likelihood Estimation) using likelihood-ratio tests (LRT). The main effects were only tested in the absence of evidence for an interaction. If there was evidence for an interaction between treatment and time, I adjusted the p-values associated with these specific linear combinations to achieve an approximate family-wise error rate of 95 %. Table continued on next page.

Group	Size class (cm TL)	Response variable (units)	Fixed effect	LRT p	Survey period	p
All species combined	<10	Density (fish m^{-2})	**treatment × time**	**0.015**	**Aug. 2009**	**0.049**
					Nov. 2009	0.081
					Jan. 2010	0.336
					Jun. 2010	0.164
					Aug. 2010	**0.010**
		Biomass (g m^{-2})	treatment × time	0.263		
			treatment	**0.007**		
	10 to 20	Density (fish m^{-2})	treatment × time	0.455		
			treatment	0.765		
		Biomass (g m^{-2})	treatment × time	0.846		
			treatment	0.858		
	<10	Richness (# of spp.)	treatment × time	0.055		
			treatment	**0.022**		
		Evenness (*J*)	treatment × time	0.945		
			treatment	0.213		
		Diversity (*H'*)	treatment × time	0.516		
			treatment	0.161		
	10 to 20	Richness (# of spp.)	treatment × time	0.152		
			treatment	0.711		
		Evenness (*J*)	treatment × time	0.443		
			treatment	0.222		
		Diversity (*H'*)	treatment × time	0.964		
			treatment	0.288		

Table B.4 (Continued)

Group	Size class (cm TL)	Response variable (units)	Fixed effect	LRT p	Survey period	p
Herbivores	<10	Density (fish m^{-2})	treatment × time	0.097		
			treatment	0.213		
		Biomass (g m^{-2})	treatment × time	0.573		
			treatment	**0.044**		
	10 to 20	Density (fish m^{-2})	treatment × time	0.892		
			treatment	0.815		
		Biomass (g m^{-2})	treatment × time	0.841		
			treatment	0.735		
Piscivores	<10	Density (fish m^{-2})	**treatment × time**	**<0.001**	Aug. 2009	0.176
					Nov. 2009	0.955
					Jan. 2010	0.144
					Jun. 2010	0.064
					Aug. 2010	0.117
		Biomass (g m^{-2})	**treatment × time**	**<0.001**	Aug. 2009	0.090
					Nov. 2009	0.400
					Jan. 2010	0.296
					Jun. 2010	0.053
					Aug. 2010	**0.047**
	10 to 20	Density (fish m^{-2})	treatment × time	0.453		
			treatment	0.843		
		Biomass (g m^{-2})	treatment × time	0.097		
			treatment	0.452		

Table B.5 List of species of herbivores and piscivores in the two size classes that were observed on experimental reefs. Asterisks indicate that the species was observed in that size class, dashes indicate that it was not.

Group	Species	Small (<10 cm TL)	Medium (10 to 20 cm TL)
Herbivores	*Acanthurus bahianus*	*	*
	Acanthurus chirurgus	*	*
	Acanthurus coeruleus	*	*
	Cryptotomus roseus	*	-
	Kyphosus spp.	-	*
	Scarus coeruleus	*	-
	Scarus taeniopterus	*	*
	Scarus vetula	*	*
	Sparisoma atomarium	*	*
	Sparisoma aurofrenatum	*	*
	Sparisoma chrysopterum	*	*
	Sparisoma radians	*	-
	Sparisoma rubripinne	-	*
	Sparisoma viride	*	*
Piscivores	*Amblycirrhitus pinos*	*	-
	Aulostomus maculatus	-	*
	Bothus lunatus	*	*
	Cephalopholis cruentatus	*	*
	Cephalopholis fulva	*	*
	Epinephelus guttatus	*	*
	Epinephelus striatus	*	*
	Mycteroperca tigris	*	*
	Ocyurus chrysurus	*	*
	Scorpaenodes caribbaeus	*	-
	Scorpaena plumieri	*	-
	Serranus tigrinus	*	*
	Synodus spp.	*	*

Table B.6 Species specific effect-to-response ratios for density and biomass. HLD - LLD: mean lionfish effect on response, LLD: mean response on LLD reefs, Ratio: effect-to-response ratio (the 20 species with the largest effect-to response ratios are listed for each response).

Response	Species	HLD - LLD (fish m^{-2})	LLD (fish m^{-2})	Ratio
Density	*Acanthurus bahianus*	-0.00025	0.00025	-1.00000
	Apogon maculatus	-0.00050	0.00050	-1.00000
	Cosmocampus spp.	-0.00025	0.00025	-1.00000
	Equetus punctatus	-0.00025	0.00025	-1.00000
	Gobionellus saepepallens	-0.00075	0.00075	-1.00000
	Haemulon parra	-0.00025	0.00025	-1.00000
	Hypleurochilus bermudensis	-0.00075	0.00075	-1.00000
	Hypoplectrus spp.	-0.00475	0.00475	-1.00000
	Lutjanus apodus	-0.00225	0.00225	-1.00000
	Micrognathus ensenadae	-0.00025	0.00025	-1.00000
	Monacanthus tuckeri	-0.00125	0.00125	-1.00000
	Opistognathus macrognathus	-0.00050	0.00050	-1.00000
	Pseudupeneus maculatus	-0.00175	0.00175	-1.00000
	Scorpaenodes caribbaeus	-0.00025	0.00025	-1.00000
	Apogon binotatus	-0.00525	0.00550	-0.95455
	Cephalopholis cruentatus	-0.00375	0.00400	-0.93750
	Apogon townsendi	-0.00350	0.00375	-0.93333
	Scarus vetula	-0.00175	0.00200	-0.87500
	Halichoeres pictus	-0.10300	0.12400	-0.83065
	Malacoctenus triangulatus	-0.01825	0.02200	-0.82955
Biomass	*Cantherhines pullus*	-0.00239	0.00239	-1.00000
	Equetus punctatus	-0.00030	0.00030	-1.00000
	Gobionellus saepepallens	-0.00006	0.00006	-1.00000
	Haemulon album	-0.00051	0.00051	-1.00000
	Haemulon melanurum	-0.00067	0.00067	-1.00000
	Haemulon parra	-0.00068	0.00068	-1.00000
	Hemiemblemaria simulus	-0.00002	0.00002	-1.00000
	Hypleurochilus bermudensis	-0.00013	0.00013	-1.00000
	Liopropoma rubre	-0.00038	0.00038	-1.00000
	Lutjanus synagris	-0.00436	0.00436	-1.00000
	Monacanthus tuckeri	-0.00269	0.00269	-1.00000
	Mycteroperca tigris	-0.00003	0.00003	-1.00000
	Opistognathus macrognathus	-0.00055	0.00055	-1.00000
	Scorpaenodes caribbaeus	-0.00089	0.00089	-1.00000
	Apogon maculatus	-0.00088	0.00088	-0.99443
	Apogon binotatus	-0.00471	0.00478	-0.98610
	Apogon townsendi	-0.00151	0.00153	-0.98473
	Coryphopterus dicrus	-0.04566	0.04847	-0.94212
	Holocentrus adscensionis	-0.04698	0.05057	-0.92907

Table B.7 Species losses on HLD and LLD reefs over the course of the experiment. BL Reefs: number of reefs on which the species was present during the baseline survey, Reefs lost: number of those on which the species was absent during the final survey. Entries in bold disappeared from all reefs on which they were present during the baseline survey (i.e. these species were extirpated from all experimental reefs on which they were initially found).

HLD		
Species (n = 38)	BL Reefs	Reefs lost
Pseudupeneus maculatus	**3**	**3**
Stegastes adustus	5	2
Gramma loreto	4	2
Malacoctenus triangulatus	4	2
Paradiplogrammus bairdi	4	2
Bodianus rufus	3	2
Chromis multilineata	3	2
Microspathodon chrysurus	3	2
Acanthurus bahianus	**2**	**2**
Apogon townsendi	**2**	**2**
Halichoeres radiatus	5	1
Chromis cyanea	4	1
Coryphopterus dicrus	4	1
Halichoeres pictus	4	1
Holacanthus ciliaris	4	1
Abudefduf saxatilis	3	1
Clepticus parrae	2	1
Coryphopterus personatus/hyalinus	2	1
Cryptotomus roseus	2	1
Halichoeres poeyi	2	1
Labrisomus species	2	1
Malacoctenus boehlkei	2	1
Opistognathus aurifrons	2	1
Amblycirrhitus pinos	**1**	**1**
Apogon maculatus	**1**	**1**
Calamus calamus	**1**	**1**
Cephalopholis fulva	**1**	**1**
Chaetodon aculeatus	**1**	**1**
Cosmocampus albirostris	**1**	**1**
Equetus lanceolatus	**1**	**1**
***Haemulon* spp. (juvenile)**	**1**	**1**
Hemiemblemaria simulus	**1**	**1**
Mycteroperca tigris	**1**	**1**
Oxyurichthys stigmalophius	**1**	**1**
Paranthias furcifer	**1**	**1**
Rhinesomus triqueter	**1**	**1**
Starksia hassi	**1**	**1**
Xyrichtys splendens	**1**	**1**

LLD		
Species (n = 19)	BL Reefs	Reefs lost
Holocanthus tricolor	**2**	**2**
Coryphopterus glaucofraenum	5	1
Halichoeres bivittatus	5	1
Coryphopterus dicrus	4	1
Halichoeres pictus	4	1
Malacoctenus gilli	4	1
Stegastes adustus	4	1
Stegastes leucostictus	4	1
Stegastes planifrons	4	1
Sparisoma atomarium	3	1
Bodianus rufus	2	1
Elacatinus horsti	2	1
Paradiplogrammus bairdi	2	1
***Cosmocampus* spp.**	**1**	**1**
Equetus punctatus	**1**	**1**
***Haemulon* spp. (juvenile)**	**1**	**1**
***Labrisomus* spp.**	**1**	**1**
Malacoctenus macropus	**1**	**1**
Ocyurus chrysurus	**1**	**1**

Table B.8 Species gains on HLD and LLD reefs over the course of the experiment. Reefs gained: number of reefs on which the species was not initially present (baseline survey), but was present at the final survey.

HLD		LLD	
Species (n = 25)	Reefs gained	Species (n = 38)	Reefs gained
Holocentrus adscensionis	3	*Apogon binotatus*	3
Abudefduf saxatilis	2	*Holocentrus adscensionis*	3
Chaetodon striatus	2	*Lutjanus apodus*	3
Holocanthus tricolor	2	*Acanthurus chirurgus*	2
Ocyurus chrysurus	2	*Apogon townsendi*	2
Sargocentron coruscum	2	*Halichoeres poeyi*	2
Stegastes planifrons	2	*Holacanthus ciliaris*	2
Acanthurus coeruleus	1	*Mulloidichthys martinicus*	2
Canthigaster rostrata	1	*Ocyurus chrysurus*	2
Chaetodon sedentarius	1	*Priolepis hipoliti*	2
Diodon hystrix	1	*Sargocentron coruscum*	2
Elacatinus horsti	1	*Scarus vetula*	2
Epinephelus guttatus	1	*Abudefduf saxatilis*	1
Haemulon plumierii	1	*Acanthemblemaria aspera*	1
Haemulon sciurus	1	*Acanthurus bahianus*	1
Nes longus	1	*Acanthurus coeruleus*	1
Pomacanthus arcuatus	1	*Amblycirrhitus pinos*	1
Scarus taeniopterus	1	*Apogon maculatus*	1
Scarus vetula	1	*Bodianus rufus*	1
Scorpaena plumieri	1	*Chaetodon striatus*	1
Sparisoma atomarium	1	*Clepticus parrae*	1
Sparisoma chrysopterum	1	*Coryphopterus personatus/hyalinus*	1
Unknown goby species	1	*Cosmocampus* spp.	1
Unknown blenny species	1	*Cryptotomus roseus*	1
		Elacatinus horsti	1
		Haemulon plumierii	1
		Halichoeres radiatus	1
		Holocanthus tricolor	1
		Hypleurochilus bermudensis	1
		Malacoctenus boehlkei	1
		Malacoctenus gilli	1
		Monacanthus tuckeri	1
		Opistognathus aurifrons	1
		Pseudupeneus maculatus	1
		Scarus taeniopterus	1
		Scorpaenodes caribbaeus	1
		Synodus spp.	1
		Unknown blenny species	1

Table B.9 Estimates and significance tests for differences in response variables between reefs assigned to the two lionfish treatments at the baseline survey (before establishment of lionfish treatments).

Group	Size class (cm TL)	Response variable (units)	Estimated difference ± SEM	p
All species	<10	Density (fish m^{-2})	-0.04 ± 0.76	0.964
		Biomass (g m^{-2})	0.26 ± 1.05	0.812
	10 to 20	Density (fish m^{-2})	0.02 ± 0.13	0.883
		Biomass (g m^{-2})	3.65 ± 7.11	0.622
	<10	Richness (# of spp.)	0.27 ± 1.69	0.875
		Evenness (*J*)	0.00 ± 0.02	0.908
		Diversity (*H′*)	0.00 ± 0.07	0.972
	10 to 20	Richness (# of spp.)	-0.29 ±1.25	0.821
		Evenness (*J*)	0.00 ± 0.02	0.870
		Diversity (*H′*)	0.00 ± 0.14	0.998
Herbivores	<10	Density (fish m^{-2})	0.00 ± 0.09	0.942
		Biomass (g m^{-2})	0.01 ± 0.20	0.942
	10 to 20	Density (fish m^{-2})	-0.00 ± 0.02	0.953
		Biomass (g m^{-2})	-0.34 ± 1.45	0.821
Piscivores	<10	Density (fish m^{-2})	-0.02 ± 0.01	0.136
		Biomass (g m^{-2})	-0.06 ± 0.04	0.125
	10 to 20	Density (fish m^{-2})	-0.00 ± 0.01	0.871
		Biomass (g m^{-2})	-0.08 ± 0.50	0.879

Table B.10 Linear correlations of species-specific density of small fishes (<10 cm TL) with NMDS axes. Table includes species with absolute correlation values >0.3 for either axis, and is sorted in order of decreasing correlation with each axis. No species had a strong negative correlation with axis 1 and only one species had a strong negative correlation with axis 2.

Axis 1		Axis 2	
Species	Correlation	Species	Correlation
Sparisoma viride	0.629	*Thalassoma bifasciatum*	0.585
Scarus iserti	0.544	*Gramma loreto*	0.526
Acanthurus coeruleus	0.495	*Chromis cyanea*	0.505
Haemulon flavolineatum	0.444	*Elacatinus genie*	0.500
Haemulon plumierii	0.394	*Coryphopterus glaucofraenum*	0.499
Stegastes planifrons	0.377	*Coryphopterus dicrus*	0.464
Stegastes adustus	0.377	*Stegastes partitus*	0.393
Canthigaster rostrata	0.370	*Acanthemblemaria aspera*	0.391
Abudefduf saxatilis	0.348	*Malacoctenus triangulatus*	0.376
Halichoeres radiatus	0.342	*Coryphopterus personatus/hyalinus*	0.326
Stegastes leucostictus	0.341	*Halichoeres pictus*	0.318
		Scarus taeniopterus	0.317
		Stegastes variabilis	0.312
		Stegastes diencaeus	0.304
		Stegastes planifrons	0.302
		Halichoeres bivittatus	-0.609

Figure B.1 Satellite photographs of 8 of the 10 experimental reefs. Scale is approximately equal among the photos. Includes reef pairs 2 (a, b), 3 (c, d), 4 (e, f), and 5 (g, h). Reef pair 1 is not included because high resolution images were not available. Includes material © 2011 DigitalGlobe, Inc. ALL RIGHTS RESERVED.

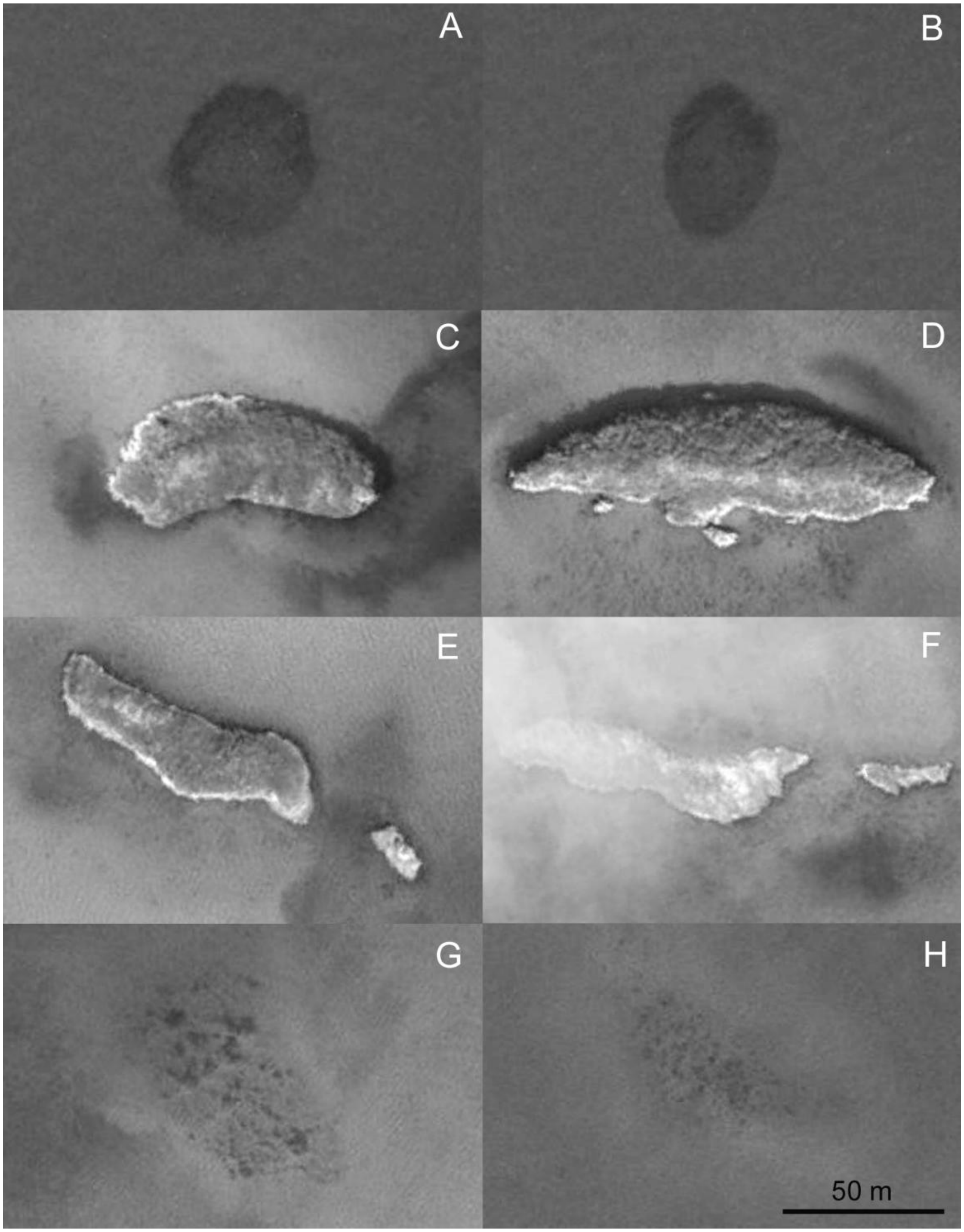

Figure B.1

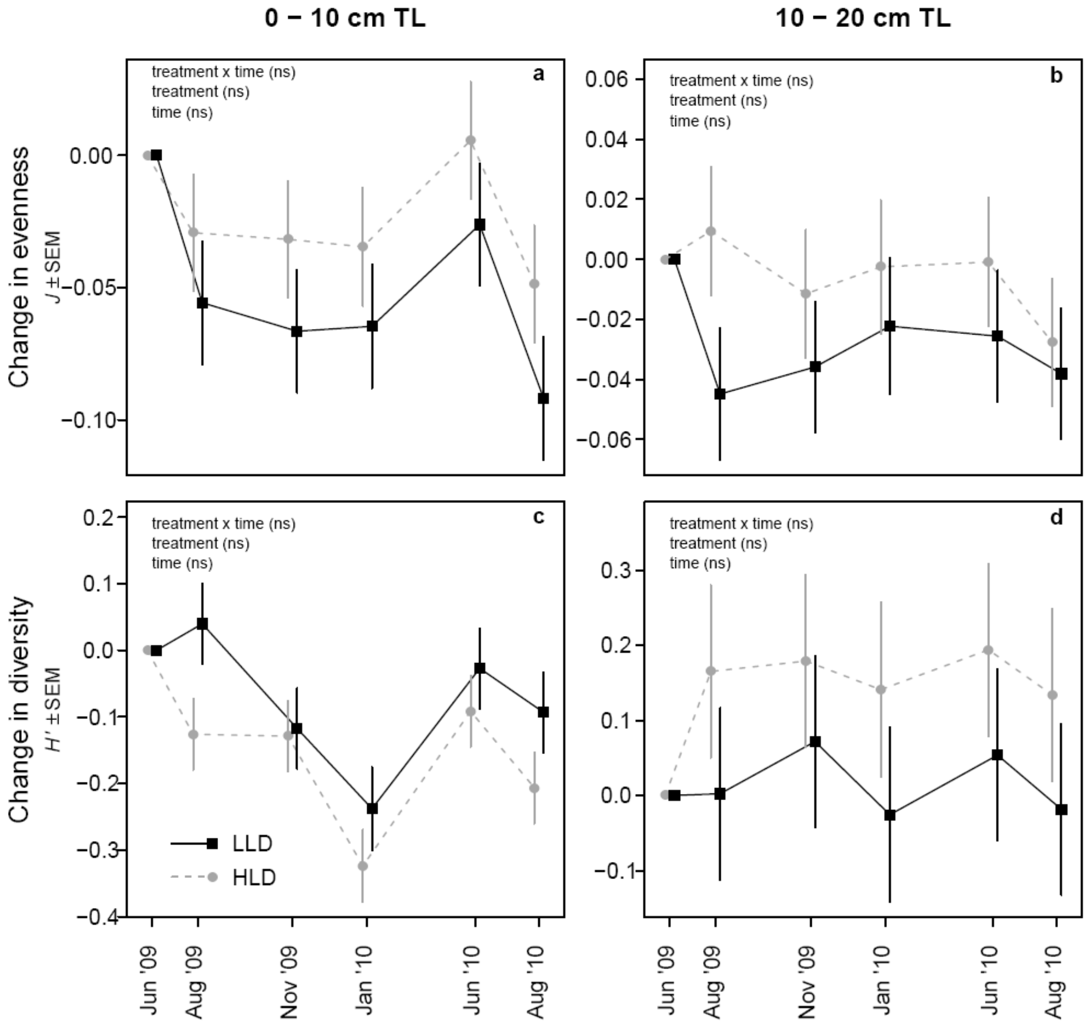

Figure B.2 Plots of change in evenness, Peilou's *J* (a, b), and change in diversity, Shannon-Wiener's *H'* (c, d) in the two size classes (<10 cm TL and 10 to 20 cm TL). The estimated values and SEMs around those estimates are from the full random and fixed effects models. Estimates for low-lionfish-density (LLD) reefs (n = 5) are depicted by black squares connected by solid lines, and those for high-lionfish-density (HLD) reefs (n = 5) are grey circles connected by dashed lines. Results of likelihood ratio tests for the fixed effects are shown at the top left of each panel (ns: p > 0.05, *p < 0.05, **p < 0.001, ***p < 0.0001). Note that y-axis scales for the two size classes are different, but the units are the same.

Figure B.3 Plots from a non-metric multidimensional scaling ordination of reef sub-samples in species space. The ordination was constructed using data from all survey periods and the panels depict the position of sub-samples in species space at each survey period. Minimum convex hull polygons have been drawn around sub-samples from each reef and numbers indicate reef pairs. Low-lionfish-density (LLD) reef sub-samples are indicated by black squares with solid lines, and high-lionfish-density (HLD) reef sub-samples are indicated by grey circles with dashed lines.

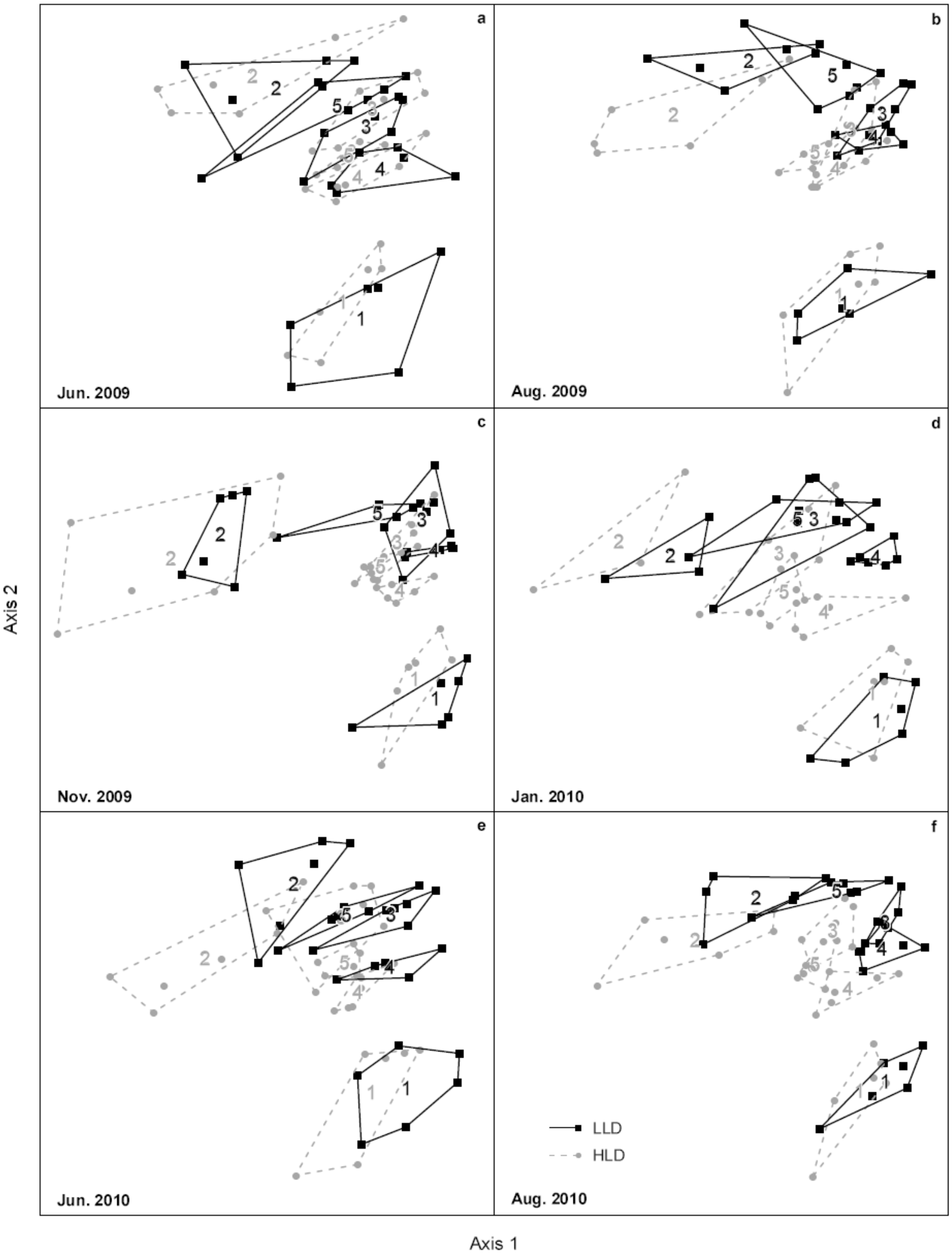
a
b
c
d
e
f
Jun. 2009
Aug. 2009
Nov. 2009
Jan. 2010
Jun. 2010
Aug. 2010
1
2
3
4
5
LLD
HLD
Axis 1
Axis 2

Figure B.3