



## AN ABSTRACT OF THE DISSERTATION OF

Tye L. Kindinger for the degree of Doctor of Philosophy in Zoology presented on June 13, 2016.

Title: Invasive Pacific Lionfish Alters Native Community Interactions on Atlantic Coral Reefs

Abstract approved: \_\_\_\_\_

Mark A. Hixon

Biological invasions have been identified as one of the prominent drivers of global environmental change. In particular, invasive predators typically have substantial negative effects on populations of native prey, even driving species to extinction in extreme cases. However, beyond direct predatory effects, little is understood regarding the specific mechanisms by which invasive predators influence native communities and ecosystems. Therefore, the objective of this dissertation was to investigate whether and how an invasive predator, the Pacific red lionfish (*Pterois volitans*), alters native community interactions on Atlantic coral reefs. The lionfish invasion is unprecedented for a marine fish in the extent of rapid geographical spread, successful establishment across numerous habitats, and strong predatory effects on native species. By conducting behavioral observations and manipulative experiments in both the laboratory and field settings, I tested for a variety of direct and indirect mechanisms by which invasive lionfish potentially influence native fish communities and coral-reef ecosystems.

I first conducted a model-bottle experiment in The Bahamas and Cayman Islands (Chapter 2) to test for aggression of a native territorial damselfish, *Stegastes planifrons*, toward

invasive lionfish. Such territoriality could provide a possible source of biotic resistance that may provide behavioral refugia for native coral-reef fish recruits from lionfish predation. However, the behavior of this damselfish in response to invasive lionfish in a clear plastic bottle did not differ from the minimal response exhibited toward the empty bottle control. Therefore, the territories of this damselfish are unlikely to provide such biotic resistance to the invasion.

To investigate whether invasive lionfish alter competition between native prey fishes, I then performed a manipulative field experiment in The Bahamas whereby I simultaneously tested for the effects of both competition and lionfish predation on two congeneric coral-reef fishes, the fairy and blackcap basslets (*Gramma loreto* and *G. melacara*, respectively). In the absence of invasive lionfish, competition within local populations of basslets under reef ledges had symmetrical effects on the juveniles of both species (Chapter 3). Interference between species drove juvenile basslets further back under ledges where feeding and growth rates of individuals were reduced. Within reefs with the invasive predator present (Chapter 4), lionfish reduced the density of juvenile fairy basslet, thereby reducing the effects of competition on juvenile blackcap basslet, and tipping the balance of competition between juveniles of these species from symmetrical to asymmetrical effects. Differential predation of invasive lionfish may be explained by a preference for fairy basslet, as demonstrated by a laboratory experiment (Chapter 5).

Lastly, I examined possible mechanisms underlying a potential invasive lionfish-herbivorous fishes-macroalgae trophic cascade on large reefs in The Bahamas (Chapter 6). During a two-year field experiment, lionfish caused a decline in the density of small herbivorous fishes on reefs, and behavioral observations revealed that the presence of lionfish reduced

grazing by both small and large fishes, which resulted in 66-80% less algae removed from reef substrata. Therefore, invasive lionfish have both consumptive and non-consumptive effects on the important ecosystem function of native herbivorous fishes: reducing the abundance of benthic algae that could otherwise displace corals.

In sum, this dissertation indicates that throughout native coral reefs, invasive lionfish (1) are not attacked by native territorial damselfish that could otherwise provide local refugia for native recruit fishes; (2) alter the outcome of interspecific competition between native basslets via differential predation that tips the balance of competition from symmetrical to asymmetrical; and (3) have both consumptive and non-consumptive effects on native herbivorous fishes, which reduces grazing and indirectly benefits benthic macroalgae to the possible detriment of corals. This research broadens our mechanistic understanding of predation in the context of invasive species, which further informs predictions relevant for management and conservation initiatives.

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Invasive Pacific Lionfish Alters Native Community Interactions on Atlantic Coral Reefs

by  
Tye L. Kindinger

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APPROVED:

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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.

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Tye L. Kindinger, Author

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First and foremost, I thank my advisor, Mark Hixon, for his guidance, support, and dedication to my development as an academic. I am fortunate to have a mentor who shares in my sincere love for the ocean, and who also feels at home when underwater. This passion was especially evident whenever we overlapped in the field, when I appreciated Mark's contagious excitement the most. He has been a personal inspiration to me as an active member in the academic community, where he simultaneously excels in teaching, research, storytelling, and public service. By fostering an environment that promotes rigorous activity in an engaging and encouraging manner, Mark has greatly enhanced my abilities as a scientist, field researcher, scientific communicator, and especially as a writer, for which I am truly grateful.

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manuscript. As a post-graduate, Eric Dilley helped me catch basslets and lionfish in order to set up my competition-predation experiment.

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## CONTRIBUTION OF AUTHORS

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# **Invasive Pacific Lionfish Alters Native Community Interactions on Atlantic Coral Reefs**

## Chapter 1 – General Introduction

As humans continue to induce environmental change and threaten biodiversity at a global scale (Vitousek et al. 1997, Pereira et al. 2010, 2012, Hautier et al. 2015), accurately predicting the response of progressively-altered ecosystems is of ever-increasing importance. Biological invasions have been identified as one of the prominent drivers of ecological change (Vitousek et al. 1997, Sala et al. 2000, Nelson et al. 2006), given that invasions can displace native species, cause local extinctions, alter community structure and food webs, and disrupt ecosystem processes (Vitousek et al. 1996, Mack et al. 2000, Mooney 2005, Simberloff 2013).

Invasive predators typically have stronger effects on prey than their native counterparts (Salo et al. 2007, Paolucci et al. 2013), and often cause large declines in native species (Grosholz 2002, Snyder & Evans 2006, Pitt & Witmer 2007, Cucherousset & Olden 2011, Gallardo et al. 2016) that can reach the point of extirpation or even global extinction in extreme cases (Clavero & García-Berthou 2005, Medina et al. 2011, Pringle 2011, Woinarski et al. 2015). However, beyond these simple (yet substantial) direct reductions in native species, little is understood about the mechanistic ability of invasive predators to influence native communities and ecosystems indirectly (Parker et al. 1999, White et al. 2006, Ehrenfeld 2010, Simberloff 2011, Ricciardi et al. 2013). *The objective of my dissertation is to investigate how an invasive predator, the Pacific red lionfish, alters native community interactions throughout Atlantic coral reefs.*

The invasion of the tropical and subtropical western Atlantic by Pacific red lionfish (*Pterois volitans*) is unprecedented for a marine fish in the extent of rapid geographical spread, successful establishment across numerous habitats, and strong predatory effects on native species (Côté et al. 2013a, Albins & Hixon 2013). Since the early 2000s, lionfish have undergone a



widespread invasion, with established populations currently ranging from the waters of North Carolina to Brazil, including the Gulf of Mexico (Schofield 2009, 2010, Ferreira et al. 2015). Lionfish are considered to be habitat generalists, having been observed in temperate hard-bottom reefs (Whitfield et al. 2007), tropical coral reefs (Green & Côté 2009, Biggs & Olden 2011, Lesser & Slattey 2011), seagrass beds (Claydon et al. 2012), mangroves (Barbour et al. 2010), and man-made structures (Smith 2010). Lionfish also are found across an expansive depth range from shallow waters through depths of over 300 m (Albins and Hixon 2013), and they have a broad salinity tolerance (Jud et al. 2015), which likely enables individuals to colonize brackish habitats, such as river estuaries (Jud et al. 2011, Jud & Layman 2012).

Invasive lionfish are especially found on coral reefs in high densities (Green & Côté 2009, Kulbicki et al. 2012) where they are novel predators, both in their appearance (striped patterning and morphology) which differs from that of all other Atlantic fishes and in their use of unique hunting strategies, including herding prey with widely-fanned pectoral fins (Côté & Maljković 2010, Green et al. 2011, Cure et al. 2012) and blowing directed jets of water at prey (Albins & Lyons 2012). As generalist predators, invasive lionfish consume an extensive variety of small native fishes (Morris & Akins 2009, Muñoz et al. 2011, Côté et al. 2013b), resulting in substantial reductions in the abundance of native prey that scale-up from smaller patch reefs (Albins & Hixon 2008, Albins 2013, Green et al. 2014, Benkwitt 2015) to large coral reefs (Albins 2015).

With such large consumptive effects, lionfish likely alter interactions between and among native species. By conducting behavioral observations and manipulative experiments in both the laboratory and field settings, I tested for direct and indirect mechanisms by which invasive lionfish potentially influence native communities and ecosystems. This dissertation consists of

four stand-alone manuscripts and one short note that are currently either published or in various stages of the peer-review publication process in scientific journals.

Chapter 2, “Behavioral response of native Atlantic territorial three spot damselfish (*Stegastes planifrons*) toward invasive Pacific red lionfish (*Pterois volitans*)”, is published in *Environmental Biology of Fishes* (2015, 98:487-498). I tested for aggression of this native territorial damselfish toward invasive lionfish as a possible source of biotic resistance that may indirectly provide refugia for native coral-reef fish recruits from lionfish predation. I conducted a field experiment in The Bahamas and Cayman Islands using a model-bottle design, which is a method that was developed for examining specifically threespot damselfish behavior (Myrberg & Thresher 1974). I compared the behavioral response of damselfish in the presence of invasive lionfish versus three native fishes, which were all presented individually in clear plastic bottles, as well as an empty bottle control.

The next three chapters consist of laboratory and field experiments that I conducted in Eleuthera, The Bahamas to determine whether invasive lionfish alters interspecific competition between native reef fishes. Together, Chapters 3 and 4 report the results of a single manipulative field experiment that I conducted to simultaneously test for the individual and/or interactive effects of native interspecific competition and invasive predation on two native coral-reef fishes. Chapter 3, “Symmetrical effects of interspecific competition on congeneric coral-reef fishes” is currently in revision in *Marine Ecology Progress Series*, and describes a study in which I tested for the existence and mechanisms of interspecific competition on the distribution and demographic parameters of native fairy and blackcap basslets (*Gramma loreto* and *G. melacara*, respectively). Throughout Caribbean reefs, basslets are segregated by depth with a narrow zone of overlap. Local populations of these fishes are found under isolated reef ledges, where fairy

basslet is known to compete intraspecifically for access to prime feeding positions at the outer edges (Webster and Hixon 2000, Webster 2004). I investigated the existence, mechanisms, and effects of interspecific competition on the local distribution and demography of basslets. I documented aggression and feeding rates of both species and conducted a manipulative experiment comparing the response of each species in competitor-removal versus unmanipulated populations of co-occurring basslets.

In addition to manipulating the presence of the potential competitor in local populations, I simultaneously manipulated the presence of invasive lionfish on reefs to investigate whether this invasive predator alters native competition between fairy and blackcap basslets. For eight weeks, I measured the change from baseline values in density and ledge position of each basslet species, and calculated the growth rates of juveniles after about a month using a standard mark-and-recapture method. Experimental populations of basslets were filmed at dusk using automated video cameras to quantify the behavior of lionfish overlapping with these focal populations. The outcome of this field experiment is described in Chapter 4, entitled “Invasive predator tips the balance of symmetrical competition between native coral-reef fishes”, and is currently in preparation for submission for publication.

Chapter 5, “Preference of invasive lionfish and native grouper between congeneric prey fishes”, is a short note that is currently in press in a special issue about the lionfish invasion in *Marine Ecology Progress Series*. This chapter consists of a controlled experiment in aquaria that was conducted with undergraduate mentee, Emily Anderson, to characterize the prey preference of invasive lionfish for native fairy and blackcap basslets. We also compared this preference with that of an ecologically-similar native mesopredator, the graysby grouper (*Cephalopholis cruentata*). We observed the hunting behavior of predators and counted the number of predatory

strikes that occurred in response to two individual prey consisting of cross-factored combinations of species (fairy and blackcap) and size (small and large).

Chapter 6, “Consumptive and non-consumptive effects of an invasive marine predator on native coral-reef herbivores”, is currently in revision for *Biological Invasions* and describes a field experiment performed with my former labmate, Mark Albins, near Lee Stocking Island, The Bahamas. We tested for both consumptive and non-consumptive effects of invasive lionfish on the density and grazing behavior (respectively) of native herbivorous fishes on coral reefs. To quantify consumptive effects of lionfish, we manipulated lionfish densities on large reefs and surveyed fish populations quarterly for two years. At the end of the experiment, the non-consumptive effects of lionfish were measured by observing fish grazing behavior on algal-covered substrata placed in microhabitats varying in lionfish presence at the reef and/or within-reef scales. From before-and-after photographs of substrata, we quantified any resulting algal loss from observed fish grazing.

This dissertation investigates a variety of mechanisms by which an invasive marine predator potentially alters native communities and ecosystems both directly and indirectly. Included are the first efforts to quantify the indirect effects of invasive lionfish, which typically is a neglected concept in studies of invasion biology (White et al. 2006). Overall, this series of studies broadens our understanding of predation in the context of invasive species, as well as the types of pathways underlying the substantial effects of biological invasions on native systems.

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**Chapter 2 – Behavioral response of native Atlantic territorial three spot damselfish  
(*Stegastes planifrons*) toward invasive Pacific red lionfish (*Pterois volitans*)**

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## ABSTRACT

The Pacific red lionfish (*Pterois volitans*) has been recognized as a top conservation issue in the world due to its ability as an invasive predator to greatly reduce recruitment of native reef fishes, and with potential long-term ecosystem-level effects. This study tested for territorial aggression of native threespot damselfish (*Stegastes planifrons*) toward invasive lionfish as a possible source of biotic resistance that may provide prey refugia for coral-reef fish recruits. Throughout July and August 2011, I conducted a field experiment in the Bahamas and the Cayman Islands using a model-bottle design specifically developed for examining threespot damselfish behavior. I compared the behavioral response of 40 damselfish to the presence of invasive lionfish and three native fishes presented individually in clear bottles, as well as to an empty bottle control. Despite lionfish having invaded these islands in different years, damselfish response did not differ between the Bahamas and the Cayman Islands. Overall, damselfish response toward invasive lionfish was not significantly different from the minimal response toward the empty bottle control. In contrast, damselfish actively responded to all native fishes, with species-specific behaviors and levels of aggression that depended on the ecological relationships between damselfish and intruding fishes. Differences in the seafloor rugosity of damselfish territories among study sites also appeared to influence damselfish response. The lack of damselfish response towards lionfish demonstrates that territories are unlikely to serve as native prey refugia, and may indicate lack of recognition of this invasive predator compared to native predators.

## 2.1 INTRODUCTION

Biological invasions can have severe ecological consequences on native ecosystems and associated socioeconomic repercussions by reducing biodiversity, altering community structure, and disrupting ecosystem function (Ruiz et al. 1997, Bax et al. 2003). As the number of marine invasions increases at an accelerating rate (Cohen & Carlton 1998, Rilov & Crooks 2008), eradication strategies for established invasive species remain poorly developed, and so far, largely ineffective (Thresher & Kuris 2004). Therefore, it is important to identify and understand any natural mechanisms of biotic resistance that effectively limit local populations of invasive species.

The range expansion of an invasive marine fish has never progressed as rapidly as that of the Pacific red lionfish (*Pterois volitans*) throughout the coral reefs of the tropical western Atlantic and Caribbean (Schofield 2009, 2010). Invasive lionfish occur in high densities (Green & Côté 2009, Kulbicki et al. 2012), with recent evidence suggesting that maximum densities have yet to be reached (Benkwitt 2013). These highly efficient predators (Côté & Maljković 2010) can greatly reduce recruitment of native reef fishes (Albins & Hixon 2008, Green et al. 2012, Albins 2013), including the juveniles of species known to be important for both reef resilience and local fisheries (Morris & Akins 2009). With concerns for potential long-term effects on invaded reefs, both direct and indirect (Albins & Hixon 2013), the lionfish invasion has been recognized as one of the top conservation issues in the world (Sutherland et al. 2010).

Lionfish management efforts have been restricted to local control via removals on targeted shallow reefs (Morris & Whitfield 2009, Akins 2012, Frazer et al. 2012, Albins & Hixon 2013), even though the geographic distribution of this invader includes a broad variety of habitats (Whitfield et al. 2007, Barbour et al. 2010, Lesser & Slattery 2011, Claydon et al. 2012,

Jud & Layman 2012) and an extensive depth range reaching over 300 m (Gilmore pers comm). Various models have indicated that manual removal efforts must remain intense and necessitates long-term commitment to effectively reduce adult lionfish densities, which further limits control mostly to small, localized areas (Morris et al. 2009, Barbour et al. 2011, Arias-González et al. 2011). Green et al. (2013) demonstrated that maintaining lionfish at targeted densities on small patch reefs can be achieved with monthly lionfish removals, which were effective at mitigating lionfish predation effects on native fish communities. In order to ameliorate the effects of invasive lionfish at a broader scale, however, feasible sources of biotic resistance by native Atlantic species must be identified and promoted.

Native communities can provide biotic resistance (sensu Elton 1958), thereby preventing establishment and spread of an invasive species via predation, competition, parasites, and/or disease (Sakai et al. 2001, Levine et al. 2004). Unfortunately, there have been no reports of lionfish disease in either the invaded nor native waters, and invasive lionfish exhibit low infection levels of endo- and ecto-parasites (Tuttle *in prep*, Morris et al. 2009). Albins (2013) found evidence of an ecologically similar native predator unable to effectively limit invasive lionfish via competition. There is currently substantial debate regarding the extent to which native groupers control the abundance of invasive lionfish (Mumby et al. 2011, 2013, Bruno 2013, Hackerott et al. 2013, Bruno et al. 2013, Valdivia et al. 2014), yet there has been only one report of large native groupers containing lionfish in their stomachs (Maljković et al. 2008). The only study to date indicating that native grouper may limit invasive lionfish suggests that native Nassau grouper (*Epinephelus striatus*) displace lionfish foraging off of small patch reefs (Pusack 2013). Unfortunately, Nassau grouper are currently listed as an endangered fish by IUCN (Albins et al. 2009), and like most large predators, is severely overfished regionally (Sadovy &

Eklund 1999, Stallings 2009). Native predators, including sharks, groupers, and moray eels, have been observed consuming injured and/or dead lionfish that had been speared (Jud et al. 2011, Pimiento et al. 2013, Kindinger *pers. obs.*), and Diller et al. (2014) conditioned large predators to consume tethered lionfish. However, all of these instances were limited in that they required human interaction.

I investigated another possible source of biotic resistance to the invasion: interspecific aggression by the native threespot damselfish (*Stegastes planifrons*). In general, interspecific aggression has typically been tested in the context of explaining behavioral mechanisms underlying an invader's success, and few studies have tested specifically for interspecific aggression of a native species as an effective source of biotic resistance against an invader. Blight et al. (2010) found a dominant native ant in the Mediterranean capable of decreasing invasion success of Argentine ants through aggressive interactions. Native ant assemblages in Northwest Patagonia were documented attacking an invasive wasp competing for food sources by aggressively biting the wasp's legs (Masciocchi et al. 2010). Eastern mosquitofish native to Florida's freshwater habitats attacked and killed two non-indigenous fishes in a mesocosm experiment (Thompson et al. 2012). Observations of invasive lionfish and stomach content analyses reveal lionfish hunt and consume several species of native damselfishes (Morris & Akins 2009, Green et al. 2011, Cure et al. 2012, Layman & Allgeier 2012, Valdez-Moreno et al. 2012, Côté et al. 2013). Despite having seen invasive lionfish hunting threespot damselfish (Kindinger *pers obs*), there is yet to be any reports of this damselfish as lionfish prey.

Studies throughout their range have shown threespot damselfish to be abundant and highly aggressive toward both conspecifics and heterospecifics (including potential predators) (Myrberg & Thresher 1974, Robertson et al. 1976, Kaufman 1977, Williams 1978, 1980,

Knowlton et al. 1990), and this species is the competitive dominant within its ecological guild (Robertson 1996). In addition, the threespot damselfish effectively excludes certain species from their guarded territories (Kaufman 1977, Williams 1980, Knowlton et al. 1990). As a species of farming damselfishes (Family Pomacentridae, genus *Stegastes*), aggression by threespot damselfish fosters the growth of filamentous turfs of algae which serve as a source of food, shelter from predators, and a nesting site (Myrberg & Thresher 1974, Thresher 1976, Robertson et al. 1981). Importantly, an ecologically similar damselfish in the Pacific has been shown to indirectly provide prey refugia for small recruit fishes by excluding predators from their territories (Green 1992). If this phenomenon occurs in the Atlantic, then territorial damselfish could perhaps provide refugia from invasive lionfish predation for native reef fish recruits until they reach relatively invulnerable body sizes.

In order to assess the potential of threespot damselfish providing refugia, I used a model-bottle study design whereby invasive lionfish and native fishes were presented in clear bottles to threespot damselfish at set distances from damselfish territories (Myrberg & Thresher 1974). This method allows for the comparison of threespot damselfish behavior towards various intruding fishes. In order to address my main objective of determining at what level -- if at all -- threespot damselfish are aggressive towards a novel predator. I addressed the following questions: (1) Do threespot damselfish exhibit a behavioral response when invasive lionfish are present? (2) How do threespot damselfish respond to the presence of invasive lionfish compared to the empty bottle control? (3) Do threespot damselfish differ in their response toward invasive lionfish and three native fish species, especially an ecologically-similar predatory grouper?

## 2.2 METHODS

### 2.2.1 Area of study and microhabitat assessment

I conducted this study during July-August 2011, observing the behavioral response of 40 threespot damselfish: 20 in the Bahamas and 20 in the Cayman Islands. In addition to enhancing the generality of the study, I chose to observe damselfish in these two locations because of their difference in timing of the lionfish invasion: lionfish were first sighted in the Bahamas in 2004 and in the Cayman Islands in 2008 (Schofield 2009). In the Bahamas, I studied damselfish at three sites in the shallow waters (sites were <4 m deep) of the Great Bahama Bank in the vicinity of Lee Stocking Island, which is part of the Exuma Cays. Study sites consisted of patch reefs composed of small coral heads and larger coral bommies surrounded by sand and seagrass beds. About 380 miles Southwest of Lee Stocking Island, I observed damselfish behavior off of Little Cayman Island at three deeper sites (6-12 m deep) located along the northern side of the island, just inshore of the Bloody Bay Wall. This area is characterized by continuous stretches of reef that includes coral heads of various sizes and large coral formations.

The benthic territories maintained year-round by threespot damselfish are less than 1 m<sup>2</sup> and are easily identified by the algal gardens covering reef substrata that the damselfish cultivate (Brawley & Adey 1977). The underlying substrata of damselfish territories differed at sites both within and between the Bahamas and Cayman Islands. Since the type of habitat could potentially affect damselfish response by influencing an individual's ability to defend its territory, I characterized the microhabitat of each damselfish territory by recording the following four habitat categories: (1) low-relief dead coral rubble (mostly *Acropora cervicornis*), (2) low-relief continuous reef, (3) high-relief large coral bommies, and (4) high-relief continuous reef. Low-relief habitats lacked vertical structure, whereas high-relief habitats consisted of vertical



structure >1 m high, which could potentially interfere with the ability of damselfish to detect intruders.

### 2.2.2 *Experimental treatments and fish capture*

Each threespot damselfish was exposed to a series of treatments consisting of a single individual of (1) invasive lionfish, or the following native fishes, all of which are commonly found on reefs near threespot damselfish territories and are chased at varying degrees by damselfish (Thresher 1976, Robertson 1984): (2) herbivorous ocean surgeonfish (*Acanthurus bahianus*), a potential food competitor; (3) white grunt (*Haemulon plumieri*), a potential egg predator; and (4) coney grouper (*Cephalopholis fulva*), a mesopredator ecologically similar to lionfish and at larger sizes is a potential predator of threespot damselfish. At both study regions, I captured 2-3 individuals per fish species, which were rotated daily for experimental use based on each individual's appearance, apparent condition, and behavior. All fish were caught underwater from non-study sites using hand nets and the fish anesthetic quinaldine when needed. Body size of individual fish, ranging from 10 to 18 cm TL, was restricted to allow for ease of movement in bottles during the experiment. At these sizes, both lionfish and coney grouper were sufficiently large to pose a threat to small recruit fishes inhabiting damselfish territories (Albins 2013). Fish were maintained in flow-through aquarium tanks both prior to and between daily observational trials.

### 2.2.3 *Model-bottle experiment*

Using a model-bottle study design (Myrberg & Thresher 1974), I presented individual fish in weighted, clear-plastic gallon bottles to haphazardly located adult damselfish (7-11 cm total length [TL]) in order to measure the relative behavioral responses exhibited by each focal

damselfish. Bottle lids were replaced with secured mesh screening to allow for flow of both water and any fish chemical cues. An empty bottle was used as a control treatment. I introduced each treatment in random order to individual damselfish territories. All fishes inside bottles were either resting or hovering upon introduction.

To measure damselfish aggression per treatment, each bottle was sequentially placed at 100, 50, and 0 cm away from the center of each territory (Figure 2.1). At each increment, I observed damselfish behavior from a distance of 3 m for 2 minutes, counting the number of times the focal damselfish made physical contact with the bottle (attack rate) and tallying which aggressive behaviors each damselfish displayed: (1) contact with the mouth while hovering in place directly next to the bottle (nip); (2) contact with the caudal fin while hovering in place directly next to the bottle (butt); (3) starting from a distance, swimming with force directly towards the bottle, making contact with mouth, and then quickly swimming away from the bottle (charge); and, (4) repeatedly charging the bottle multiple times (continuous attack). These categories encompass threespot damselfish behavior known to effectively exclude intruders (Thresher 1976). I also looked for avoidance behavior by damselfish, such as entering refuge sites within their territories (Helfman 1989).

I then returned the bottle to the closest distance to the territory at which the damselfish had previously made no physical contact with the bottle, then gradually moved the bottle closer to the center of the territory until the damselfish approached the bottle and made physical contact. If the damselfish had previously attacked the bottle at 100 cm away from the territory, I placed the bottle at 150 cm where all damselfish ceased attacking the bottle, and gradually moved the bottle closer to the territory from there. This method provided a measurement of the “maximum distance of attack” (sensu Myrberg & Thresher 1974) per treatment.

#### 2.2.4 Statistical analyses

All assumptions of normality and homogeneity of variance were not met based on residual analyses, and transformations failed to normalize the data. To test for a difference in damselfish response between the Bahamas and the Cayman Islands, I used nonparametric Wilcoxon signed-rank tests for repeated measurements of the attack rate and maximum distance of attack. Binary counts of whether individual damselfish attacked each treatment or not when placed inside damselfish territories (distance of 0 cm) were also compared between the two study regions using McNemar's test. Results from all tests revealed that damselfish response did not significantly differ between regions for all three response variables measured: (1) attack rate (Wilcoxon signed-rank test,  $n=40$ ,  $V=5857$ ,  $P=0.1121$ ); (2) maximum distance of attack (Wilcoxon signed-rank test,  $n=40$ ,  $V=1702$ ,  $P=0.0902$ ); and, (3) number of damselfish that attacked (McNemar's test,  $n=40$ ,  $\chi^2=0.2273$ ,  $P=0.6336$ ). Damselfish from both locations were thus combined during all subsequent statistical analyses.

With the exception of the surgeonfish treatment, there was no discernable difference in damselfish attack rates among treatments until bottles were placed directly in the center of damselfish territories (Fig. A.1), so I compared the number of damselfish that attacked and the attack rate in response to each treatment measured only at this 0 cm distance. The proportion of damselfish (out of 40 individuals) that attacked each treatment were compared using a nonparametric Cochran's Q test. I rank-transformed the attack rate and maximum distance of attack, and then tested for differences in response among treatments and among microhabitats of damselfish territories by performing one-way repeated measures analyses of variance (ANOVAs). Results from these ANOVAs were compared with the results from Friedman tests, and were found to provide consistent conclusions. Therefore, I report only results from the one-

way repeated measures ANOVA, because this provides a more robust analysis with greater statistical power compared to the Friedman test (Zimmerman & Zumbo 1993).

In addition, I performed post-hoc pairwise comparisons of all three response variables among treatments and among microhabitats (when applicable) with Wilcoxon signed-rank tests. Reported p-values from these multiple comparisons were corrected using Holm's adjustment method, which does not assume independence of groups when controlling the family-wise error rate (Holm 1979). All statistical tests were conducted using the statistical software *R* version 3.0.0 (*R* Core Team 2014) with the associated packages, *car* (Fox et al. 2009), *nlme* (Pinheiro & Bates 2000) and *RVAideMemoire* (Hervé 2014).

## 2.3 RESULTS

Treatment had a significant effect on all damselfish response variables: (1) proportion of damselfish that attacked (Fig. 2.2, Cochran's Q test,  $n=40$ ,  $Q_4=72.7917$ ,  $P<0.0001$ ); (2) attack rate (Fig. 2.3, repeated measures ANOVA,  $n=40$ ,  $F_4=89.1661$ ,  $P>0.0001$ ); and (3) maximum distance of attack (Fig. 2.3, repeated measures ANOVA,  $n=40$ ,  $F_4=68.3478$ ,  $P<0.0001$ ). Post-hoc pairwise Wilcoxon signed-rank tests of all three variables revealed that damselfish response did not significantly differ between the empty-bottle control and invasive lionfish treatment (proportion of damselfish,  $P=1.0000$ ; attack rate,  $P=0.7296$ ; maximum distance of attack,  $P=0.2814$ ), which were significantly lower levels of damselfish response than those exhibited towards the native fish treatments ( $P<0.05$ ), including the ecologically-similar coney grouper. Damselfish response towards the native fishes remained consistent among all three variables, with a general trend of significantly increasing levels of response (pairwise Wilcoxon signed-

rank tests,  $P < 0.05$ ) towards the grouper, grunt, and surgeonfish treatments, respectively (Figs. 2.2 and 2.3).

Only nine out of the 40 threespot damselfish attacked the empty-bottle control, and similarly, only 10 damselfish attacked the invasive lionfish treatment (Fig. 2.2). Five of these damselfish attacked every treatment, which suggests these may have been individuals with higher levels of aggression. When bottles were placed directly in the center of territories, damselfish never made physical contact with the empty-bottle control nor invasive lionfish treatment more than 10 times within the two-minute observation period. Individual damselfish attacked the grouper, grunt, and surgeonfish treatments as many as 45, 59, and 100 times, respectively, all within two minutes. The furthest distance damselfish attacked the empty-bottle control was 30 cm away from their territories, whereas the maximum distance damselfish attacked invasive lionfish was 50 cm. In contrast, damselfish attacked all native fishes at distances over 50 cm, with damselfish attacking the coney grouper up to 70 cm away. The greatest distance an individual damselfish attacked any fish was 110 cm away from its territory in response to a surgeonfish.

Damselfish displayed only two aggressive behaviors in response to the empty-bottle control and the invasive lionfish treatment, but responded to the native fish treatments with all four aggressive behaviors (Fig. 2.4). The majority of damselfish showed no response to the empty-bottle control and the invasive lionfish treatment, and the individuals that did respond used mostly nips, with only one instance each of a damselfish continuously attacking the empty bottle control and charging the invasive lionfish treatment. This nip behavior was commonly observed in response to all fishes, whereas damselfish continuously attacked only the grunt and

the surgeonfish, and most often butted the coney grouper. Avoidance behavior by damselfish was not observed during any experimental trials.

In the Bahamas, the microhabitat of observed damselfish territories consisted of low-relief dead coral rubble (n=11) and high-relief large coral bommies (n=9), whereas in the Cayman Islands, damselfish territories were observed on high- and low-relief continuous reef (n=13 and 7, respectively). The type of microhabitat where damselfish territories were located had a moderate effect on overall damselfish response (repeated measures ANOVAs: attack rate, n=40,  $F_3=3.3797$ ,  $P=0.0286$ ; maximum distance of attack, n=40,  $F_3=3.1672$ ,  $P=0.036$ ). Damselfish on high-relief continuous reef attacked treatments both at distances closer to their territories and with lower attack rates than damselfish observed on low-relief dead coral rubble (pairwise Wilcoxon signed-rank tests: attack rate,  $P=0.035$ ; maximum distance of attack,  $P=0.042$ ), and this pattern in damselfish response remained consistent across all native fish treatments (Fig. A.2).

## 2.4 DISCUSSION

One likely explanation for a native species lacking an effective behavioral response to an invasive predator is prey naïveté (Diamond & Case 1986, Freeman & Byers 2006, Cox & Lima 2006). Such naïveté may result in a native species failing to recognize predation threats, having an inappropriate antipredator response, or having an appropriate response, but one that is ineffective (Banks & Dickman 2007). In this study, threespot damselfish showed minimal behavioral response to the presence of invasive lionfish that was most similar to the response elicited by an inanimate object, the empty bottle. Damselfish responded to all native fishes with species-specific levels of aggression that were consistent with previous behavioral studies of this

species (Myrberg & Thresher 1974, Thresher 1976). In particular, the level of aggression and variety of aggressive behaviors displayed by damselfish toward the native predator (coney grouper) were consistently greater than those elicited by invasive lionfish, which suggests that damselfish are unable to recognize lionfish as a potential predator.

Helfman (1989) determined that threespot damselfish respond to predators with a variety of avoidance behaviors, and the orientation and size of predators affect the level of threat perceived by individual damselfish. The coney grouper and lionfish used in this study were never oriented in any hunting postures inside the bottles. In addition, the sizes of coney grouper were never large enough to effectively consume adult damselfish, which could explain the lack of damselfish avoidance behaviors in response to this native predator. Regardless, damselfish still responded with aggression towards coney grouper. Similarly-sized coney and graysby (*Cephalopholis cruentatus*) groupers were often observed swimming through the underlying habitats of damselfish territories, especially in areas of dead coral rubble, so perhaps these small groupers pose a competitive threat to damselfish shelter.

While the “nip” behavior seemed to be a general response by threespot damselfish, they used a “butting” behavior toward coney grouper more so than towards any other species, whereby they made physical contact with the bottle using only the caudal fin. In contrast, damselfish continuously attacked the native grunt and surgeonfish, which resulted in damselfish remaining in close contact with the bottle while performing continuous series of head-first charges. Perhaps damselfish are relatively cautious when warding off a potential predator by limiting physical contact with the predator and resorting to butting attacks with the caudal fin rather than the head.

Invasive lionfish are capable of consuming prey as large as about 50% of their body length (Morris & Akins 2009), so some of the lionfish used in this study were large enough to consume some of the observed threespot damselfish. Despite the potential benefit for damselfish to perceive lionfish as a predatory threat, no avoidance behaviors were displayed, and in contrast to the coney grouper, damselfish never used the butting behavior towards lionfish. Lionfish hunting within and around damselfish territories could also be perceived as a general intrusion to damselfish, such as when threespot damselfish attack intruding divers (Helfman 1989, Kindinger pers. obs.), yet damselfish consistently exhibited minimal response toward lionfish.

The cue similarity hypothesis highlights the importance of comparing cues between native and non-native predators, and understanding whether prey use general versus specific cues while assessing risk during detection and recognition of predators (Sih et al. 2010). Both the appearance and behavior of lionfish are unique compared to native predators in the Atlantic. Lionfish have cryptic coloration and striped patterning, with elongated fin rays that have been postulated to enhance mimicry and/or camouflage (Albins & Hixon 2013). The hunting behaviors of lionfish are described as a slow stalking of prey and use of fanlike pectoral fins for herding prey (e.g., Randall 2005, Green et al. 2011, Cure et al. 2012), as well as a unique blowing behavior, whereby lionfish aim jets of water at prey, which apparently increases the probability of head-first capture (Albins & Lyons 2012). It seems plausible that invasive lionfish and native predators provide dissimilar cues to potential prey.

Native species can learn to recognize novel predators (Payne et al. 2004, Carlsson et al. 2009) and there is evidence of some fishes having learned predator recognition and antipredator response (Kelley & Magurran 2003). Marsh-Hunkin et al. (2013) reported that native gobies in the Bahamas recognize and respond to invasive lionfish cues. This discrepancy in findings with



threespot damselfish may be explained by potential differences in the relative use of general versus species-specific cues between Atlantic damselfishes and gobies. General cues include chemicals (Sih et al. 2010), as well as the visual cue of any moving organism or object that is larger than a minimum size threshold (Dill 1974, Sih 1986).

Native prey are also expected to shift towards adaptive antipredator behavior either through evolutionary time (Strauss et al. 2006, Losos et al. 2006) or through ecological time within a generation (Berger et al. 2001, Caro 2005). Even though invasive lionfish have been established in the Bahamas years longer than populations in the Cayman Islands (Schofield 2009), I found no evidence of a shift in threespot damselfish behavior towards this invasive predator. Since lionfish have been observed hunting threespot damselfish (Kindinger pers obs), perhaps with continued overlap in distribution over larger temporal scales threespot damselfish will eventually respond to lionfish. However, a native Pacific damselfish presumed to share an evolutionary history with red lionfish failed to react to both visual and chemical lionfish cues, even once conditioned to those specific cues (Lönnstedt & McCormick 2013). Further study is needed to enhance our understanding of lionfish recognition by prey fishes in general, and to help elucidate how the behavior and ecology of native fishes will eventually change in response to the lionfish invasion.

Threespot damselfish response varied depending on the microhabitat in which their territories occurred. If there is potential for this damselfish to provide prey refugia from any predators, it may be that this phenomenon is context-dependent on local habitat characteristics. In this study, reef formations that damselfish used as substrate for their algal gardens on high-relief continuous reef consisted mostly of tall (>1 m) isolated structure, which generated a vertical component into the total guarded area and often appeared to be a visual obstruction for

detecting intruders. As a result, it required relatively more time for some damselfish to encounter fish in model bottles placed near their territories. All other types of observed microhabitat consisted of damselfish territories with vantage points containing fewer visual obstructions, especially territories located on dead coral rubble, which had the lowest rugosity.

Threespot damselfish behavior had not been assessed since the invasion of lionfish throughout the Atlantic Ocean. Here, I have determined that damselfish behavior in response to intruding native fishes corroborates the original patterns described by previous model-bottle studies (Myrberg & Thresher 1974, Thresher 1976). Based on the low level of behavioral response towards invasive lionfish, it is unlikely that the threespot damselfish is effectively excluding lionfish, and thus is not providing any sort of refuge from invasive lionfish predation for native recruit fishes. Importantly, if damselfish are effectively providing refugia for native fishes by excluding native predators from their territories, but fail to deter invasive lionfish, then lionfish could potentially exploit damselfish territories as possible sources of prey. Understanding these potential interactions can provide insight into the relative ability of native communities to provide biotic resistance, and may inform predictions of the long-term effects of an invasive marine predator on native community structure.

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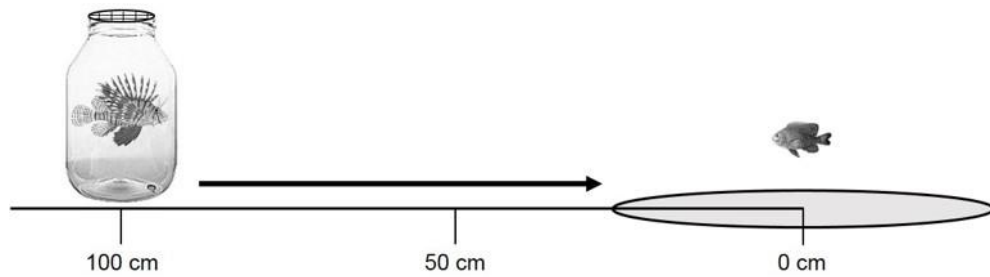
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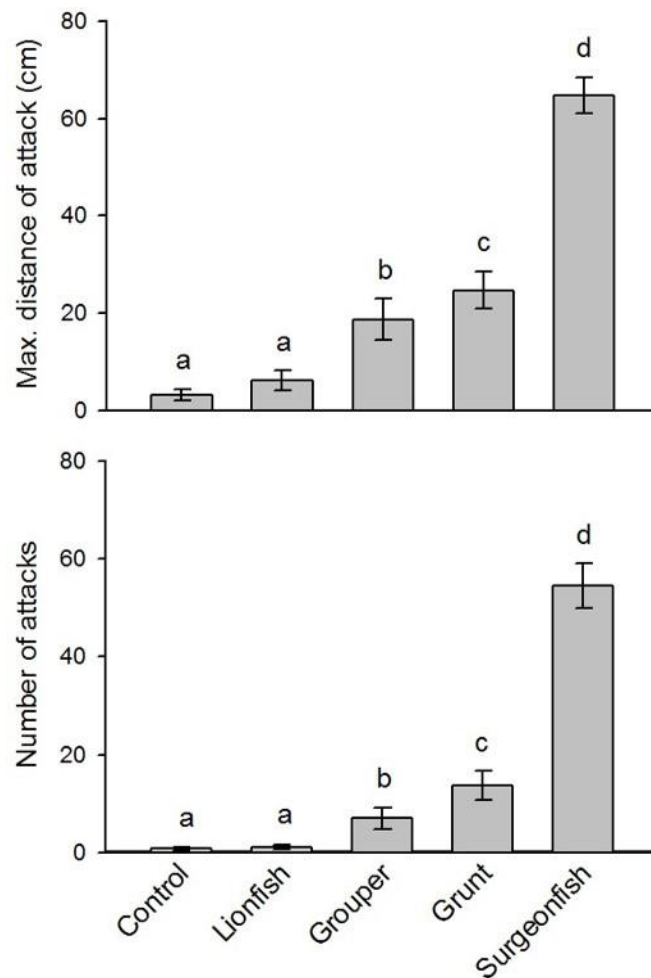
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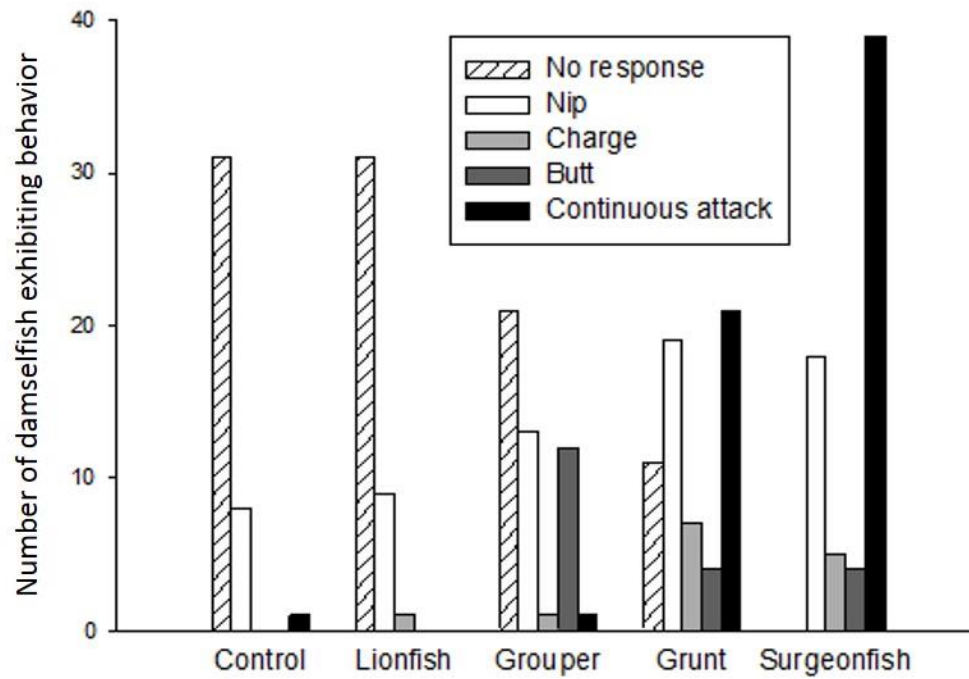
**Fig. 2.1** Model-bottle study design. Shaded ellipse represents the damselfish's guarded territory, with the focal damselfish positioned above. Bottles in each treatment (invasive lionfish treatment pictured here) were sequentially placed at 100, 50, and 0 cm away from the center of the territory, and damselfish attack rate and behavior was observed for two minutes at each increment. Then, the model bottle was moved to a distance where the focal damselfish had not responded, and then gradually moved closer to the territory until the damselfish made physical contact (i.e. maximum distance of attack). Images courtesy of FAO.



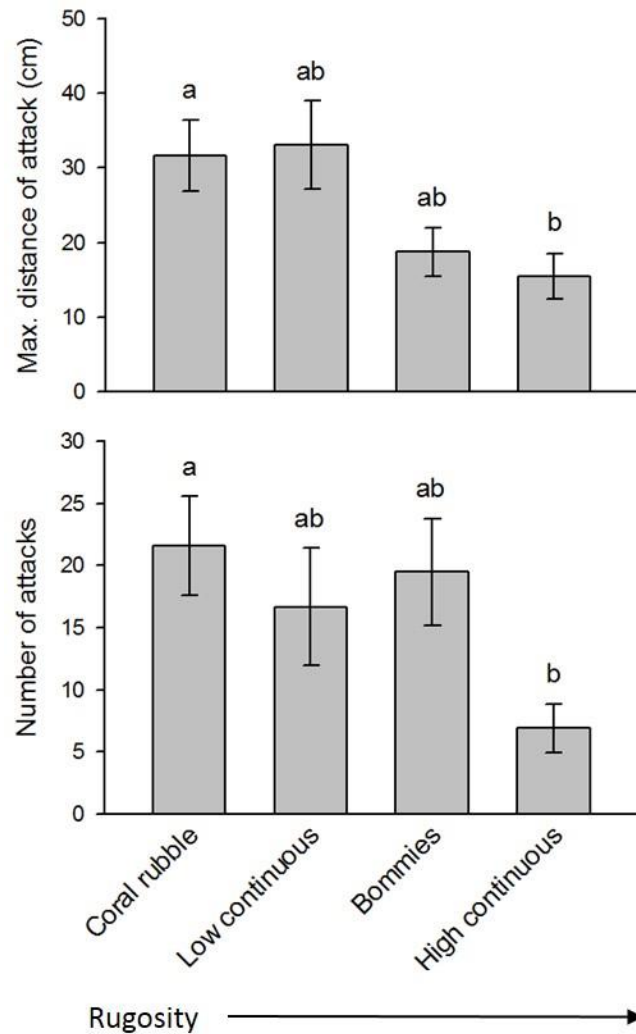
**Fig. 2.2** Proportion of damselfish (n=40) that attacked each model-bottle treatment when placed in the center of the damselfish territory (0 cm distance). Proportions with different letters are significantly different (pairwise Wilcoxon signed-rank tests with Holm's correction method,  $P < 0.05$ ).



**Fig. 2.3** Mean damselfish response ( $\pm$ SEM) to each model-bottle treatment (n=40 damselfish) measured as the maximum distance of attack and the attack rates when treatments were placed in the center of damselfish territories. Response levels with different letters are significantly different (pairwise Wilcoxon signed-rank tests with Holm's correction method,  $P < 0.05$ ).



**Fig. 2.4** Number of damselfish exhibiting each behavior observed in response to the five model-bottle treatments (n=40 damselfish). In order of increasing level of aggression, behaviors consisted of no response, nip, charge, butt, and continuous attack (see Methods for further description).



**Fig. 2.5** Mean damselfish response ( $\pm$ SEM) in each of four microhabitats in which damselfish territories occurred (left-to-right in order of increasing rugosity): dead coral rubble, low-relief continuous reef, coral bommies, and high-relief continuous reef. Low-relief habitats lacked vertical structure and high-relief habitats consisted of vertical structure >1 m high. Response levels with different letters are significantly different (pairwise Wilcoxon signed-rank tests with Holm's correction method,  $P < 0.05$ ).

### **Chapter 3 – Symmetrical effects of interspecific competition on congeneric coral-reef fishes**

Tye L. Kindinger

Marine Ecology Progress Series  
*In revision*

## ABSTRACT

Zonation in marine fishes occurs along depth gradients in both temperate and tropical habitats, yet the importance of competition in causing these patterns has been unequivocally demonstrated only in temperate systems. Throughout Caribbean reefs, fairy and blackcap basslets (*Gramma loreto* and *G. melacara*, respectively) are segregated by depth with a narrow zone of overlap. Local populations of these fishes are found under isolated reef ledges, where fairy basslet is known to compete within-species for access to prime feeding positions at the outer edges. I investigated the existence, mechanisms, and effects of interspecific competition on the local distribution and demography of basslets. I documented aggression and feeding rates of both species and conducted a manipulative experiment comparing the response of each basslet in competitor-removal versus unmanipulated populations of both species. Positioning of both species under ledges was consistent with an overall size hierarchy, with larger fish progressively closer to the outer edges of ledges. Fairy basslet were more aggressive, yet competition had symmetrical effects on the juveniles of both basslets. Interference between species drove juvenile basslets further back under ledges where feeding and growth rates of individuals were reduced. There was no effect of competition on the density of basslets during this eight-week experiment. Aggression occurred between larger basslets, but with no consequential effects on any parameters measured. This study demonstrates symmetrical effects of interspecific competition on juvenile coral-reef fishes, which rarely has been documented.

## 3.1 INTRODUCTION

Distinct patterns of community structure occur universally in species along environmental gradients, and this zonation is determined by both abiotic and biotic mechanisms.



For example, striking zonation on rocky intertidal shores (Stephenson & Stephenson 1972) can be driven simultaneously by competition, predation, and physical factors (Connell 1975).

Competition is a fundamental process that can underlie patterns of abundance and distribution (Connell 1983, Schoener 1983, Gurevitch et al. 1992), thereby influencing zonation in terrestrial and aquatic systems (e.g., Connell 1961, Hairston 1980, Lubchenco 1980, Neet & Hausser 1990, Bertness 1991, Wilson & Tilman 1991).

Vertical zonation in marine fishes often occurs along a depth gradient throughout subtidal regions and beyond, and has been described in temperate habitats such as rocky reefs and kelp beds (Stephens Jr et al. 2006), as well as throughout tropical coral reefs (Williams 1991). Large-scale manipulations consisting of reciprocal removals of potential competitors in temperate systems have demonstrated the importance of interspecific competition in causing such bathymetric zonation of fishes (Hixon 1980, Larson 1980, Holbrook & Schmitt 1986). In contrast to temperate systems, the importance of competition in causing patterns in the local distribution of these fishes has seldom been demonstrated experimentally (but see Robertson & Gaines 1986, Robertson 1996) despite a growing number of studies exploring competition in coral-reef fishes (Bonin et al. 2015, Forrester 2015).

Fairy and blackcap basslets (*Gramma loreto* and *G. melacara*, respectively) are small coral-reef fishes (8-10 cm maximum size) commonly found under reef ledges (rock overhangs) where individuals shelter in cracks and holes, and feed primarily on the same suite of passing copepods and other zooplankton (Böhlke & Randall 1963). Throughout reefs of the greater Caribbean region, these congeners are segregated by depth with a narrow zone of overlap: greater abundances of fairy basslet are observed in shallower water (1-30 m), and blackcap basslet increase in abundance in deeper water (30-180 m) where the abundance of fairy basslet

diminishes (Starck et al. 1978). Böhlke and Randall (1963) described these species as being syntopic (occupying the same ledges) at intermediate depths ranging from 30 to 50 m, depths that are not logistically conducive for performing manipulative experiments with SCUBA. Recently, however, syntopic populations were observed in The Bahamas at depths as shallow as 9 m (Kindinger pers. obs.), providing a unique opportunity to experimentally test the hypothesis that these species compete. While populations of blackcap basslet in isolation from fairy basslet remain too deep (>40 m) to definitively test for the causes of zonation (sensu Hixon 1980, Larson 1980, Holbrook & Schmitt 1986), investigating the existence and mechanisms of competition within the zone of overlap can determine the drivers of abundance and distribution in basslets at the scale of local populations under reef ledges.

Tagging studies (Webster & Hixon 2000, Webster 2003, 2004) and during this study (described below) indicate that individuals of both species have extremely high site fidelity with negligible immigration and emigration among ledges. Therefore, each spatially isolated reef ledge contains an independent local basslet population. Within these local populations, intraspecific, size-based competition has been well-documented in fairy basslets, where larger individuals aggressively defend the front of ledges by chasing smaller individuals encroaching on their positions (Webster & Hixon 2000, Webster 2004). Positions at the front of ledges facilitate higher feeding rates on passing plankton (Webster & Hixon 2000) and reduce overlap with resident predators (Webster 2004). Given this understanding of within-species competition, I hypothesized that interspecific competition influences the local distribution, growth, and density of fairy and blackcap basslets where these fishes co-occur under reef ledges via aggression.

To test this hypothesis, I first observed local populations of basslets within the zone of overlap and characterized fish behavior under ledges where the species co-occur. I predicted that (1) if interference competition exists between basslets, then interspecific aggression should be evident. I then performed a controlled manipulative experiment to compare the response of each species in the presence versus the absence of the potential competitor. I predicted that (2) if interspecific competition affects both basslets, then each species should exhibit in the manipulated absence (versus presence) of the competitor (a) a shift in local distribution closer to the front of ledges, where they will have (b) higher feeding rates, (c) higher individual growth rates, and (d) increases in density.

## **3.2 METHODS**

### *3.2.1 Basslet behavior*

During July and August of 2013, I observed the behavior of fairy and blackcap basslets in local populations under reef ledges within the depth zone inhabited by both species (hereafter, zone of overlap). Populations were located within two isolated, large reefs (322 and 533 m<sup>2</sup>) surrounded by sand off the southwest end of Eleuthera, The Bahamas, where I maintained native fish communities by regularly removing invasive lionfish (weekly) with hand nets and pole spears. I selected three local populations in each reef (n=6 populations total, Table B.1A) that were located under ledges varying in surface area from 0.90 to 9.99 m<sup>2</sup>. Initial densities of fairy and blackcap basslet ranged from 2.30 to 13.3 and 0.21 to 11.1 fish m<sup>-2</sup>, respectively.

#### *3.2.1.1 Aggression*

To quantify interference competition between basslets, I observed aggressive chases by filming each focal population (n=6) with a digital video camera in an underwater housing for

four minute periods. Because the activity levels of planktivorous fishes can vary throughout the day (Hobson 1991), I filmed every population twice in dawn (06:08-06:50, or 37-83 minutes post-sunrise), midday (11:59-16:24), and dusk (18:15-20:00, or 8 minutes before through 60 minutes after sunset). From the video footage, I counted and characterized each chase that occurred between basslets by the respective species and sizes (TL) of the aggressor and recipient. To test whether the role of basslets in observed chases differs between species, I calculated the relative frequency in which each fish was an aggressor versus recipient. Within each role, I also tested whether each fish chased (aggressor) and/or was chased (recipient) more often by heterospecifics versus conspecifics.

Density of basslets among local populations varied (see above), potentially influencing the likelihood of individual fish encountering each other. Hence, prior to statistical analyses, I standardized among-population variance in basslet density by dividing the response of each focal basslet by the proportional density of the interacting species (density of interacting basslet/total density of basslets in population). I performed statistical analyses (described below) of the response of each basslet species (separately). Specifically, I tested the relationship between the relative frequency of chases and the *size* class of fish (2 cm: 1.5-2.0 cm; 3 cm: 2.5-3.0 cm; 4 cm: 3.5-4.0 cm; 5 cm: 4.5-5.0 cm), *time of day* (dawn, midday, dusk), and/or *role* of basslets (aggressor or recipient). Similarly, I tested if chase number involving each aggressor species (separately) was correlated with the aggressor size (*agg size*), recipient species (*rec species*), and/or *time of day*. I repeated this process to test the relationship between chase number when fish were recipients and recipient size (*rec size*), aggressor species (*agg species*), and/or *time of day*.

### 3.2.1.2 Feeding rate

To determine the importance of positioning under ledges for acquiring planktonic food, I observed the feeding rate of basslets in the six focal populations during the same dives conducted to measure aggression (twice per local population in each of three times of day). Following the methods of Webster and Hixon (2000), I visually divided each ledge into four positions from the back to the front. In each position, I selected one 2.0-2.5 cm fish and counted the number of feeding bites observed in one minute, repeating this process with individuals of both species. If a fish within the size range was not present within a ledge position, I counted the bites of the nearest fish of the focal size. I converted counts to rates (number of feeding bites/60 seconds) and tested the relationship between feeding rates and *ledge position* (continuous variable), *time of day* (dawn, midday, or dusk), and/or *species* (fairy or blackcap basslet). Consistent with the relationship observed in fairy basslet by Webster and Hixon (2000), I also observed a linear relationship between the feeding rate and *ledge position* in both basslet species (Fig. 3.3). Therefore, *ledge position* was a continuous variable.

### 3.2.2 Manipulative experiment

Throughout the summer months of 2014 (June-August), I tested for effects of interspecific competition on fairy and blackcap basslets in local populations within the zone of overlap via a controlled manipulative experiment. In each of three isolated, large reefs (344-1023 m<sup>2</sup>) off the southwest end of Eleuthera, The Bahamas, I selected three populations of co-occurring basslets (Table B.1B). Ledges were located within a limited depth range of 13.4 to 15.8 m and initial densities of fairy and blackcap basslet ranged from 2.37 to 12.6 and 0.84 to 11.1 fish m<sup>-2</sup>, respectively.

Following baseline censuses of these populations (detailed methods below), I performed controlled reciprocal removals of each species, resulting in three treatments per reef: (1) unmanipulated populations of both species (control); (2) removal of fairy basslet, leaving blackcap basslet (fairy removal); and (3) removal of blackcap basslet, leaving fairy basslet (blackcap removal). Every week, I maintained these basslet treatments by removing fish with small aquarium hand nets and the fish anesthetic quinaldine. I also performed weekly removals of invasive lionfish with hand nets and pole spears to maintain native fish communities on reefs containing experimental populations.

### ***3.2.2.1 Ledge position***

To test the effect of interspecific competition on the distribution of basslets under ledges, I performed baseline and weekly censuses during pre- and post-manipulation (respectively) of potential competitors for a total of nine weeks. Censuses of each population ( $n=9$  total) consisted of mapping the ledge position and visually estimating the TL of every fish. Following the methods of Webster & Hixon (2000), I used these maps to measure the absolute ledge position of each fish (distance between fish and the front of ledge) and then standardized these values by the size of each respective ledge, resulting in relative ledge positions:  $1 - (\text{absolute position} / \text{ledge depth})$ .

For each local population, I calculated a single mean value of the relative ledge position per size class (2-5 cm) of fairy and blackcap basslet (separately) during each week of observation. These measures were then converted to the weekly change in ledge position from baseline values ( $\text{position}_{\text{week}(t)} - \text{position}_{\text{week}(0)}$ ). For each species, I analyzed the change in ledge

position by size class (2-5 cm), testing whether the response differed through *time* and/or between basslet treatments (*comp*, basslet-removal versus unmanipulated control).

### **3.2.2.2 Growth rate**

I used a mark-and-recapture method to test the effect of interspecific competition on the growth of basslets. In all nine focal populations, I captured the smallest fish possible (fairy basslet mean initial TL  $\pm$  SEM:  $2.24 \pm 0.05$  cm; blackcap basslet mean initial TL  $\pm$  SEM:  $2.34 \pm 0.05$ ) using small aquarium hand nets and the fish anesthetic quinaldine. Prior to the release of each fish, I measured total length (TL) to the nearest millimeter (mm) and injected a unique visible tag of fluorescent elastomer (Frederick 1997). Fish were recaptured and measured after about a month (31-36 days, July-August). Individual growth rates were calculated by dividing the change in TL by the number of days between initial and final measurements. Since among-population density variance could influence resource access by individuals, I standardized by dividing each growth rate by mean basslet density in each respective population during the interval of time each fish was observed. Growth rates of fairy basslet were compared between blackcap-removal and control populations (n=15 and 19 fish, respectively) and growth rates of blackcap basslet were compared between fairy-removal and control populations (n=18 and 11 fish, respectively).

### **3.2.2.3 Population density**

In The Bahamas, population densities of fairy basslet peak in late summer as individuals recruit to reefs (Webster 2003). To test for an effect of interspecific competition on the local density of basslets, I calculated the weekly density of 2-5 cm size classes of each species from censuses of focal populations (n=9 populations). These measures were converted to the weekly

changes from baseline values ( $\text{density}_{\text{week}(t)} - \text{density}_{\text{week}(0)}$ ). Within each species, the response was analyzed by size class, testing whether the change in density differed through *time* and/or between basslet-removal versus unmanipulated control populations (*comp*).

### 3.2.3 Statistical analyses

All statistical analyses were performed by fitting linear mixed effects models (LMMs) to account for the spatial nesting of ledges (local basslet populations) within reefs. Full models were fit for each response variable with the respective fixed effects as described above, and *ledge* nested within *reef* as random effects (Pinheiro & Bates 2000, Bolker et al. 2009, Zuur et al. 2009). With the exception of *ledge position*, all fixed effects were categorical variables (including *time*), because I had no a priori reason to assume any linear relationships with response variables.

When visual examination of residuals indicated a violation of normality in any model, I log-transformed the response. Full models included weighted terms that allowed variances to differ among reefs and AR1 structures in models with the fixed effect, *time*, to further account for temporal autocorrelation. Full and reduced models (with versus without weighted terms and/or AR1 structures) were then fit using restricted maximum likelihood and compared full and reduced models estimation (REML) and using Akaike's Information Criterion (AIC) and likelihood ratio tests (LRTs). Best-fit models met all assumptions of normality, homogeneity, and independence based on visual examination of model residuals.

The significance of fixed effects was assessed using LRTs of these models refit using maximum likelihood estimation (Zuur et al. 2009), and any variables that were not significant were sequentially dropped from the model. Final models were refit using REML in order to



calculate effect sizes and parameter estimates. If LRTs indicated a significant interaction between two fixed effects, I performed multiple comparisons and adjusted all p-values of linear contrasts to maintain an approximate 5% family-wise error rate (Hothorn et al. 2008). All statistical analyses were conducted using the statistical software *R* version 3.1.2 (*R* Core Team 2014) with the associated packages, *nlme* (Pinheiro et al. 2014, version 3.1-118) and *multcomp* (Hothorn et al. 2008, version 1.3-7).

### 3.3 RESULTS

#### 3.3.1 Basslet behavior

##### 3.3.1.1 Aggression

Basslets of all sizes aggressively chased each other, but overall, fairy basslet were more aggressive than blackcap basslet. I observed fairy basslet chasing other individuals a total of 355 times: 303 times chasing fairy basslet and 53 times chasing blackcap basslet. In contrast, blackcap basslet chased a total of 80 individuals: 60 blackcap basslet and 20 fairy basslet. In almost every instance of aggression, basslets chased individuals that were equal or smaller in size, with the exception of five chases where 2 cm fairy aggressors chased 3 cm (n=3) and 4 cm (n=2) blackcap recipients.

In chases between basslets, the relative frequency of roles were different in each species (Table B.2, Fig. 3.1, fairy basslet: *role* LRT  $p=0.002$ , blackcap basslet: *role* LRT  $p=0.034$ ), where fairy basslet were aggressors  $95.8 \pm 4.22\%$  of the time (aggressor vs. recipient:  $0.96 \pm 0.31$  chases  $\pm$  SEM,  $p=0.002$ ) and blackcap basslet were recipients  $95.4 \pm 4.15\%$  of the time (recipient vs. aggressor:  $0.95 \pm 0.02$  chases  $\pm$  SEM,  $p=0.034$ ). Fairy aggressors chased both species in similar amounts, with no significant difference in the number of chases directed at

fairy versus blackcap recipients (Table B.3, Fig. 3.2A). However, the recipient species of blackcap aggression did significantly differ (Table B.3, Fig. 3.2B). Blackcap aggressors chased conspecifics  $42.7 \pm 4.95\%$  ( $0.56 \pm 0.18$  interactions  $\pm$  SEM) more than heterospecifics.

Whether fairy basslet were chased was related to the size of the fairy recipient and the species of the aggressor (*rec size* x *agg species* LRT  $p < 0.001$ ). All but 5 cm fairy recipients were chased more by fairy than blackcap aggressors, and both species rarely chased 5 cm individuals (Table B.3, Fig. 3.2C). In contrast, blackcap basslet of all sizes were chased by both species, with no significant difference in the number of chases between aggressor species (Table B.3, Fig. 3.2D).

### **3.3.1.2 Feeding rate**

Feeding rates of 2.0-2.5 cm individuals were related to the positioning of basslets under ledges. Interactions between ledge position and time of day (LRT  $p < 0.007$ ), as well as between ledge position and species (LRT  $p = 0.050$ , Table B.4) were correlated with feeding rates. The rates of both species increased linearly from ledge positions at the back to the front of ledges (Fig. 3.3), and decreased throughout the day with significantly lower rates at dusk when compared to rates during both dawn and midday (Table B.4, Fig. 3.3). Across all ledge positions, fairy basslet exhibited rates that were on average ( $\pm$  SEM)  $1.02 \pm 0.01$  bites  $\text{min}^{-1}$  greater than blackcap basslet.

### **3.3.2 Manipulative experiment**

#### **3.3.2.1 Ledge position**

The distribution of basslets under ledges through time varied by size consistent with an overall size hierarchy. The smallest individuals were observed the furthest back under ledges,

and individuals of increasing size maintained positions that were progressively closer to the front of ledges (Figs. B.1A and B.1C). Following the removal of blackcap basslet, 2 and 3 cm fairy basslet shifted closer to the front of ledges (Table 3.1, *comp x time* LRT  $p=0.001$  and *comp* LRT  $p=0.015$ , respectively). By the end of the experiment (eight weeks), 2 cm fairy basslet were on average ( $\pm$  SEM)  $46.3 \pm 13.9\%$  closer to the front of ledges (Fig. 3.4C), and 3 cm fairy basslet were consistently closer to the front of ledges through time by  $14.4 \pm 4.19\%$  (mean  $\pm$  SEM) in blackcap-removal versus control populations.

Similarly, after removing fairy basslet from populations, 2 cm blackcap basslet shifted closer to the front of ledges through time (Table 3.1, *comp x time* LRT  $p=0.043$ ), reaching positions that were  $61.3 \pm 13.8\%$  (mean  $\pm$  SEM) closer to the front of ledges than in control populations by the end of eight weeks (Fig. 3.4D). 3 cm blackcap basslet were on average ( $\pm$  SEM)  $14.8 \pm 8.40\%$  closer to the front of ledges through time in fairy-removal versus control populations, but this difference was not significant (Table 3.1, *comp* LRT  $p=0.083$ ). The removal of the potential competitor did not have a significant effect on the ledge positions of 4 and 5 cm size classes of either basslet (Table B.5).

### 3.3.3.2 Growth rate

Interspecific competition affected the growth rates of ~2 cm fairy and blackcap basslets (Table 3.1, *comp* LRT  $p<0.001$  and  $p=0.032$ , respectively). Both species exhibited increased growth rates in competitor-removal versus unmanipulated control populations (Figs. 3.4E and 3.4F) that were on average ( $\pm$  SEM)  $75.2 \pm 4.47\%$  (fairy basslet) and  $70.1 \pm 2.58\%$  (blackcap basslet) higher in the absence of the competitor ( $0.002 \pm 0.00$  and  $0.001 \pm 0.01$  cm day<sup>-1</sup>, respectively).

### 3.3.3.3 Population density

Consistent with expected seasonal patterns of recruitment, densities of smaller basslets (2 and 3 cm) tended to increase through time, whereas larger fishes (4 and 5 cm) maintained relatively consistent densities (Figs. B.1B and B.1D). Interspecific competition did not affect the density of 2 cm basslets (Table 3.1, Figs. 3.4A and 3.4B), nor the densities of any larger size classes of fish (Table B.5).

## 3.4 DISCUSSION

Interspecific competition via aggression negatively affects the distribution and growth of juvenile basslets (mostly 2 cm) in local populations under reef ledges. Observations of fish behavior and the results of the manipulative experiment were consistent with expectations of substantial competition between these species. Clear interference competition was observed between basslets, and the juveniles of both species exhibited shifts in distribution towards the front of ledges (where feeding rates were higher) and increased growth rates in the absence (versus presence) of the competitor. Contrary to expectations, interspecific competition did not influence the local population density of either basslet. However, an observational period of eight weeks may have been too short of an experiment to see such effects (cf. Hixon & Jones 2005). Once basslets reach larger sizes, interspecific aggression still occurred, but with no consequential effects on any of the demographic parameters measured in this study.

Despite an overall imbalance in aggression, with fairy basslet engaged in many more chases than blackcap basslet, the effects of interspecific competition on the ledge position and growth of juveniles were symmetrical between species. This inconsistency suggests the need to consider the potential energetic costs associated with aggression *per se*, both in terms of the

energetic demands required for physical movement when chasing and/or being chased, as well as a reduction in time allocated for feeding (and other vital behaviors). Further research is also needed to directly compare the effects of intra- versus interspecific competition (e.g., Forrester et al. 2006), because observations in this study revealed that fairy basslet were engaged in over five times the number of within-species chases compared to blackcap basslet, in addition to over twice the amount of between-species chases than blackcap basslet.

Intraspecific competition within fairy basslet maintains a size hierarchy within local populations, whereby larger individuals are found in ledge positions closer to the front of ledges and thus have higher feeding rates (Webster & Hixon 2000). Observations from this study demonstrate that a size hierarchy is retained in local populations consisting of both fairy and blackcap basslets, and a positive correlation between feeding rates of fish and positioning from the backs to fronts of ledges is consistent in both species. Native predators of basslets have also been previously documented spending more time at the back of reef ledges (Webster 2004). Therefore, as interspecific competition causes shifts in the distribution of juvenile basslets towards the backs of ledges, individuals may simultaneously experience lower feeding rates and an increase in spatial overlap with predators. Both of these mechanisms may contribute to the measured decreases in growth rates of juvenile basslets from the presence of the competitor, with lower feeding rates indicating less food being obtained (and therefore less energy for growth), and an increase in risk of predation potentially increasing the amount of time and energy basslets allocate for predator avoidance and/or antipredator response (i.e., non-consumptive effects, see reviews by Lima & Dill 1990, Werner & Peacor 2003, Peckarsky et al. 2008, among others).

Very few studies have tested for effects of interspecific competition on the growth of coral-reef fishes, and findings have been highly inconsistent (Bonin et al. 2015, Forrester 2015).

To my knowledge, there is only one other study that has demonstrated reciprocal negative effects on growth between species (Forrester et al. 2006). My findings slightly differ in that Forrester et al. (2006) found effects of competition on the growth of adult fishes, and I measured the growth of only juvenile fishes. However, it seems unlikely that the growth of adult basslets is affected by competition, because competition did not alter the positioning (nor density) of adult fish under ledges in this study. Further testing of such sub-lethal effects of interspecific competition (e.g., growth and reproduction) on coral-reef fishes is needed to better understand the generality and symmetry of these effects.

Interspecific competition that is highly asymmetric has been shown to influence the distribution of coral-reef fishes among microhabitats (e.g., Ebersole 1985, Robertson & Gaines 1986, Clarke 1989, Munday et al. 2001, McCormick & Weaver 2012). At a similar scale (within local populations), I have demonstrated that symmetrical competition between species can also determine the distribution of juvenile coral-reef fishes. However, this mechanism is not common (Bonin et al. 2015, Forrester 2015). Earlier research by (Munday 2004) and recent work by (Pereira et al. 2015) demonstrated that the juveniles of two Pacific coral-dwelling gobies also compete for habitat with similar competitive abilities, but this is currently the only other documented instance of symmetrical competition between coral-reef fishes.

The zonation of each basslet species across larger spatial scales is likely driven by a variety of abiotic and biotic mechanisms that may not be mutually exclusive. Abiotic conditions such as water temperature, visible light, fluid pressure, water circulation, etc. likely vary with depth and potentially form a gradient that influences the depth limits of basslets. These factors may directly affect the depth distribution of basslets based on the environmental tolerance and corresponding fitness and survival, and/or influence the dispersal of larval fishes. Also, these

factors may indirectly affect populations of basslets by driving the distribution of their planktonic food and/or predators.

Asymmetrical competition among coral-reef fishes, such as surgeonfishes and damselfishes, can determine the distribution of these species across reef zones (Robertson & Gaines 1986, Robertson 1995). If the depth range of basslets also contains habitats that are highly-preferred by both species, then asymmetry in aggression characterized in this study may influence the overall zonation of these fishes. Additional biotic factors that could potentially be important in driving this broad-scale distribution include habitat selection by larval basslets as they recruit to reefs (Shima & Osenberg 2003), and priority effects where resident fishes (e.g., predators, conspecifics, etc.) influence incoming recruits (Shulman et al. 1983, Almany 2003, 2004, Shulman 2015). Relative predation risk could also differ between species with depth, given that blackcap basslet may be more cryptic (i.e., much darker in coloration) than their competitor. This difference may be particularly striking at deeper depths where there is less ambient light available for visual predators. Mortality rates of basslets could further vary if the overall community structure differs across a broad depth range, potentially modifying the strength or even presence of direct and indirect interactions that involve basslets.

Coral-reef fishes are the most diverse and complex assemblages of vertebrates in the world (Sale 2002), and understanding the processes that enable these ecosystems to support such species-rich communities remains a fundamental question in marine ecology. Here, I demonstrated the symmetrical effects of interspecific competition on the distribution and growth of two congeneric coral-reef fishes in local populations. Additional experimental work investigating competition between marine fishes is needed (Hixon 2006, Link & Auster 2013, Bonin et al. 2015, Forrester 2015) to increase the number of species and families on which we

base our understanding of competition, and to assess the importance of interspecific competition in determining the zonation and range limits of these organisms. Identifying the processes that influence the distribution of organisms is essential for understanding broad-scale patterns in biodiversity, and for predicting the response of species to global environmental change (Parmesan et al. 2005).

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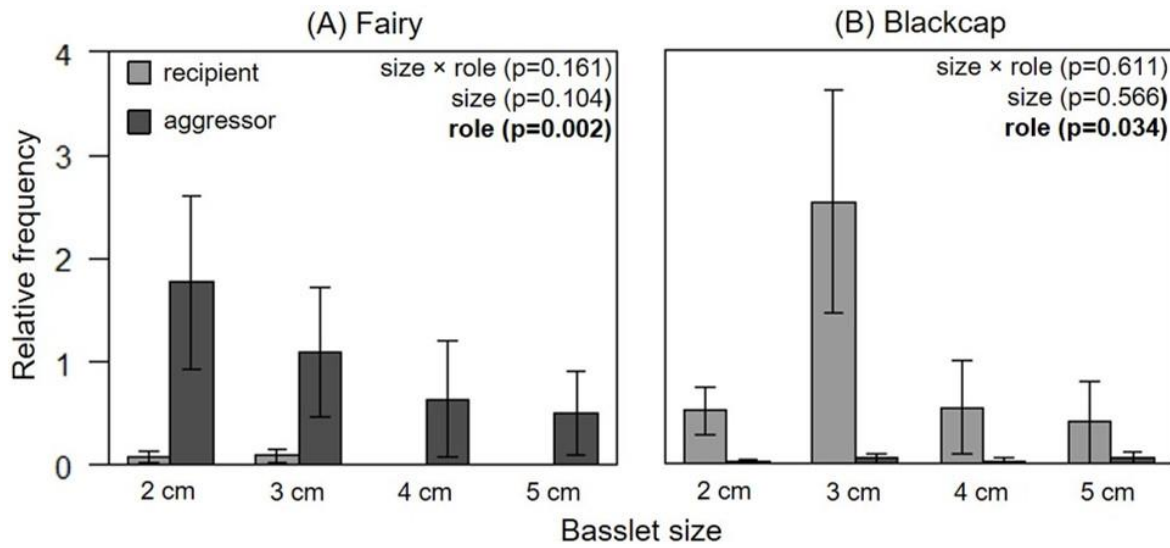
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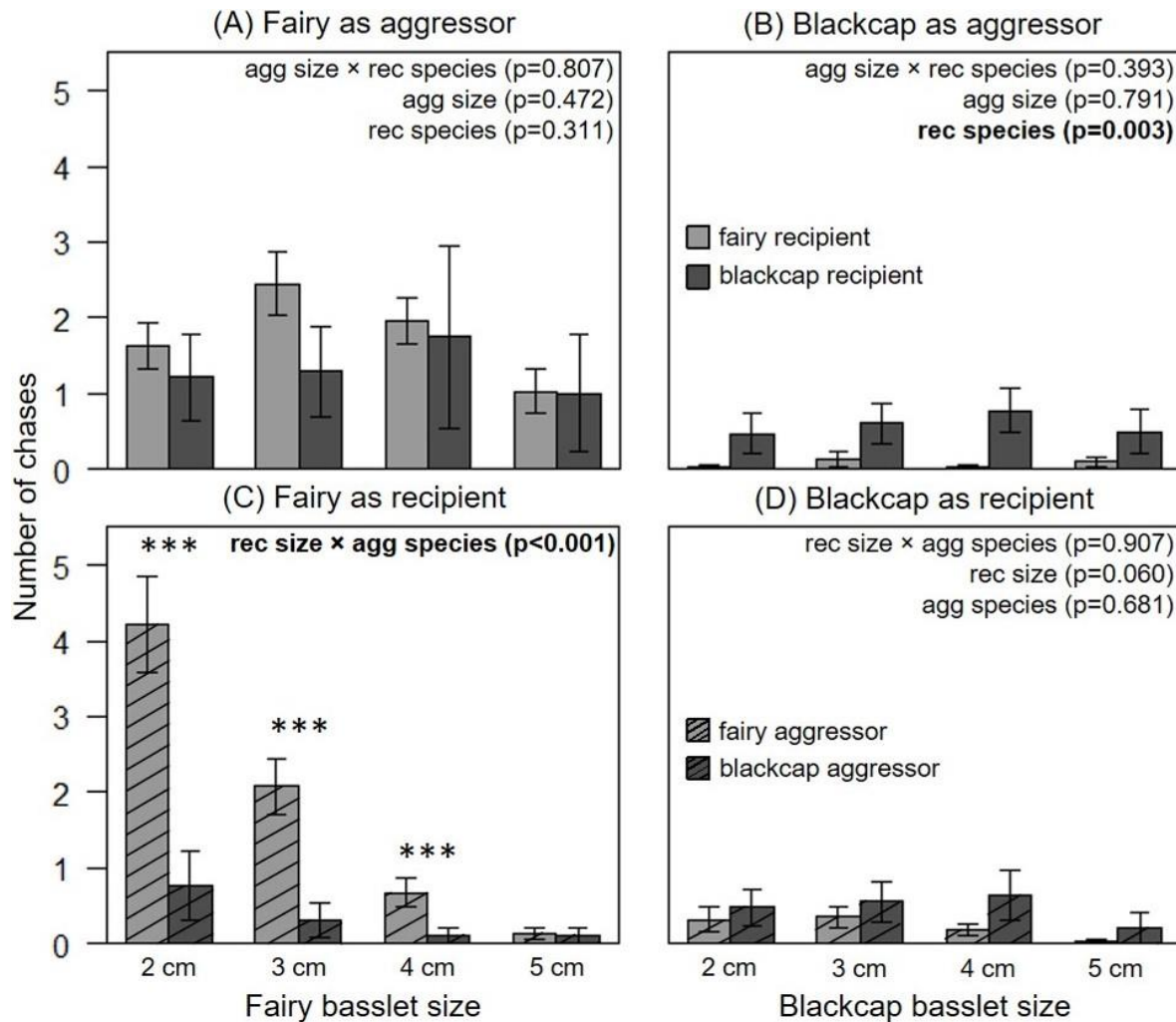
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**Table 3.1** Results of likelihood ratio tests (LRTs) of the hypothesized effect of the potential competitor (*comp*) and *time* on the change in ledge position and density of 2 and 3 cm basslets, and the effect of the potential competitor on the individual growth rates of ~2 cm basslets in a manipulative experiment. Response of basslets were compared between local populations with the potential competitor removed versus unmanipulated populations of both species (n=3 populations per treatment). If there was evidence of a significant interaction (*comp* × *time*), p-values associated with these specific linear combinations were adjusted ( $p_{\text{cor}}$ ) to achieve an approximate family-wise error rate of 5%. Variables with significant effects and corresponding p-values are in bold.

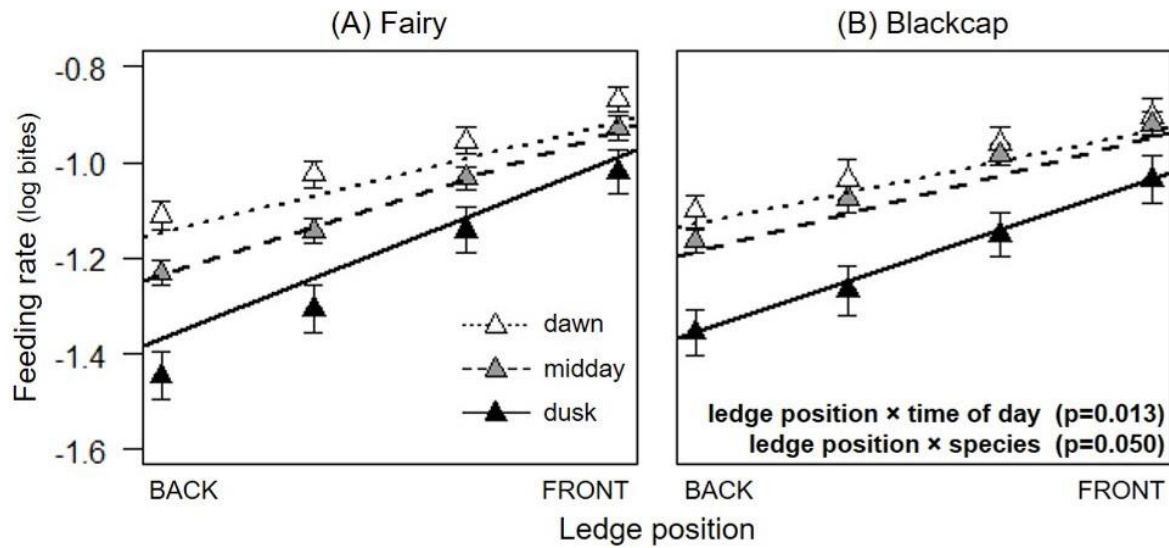
Basslet species	Response variable	Basslet size	Fixed effect	LRT p	Week	$p_{\text{cor}}$
Fairy	Change in ledge position	2 cm	<b>comp</b> × <b>time</b>	<b>0.001</b>	1	0.467
					2	0.998
					3	0.453
					4	0.611
					5	0.250
					<b>6</b>	<b>0.050</b>
					<b>7</b>	<b>0.034</b>
					<b>8</b>	<b>0.004</b>
	Growth rate	~2 cm	comp × time	0.143		
			<b>comp</b>	<b>0.015</b>		
			time	0.571		
			<b>comp</b>	<b>&lt;0.001</b>		
Blackcap	Change in ledge position	2 cm	comp × time	0.709		
	Change in density	2 cm	comp × time	0.546		
Blackcap	Change in ledge position	2 cm	<b>comp</b> × <b>time</b>	<b>0.043</b>	1	0.254
					2	0.997
					3	0.642
					4	0.088
					<b>5</b>	<b>&lt;0.001</b>
					<b>6</b>	<b>0.003</b>
					<b>7</b>	<b>&lt;0.001</b>
					<b>8</b>	<b>&lt;0.001</b>
	Growth rate	~2 cm	comp × time	0.578		
			comp	0.083		
			<b>time</b>	<b>0.050</b>		
			<b>comp</b>	<b>0.032</b>		
Blackcap	Change in density	2 cm	comp × time	0.987		
	Change in density	2 cm	<b>comp</b>	<b>0.004</b>		
Blackcap	Change in density	3 cm	comp × time	0.298		
Blackcap	Change in density	3 cm	comp	0.910		
Blackcap	Change in density	3 cm	<b>time</b>	<b>&lt;0.001</b>		



**Fig. 3.1** Relative frequency in which 2-5 cm *size* classes of fairy (A) and blackcap (B) basslets were aggressors versus recipients (*role*) in chases between species observed in local populations of both species ( $n=6$  populations). Shading of bars represent the role of fishes and error bars are standard error of the mean. Results of likelihood ratio tests are shown in the upper right of each plot and variables with significant correlations and  $p$ -values are in bold.

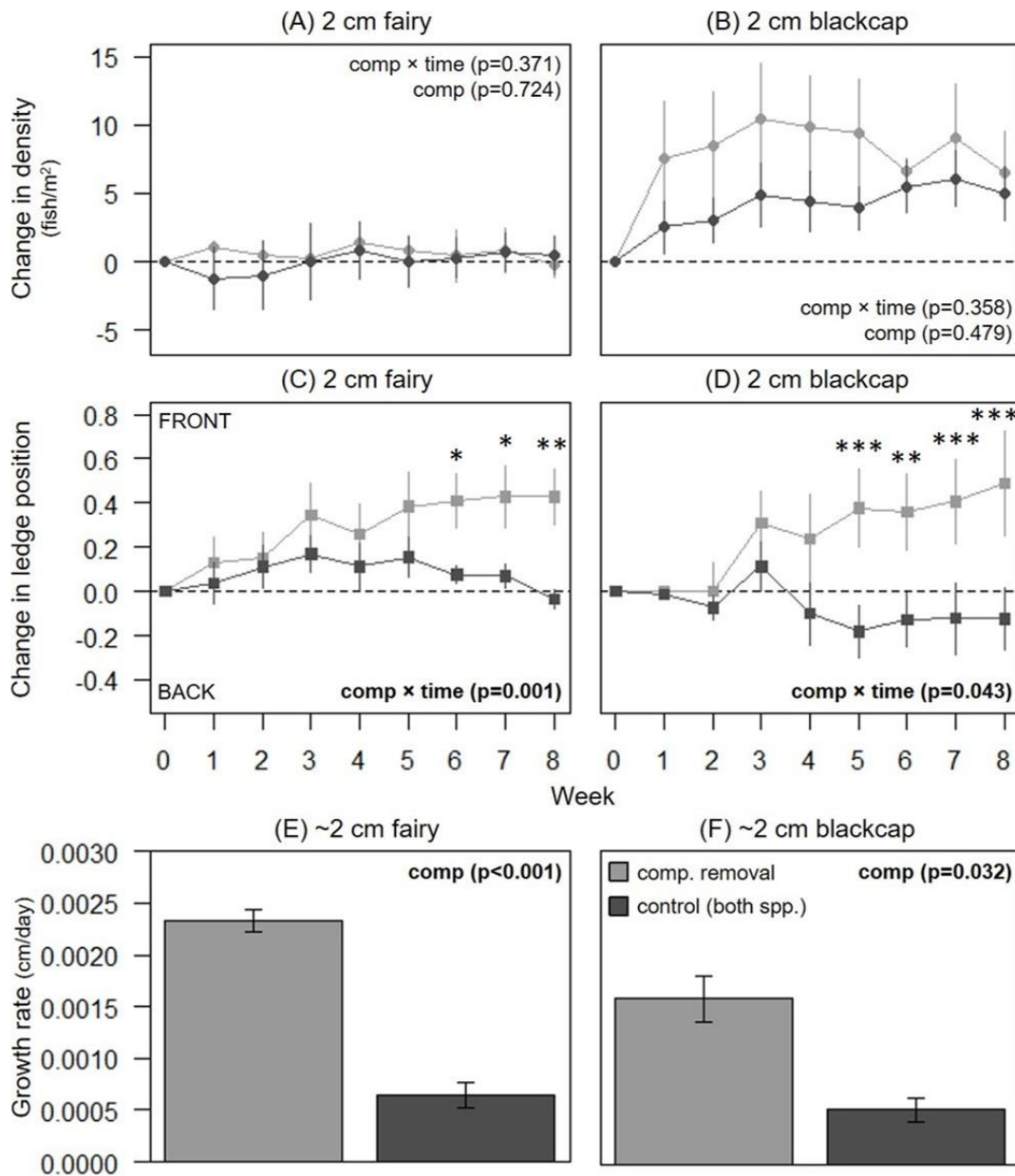


**Fig. 3.2** Number of instances in which 2-5 cm size classes (*agg size* or *rec size*) of fairy (left plots) and blackcap (right plots) basslets chased (upper plots, solid bars) and were chased (lower plots, striped bars) by each species (shading of bars) in local populations of both fishes ( $n=6$  populations). Error bars are standard error of the mean. Results of likelihood ratio tests are shown in the upper right of each plot and variables with significant correlations and p-values are in bold. In the instance where the interaction between recipient size and aggressor species was significant (*rec size*  $\times$  *agg species*), the marginal differences between aggressor species were examined in each size class; adjusted p-values to obtain an approximate family-wise error rate of 5% are indicated for each size class (significance:  $*p < 0.05$ ,  $**p < 0.01$ ,  $***p < 0.001$ ).



**Fig. 3.3** Feeding rate of 2.0-2.5 cm fairy (A) and blackcap (B) basslets (species) in positions from the back to front of ledges (ledge position) in local populations of both species ( $n=6$ ) during dawn, midday, and dusk (time of day, indicated by shading and lines). Mean values are log-transformed and error bars are standard error of the mean. Results of likelihood ratio tests are shown in the lower right of the figure and significant variables are in bold. Lines were calculated from the final models with ledge position as a continuous variable.





**Fig. 3.4** Change in density (A and B) and ledge position (C and D) through time (week), and growth rates of ~2 cm individuals (E and F) of fairy and blackcap basslets (left and right plots, respectively) following the removal of the potential competitor versus unmanipulated control populations ( $n=3$  populations per treatment; lighter and darker shading, respectively). Error bars are standard error of the mean. Results of likelihood ratio tests are shown in each plot and variables with significant effects and p-values are in bold. In the instances where the interaction between competitor presence and time was significant ( $\text{comp} \times \text{time}$ ), the marginal differences between treatment were examined during each week; adjusted p-values to obtain an approximate family-wise error rate of 5% are indicated (significance: \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ ).

**Chapter 4 – Invasive predator tips the balance of symmetrical competition between native coral-reef fishes**

Tye L. Kindinger

*In preparation*

## ABSTRACT

By causing large reductions in native prey, invasive predators may modify native species interactions, yet little is understood regarding whether and how these predators influence native communities and ecosystems. I conducted a manipulative field experiment in The Bahamas to investigate the possibility that the invasive Pacific red lionfish (*Pterois volitans*) alters competition between planktivorous fairy and blackcap basslets (*Gramma loreto* and *G. melacara*, respectively). Competition between these coral-reef fishes is known to have symmetrical effects on the juveniles of both species, whereby the feeding positions under reef ledges and growth rates of these individuals are hindered. Following baseline censuses of local populations of both basslet species, I simultaneously manipulated the presence of lionfish on entire reefs, and the presence of basslets in local populations under isolated ledges within each reef, resulting in three treatments: unmanipulated control populations of both basslets, removal of fairy basslet, and removal of blackcap basslet. For eight weeks, I measured the change in density and feeding position of 2-5 cm size classes of each basslet species, and calculated the growth rates of individuals using a standard mark-and-recapture method. Experimental populations of basslets were filmed at dusk using automated video cameras to quantify the behavior of lionfish visiting these populations. Video playback revealed that lionfish hunted across all feeding positions under ledges, regardless of which basslet species were present. Lionfish differentially reduced the density of juvenile (2 cm) fairy basslet, thereby reducing the effects of interspecific competition on juvenile blackcap basslet as evidenced by corresponding shifts in feeding position towards coveted edges of ledges and increases in growth rates of juveniles that were comparable to the response of these fish in populations where fairy basslet had been experimentally removed. Thus, an invasive predator altered the outcome of

interspecific competition via differential predation that tipped the balance of competition between native prey species from symmetrical to asymmetrical effects on juveniles. This study also demonstrates that an invasive predator can have negative direct and positive indirect effects on native prey, further broadening our mechanistic understanding of the interactive effects of predation and competition in the context of invasive species.

#### **4.1 INTRODUCTION**

Ubiquitous and fundamental processes that structure ecological communities, such as predation and competition, are typically examined separately such that interactions between these processes are seldom understood (reviews by Sih et al. 1985, Gurevitch et al. 2000). Additionally, most of our knowledge on the importance of interactions between predation and competition comes from terrestrial and freshwater systems and is rarely tested explicitly in marine systems (reviews by Sih et al. 1985, Osenberg and Mittelbach 1996, Gurevitch et al. 2000, Chase et al. 2002). Predation by invasive species can have particularly large effects on prey that are typically stronger than the effects of native predators (Salo et al. 2007, Paolucci et al. 2013) and often result in large declines in native species (reviews by Pitt and Witmer 2007, Gallardo et al. 2016), which in extreme cases can lead to local or global extinction (reviews by Clavero and García-Berthou 2005, Woinarski et al. 2015). Such substantial declines in native prey caused by invasive predators likely modify competitive interactions among native species. However, beyond these reductions in taxa, little is understood regarding whether and how invasive predators influence native communities and ecosystems (Parker et al. 1999, White et al. 2006, Ehrenfeld 2010, Simberloff 2011, Ricciardi et al. 2013).

In general, the interaction between predation and competition can produce a range of possible outcomes, depending on the nature and intensity of both processes (Chesson and Huntly 1997, Abrams 2001, Chase et al. 2002, Chesson and Kuang 2008). Predation that decreases the population size of competitors could moderate competition as resources become less-limiting. Predators that exhibit switching behavior and consume whichever species occurs in greater abundance (Murdoch 1969, Roughgarden and Feldman 1975) could also prevent either prey species from competitively excluding the other. Differential predation could moderate or intensify competition that is asymmetrical between prey species, depending on whether the dominant or subordinate competitor (respectively) is disproportionately consumed. Differential predation could also tip the balance of competition that is symmetrical in favor of one prey species over the other. Lastly, predation that extirpates local populations of one or both prey species could cause competition to cease altogether.

I tested whether and how an invasive predator modifies native interspecific competition by performing a manipulative field experiment in which I measured the response of each prey species in both the presence and absence of its competitor cross-factored with the presence and absence of the invasive predator. Focal prey were congeneric fishes commonly found on coral reefs throughout the Caribbean region (Böhlke and Randall 1963, Starck et al. 1978) that are popular in the aquarium trade: fairy basslet (*Gramma loreto*) and blackcap basslet (*G. melacara*). Independent local populations of these planktivorous basslets inhabit the undersides of spatially isolated reef ledges, with negligible immigration and emigration among ledges (Webster and Hixon 2000, Webster 2003, 2004, Ingeman and Webster 2015, Kindinger *in revision*). Basslets are known to aggressively compete both within (Webster and Hixon 2000, Webster 2004) and between species (Kindinger *in revision*) for feeding positions under ledges, which maintains a

size hierarchy among members of local populations. Larger basslets occupy prime feeding locations at the fronts of ledges where individuals exhibit higher feeding rates, presumably due to increased access to passing zooplankton, whereas smaller fishes are found closer to the backs of ledges where they feed less (Webster and Hixon 2000) and more often encounter resident predators (Webster 2004). Importantly, competition between fairy and blackcap basslets in local populations is known to have symmetrical effects on the juveniles of both species, driving shifts in the distribution of affected individuals further towards the backs of ledges where their growth rates are reduced (Kindinger *in revision*).

I investigated whether the competitive interaction between native basslets is altered by an invasive predator, the Pacific red lionfish (*Pterois volitans*). This invasion is unprecedented for a marine fish in the extent of rapid geographical spread throughout the greater Caribbean region (including the Gulf of Mexico), successful establishment across numerous habitats, and strong predatory effects on native species (Côté et al. 2013a, Albins and Hixon 2013). In particular, invasive lionfish causes substantial reductions in the abundance and species richness of native prey fishes that scale-up from smaller patch reefs (Albins and Hixon 2008, Albins 2013, Green et al. 2014, Benkwitt 2015) to large coral reefs (Albins 2015). Importantly, both blackcap basslet and fairy basslet have been found in the stomachs of invasive lionfish (Morris and Akins 2009). Further, a recent study by Ingeman (*in revision*) demonstrated that in only four weeks, invasive lionfish can increase the likelihood that local populations of fairy basslet are extirpated.

Given that competition between basslets has symmetrical effects on juveniles (Kindinger *in revision*) and that lionfish can extirpate local populations of fairy basslet (Ingeman *in revision*), I tested several alternative hypotheses regarding the effects of invasive lionfish on interspecific competition between native basslets: (1) lionfish predation affects both basslet

species substantially, thereby moderating interspecific competition; (2) predation by lionfish is frequency-dependent, thereby benefitting whichever basslet species is less abundant; (3) lionfish predation differentially affects fairy basslet, thereby benefitting blackcap basslet; (4) lionfish predation differentially affects blackcap basslet, thereby benefitting fairy basslet; and (5) lionfish predation is so intense that one or both basslets are extirpated. I predicted that the change in density of basslets through time should reflect predation of invasive lionfish. I also predicted that the feeding positions and individual growth rates of juvenile basslets should shift through time in ways that are beneficial (i.e., shift in position towards the fronts of ledges and exhibit an increase in growth rate) for either both species (hypotheses 1 and 2), just one species (hypotheses 3 and 4, or hypothesis 5 if one species is extirpated), or perhaps neither species (hypothesis 5 if both species are extirpated).

## 4.2 METHODS

### 4.2.1 *Experimental design*

To test whether invasive lionfish alter competition between native basslets, I conducted a field experiment from June through August of 2014 where I simultaneously manipulated the presence of lionfish on reefs located off the southwest end of Eleuthera, The Bahamas, and the presence of basslets under ledges within these reefs. Six large reefs (344-1023 m<sup>2</sup>) isolated by at least 150 m of open sand were paired by similar habitat (depth, surface area, reef structure, etc.) and randomly assigned a low- or high-lionfish treatment (Table C.1). Within each reef, I selected three local populations of competing basslets (Table C.1) that occupied isolated reef ledges ( $\geq 4$  m from the nearest basslet population), which is an approach successfully used in

previous studies of basslets (Webster and Hixon 2000, Webster 2003, 2004, Ingeman and Webster 2015).

I conducted baseline censuses of every population ( $n=18$ ), mapping the feeding position and visually estimating the total body length (TL) of each basslet to the nearest half-centimeter. Following these initial observations, I manipulated the presence of the predator (low- and high-lionfish reefs,  $n=3$  reefs per treatment) and performed controlled reciprocal removals of each competitor species in populations, resulting in three treatments per reef: (1) unmanipulated populations of both basslets (controls); (2) removal of fairy basslet, leaving blackcap basslet (fairy removals); and (3) removal of blackcap basslet, leaving fairy basslet (blackcap removals). I removed lionfish from low-lionfish reefs with hand nets and pole spears, and augmented the density of lionfish within naturally occurring limits by transplanting individuals onto high-lionfish reefs. Basslets were removed from populations with small aquarium hand nets and the fish anesthetic quinaldine. Lionfish and basslet treatments were maintained throughout the experiment by performing weekly removals of any newly settled individuals. As a result, mean lionfish densities differed between low- and high-lionfish reefs by at least one order of magnitude, and mean densities of focal basslet species were on average  $11.5 \pm 3.04$  times greater than that of the removed basslet species within basslet-removal treatments (Table C.1).

#### *4.2.2 Basslet response*

To quantify changes in density and/or shifts in feeding position of basslets, I conducted weekly censuses (described above) of each focal population for eight weeks. I calculated the weekly change in density from the baseline values ( $\text{density}_{\text{week}(t)} - \text{density}_{\text{week}(0)}$ ) of 2-5 cm size classes (2 cm: 1.5-2.0 cm; 3 cm: 2.5-3.0 cm; 4 cm: 3.5-4.0 cm; and 5 cm: 4.5-5.0 cm) of each



basslet species. Consistent with previous methods (Webster and Hixon 2000), I also measured the absolute feeding position (distance between fish and the front of ledge) of every individual from the weekly maps and converted these values to relative feeding positions:  $1 - (\text{absolute position} / \text{ledge depth})$ . For each population, I then calculated the weekly change in mean values per size class (2-5 cm) of each basslet species ( $\text{position}_{\text{week}(t)} - \text{position}_{\text{week}(0)}$ ).

To compare the growth of basslets among treatments, I used a mark-and-recapture method to measure the growth rates of small fish in every focal population (fairy basslet mean initial TL  $\pm$  SEM:  $2.29 \pm 0.05$  cm; blackcap basslet mean initial TL  $\pm$  SEM:  $2.39 \pm 0.05$  cm). Each fish captured with small aquarium hand nets and the anesthetic quinaldine was measured to the nearest mm (TL) and injected with a unique visible tag of fluorescent elastomer (Frederick 1997) prior to release. After about a month (31-36 days in July-August), I recaptured and remeasured these tagged fish (see Figs. 4.1 and 4.2 for sample sizes). Growth rates were calculated by dividing the change in TL by the number of days between initial and final measurements. These rates were further divided by the mean density of basslets in each population during the weeks between measurements to account for any potentially confounding effect of reducing the overall density of fish (regardless of species) via basslet-removal treatments.

I tested for the effects of the interaction between competition and predation on the response of each basslet species by fitting linear mixed effects models (LMMs) to account for the varying spatial scales of treatments: all models included *ledge* (competitor treatment) nested within *reef* (predator treatment) as random effects (Pinheiro and Bates 2000, Bolker et al. 2009, Zuur et al. 2009). Full models of the change in density and feeding position of each size class of basslet (basslet species were analyzed separately) included the fixed effects, *competition*

(competitor-removal versus control populations), *predation* (low- versus high-lionfish reefs), and *time* (weeks), as well as all potential interactions among these variables; full models of the growth rates of small basslets did not include *time*. Fixed effects were categorical variables, because I had no a priori reason to assume any linear relationships with response variables.

Full models included weighted terms allowing variances to differ among reefs and AR1 structures to account for temporal autocorrelation in models including *time*. Full and reduced models (with versus without weighted terms and/or AR1 structures) were fit using restricted maximum likelihood (REML) and compared using Akaike's Information Criterion (AIC) and likelihood ratio tests (LRTs). Examination of residuals indicated best-fit models met all assumptions of normality, homogeneity, and independence. Models were then refit using maximum likelihood estimation (Zuur et al. 2009), and the significance of fixed effects was assessed with LRTs. Variables that were not significant were sequentially dropped from models. Effect sizes and parameter estimates were calculated from final models refit using REML.

If LRTs indicated a significant three-way interaction among *competition*, *predation*, and *time*, then I fit additional LMMs (using the same procedure as above) of the response of populations in low- and high-lionfish reefs, separately, to test for an effect of *competition* and/or *time* on populations within each predator treatment. In instances of significant two-way interactions in LMMs, I made simultaneous inferences and adjusted associated p-values to maintain an approximate 5% family-wise error rate (Hothorn et al. 2008).

#### 4.2.3 *Lionfish behavior*

To quantify behavior of lionfish that visited experimental populations of basslets, I filmed all such ledges on high-lionfish reefs with GoPro® video cameras in underwater housings.

I simultaneously filmed all three basslet treatments in each reef twice for 2.5 to 3.5 hours at a time, for a total of over 50 hours of video footage. Invasive lionfish exhibit increased activity in conditions of lower ambient light during the crepuscular hours of the day, and in overcast cloudy conditions (Côté and Maljković 2010, Cure et al. 2012). Thus, I filmed focal ledges during the hours leading up to sunset (video start: 16:00-16:31; video end: 18:19-19:58; sunset: 19:35-19:45), which was sufficient for observing lionfish hunting at these deeper depths (11.9-17.4 m).

From video playback, I recorded the behavior and ledge position of each lionfish, which was estimated by visually dividing each ledge into four equal sections from the back to the front. Lionfish behavior included: resting (inactive, body against reef or seafloor); hovering (body off of substrata, but relatively stationary); swimming (directional movement across the reef); and hunting (characteristic posture of head facing prey and pectoral fins flared). These encompass the breadth of behaviors that invasive lionfish exhibit throughout diurnal and crepuscular hours of the day (Côté and Maljković 2010, Cure et al. 2012). I calculated the proportion of time (per video) lionfish visited experimental populations of basslets, and the proportion of time lionfish were observed in each ledge position. From a subset of these observations in which lionfish were hunting, I further calculated the proportion of time lionfish hunted in each ledge position.

Following the statistical procedures described above, I fit LMMs to test if the proportion of time lionfish were observed under focal ledges was correlated with which species of basslet were present (*basslet treatment*: control, fairy removal, blackcap removal) and/or lionfish *behavior*. Similarly, I tested whether the proportion of time lionfish were observed was related to *basslet treatment* and/or *ledge position* of lionfish. Lastly, because I was especially interested in whether lionfish hunted for greater amounts of time in certain ledge positions, I tested for a

correlation between the *ledge position* of lionfish and/or *basslet treatment* with the proportion of time lionfish were observed hunting.

Upon completion of the model-selection procedure described above, in the instance when the proportion of time lionfish were observed differed among lionfish *behavior*, I used Tukey's Honestly Significant Difference (HSD) method to conduct post-hoc pairwise comparisons of the proportions of time lionfish displayed each behavior. All statistical analyses used in this study were conducted using the statistical software *R* version 3.1.2 (*R* Core Team 2014) with associated packages, *nlme* (Pinheiro et al. 2014) and *multcomp* (Hothorn et al. 2008).

## 4.3 RESULTS

### 4.3.1 Basslet response

The results of the field experiment were consistent with the prediction that lionfish differentially affect fairy basslet, thereby benefitting blackcap basslet: lionfish decreased the density of 2 cm fairy basslet (Fig. 4.1A and 4.1B, Table C.2), and the feeding position and growth rate of ~2 cm blackcap basslet were enhanced (Fig. 4.2C-4.2F, Table C.3). Despite populations often consisting of larger mean densities of blackcap versus fairy basslets (Table C.1), lionfish had an effect only on the density of 2 cm fairy basslet (*predation*  $\times$  *time* LRT  $p=0.012$ ). The density of these fish differed between predator treatments by the sixth week of manipulation ( $p_{\text{cor}} < 0.001$ , Table C.2), with a decline in density on high-lionfish reefs on average ( $\pm$  SEM)  $6.50 \pm 2.05$  fish  $\text{m}^{-2}$  greater than on low-lionfish reefs by the end of the experiment.

The effect of competition on the feeding position of 2 cm blackcap basslet was dependent on the presence of lionfish (*competition*  $\times$  *predation*  $\times$  *time* LRT  $p=0.012$ ). On low-lionfish reefs, competition had an effect on the feeding position of blackcap basslet through time

(*competition*  $\times$  *time* LRT  $p=0.043$ , Fig. 4.2C), with changes in position that differed between competitor treatments by the fifth week of manipulation ( $p_{\text{cor}} < 0.001$ , Table C.3). By the end of the experiment, blackcap basslet were  $61.3 \pm 13.8\%$  (mean  $\pm$  SEM) further towards the backs of ledges in control versus fairy-removal populations. Competition had no effect on high-lionfish reefs (Table C.3), where 2 cm blackcap basslet shifted closer towards the fronts of ledges through time (LRT  $p < 0.001$ ), regardless of competitor treatment (Fig. 4.2D).

Similarly, the effect of competition on the growth rate of small blackcap basslet differed between lionfish treatments (*competition*  $\times$  *predation* LRT  $p=0.049$ ) as expected if lionfish predation differentially benefits this species. Growth rates of blackcap basslet differed between competitor treatments on low-lionfish reefs (*competition* LRT  $p=0.046$ , Fig. 4.2E), but did not differ on high-lionfish reefs (*competition* LRT  $p=0.680$ , Fig. 4.2F). The growth rate of blackcap basslet was  $70.1 \pm 2.58\%$  (mean  $\pm$  SEM) lower in control versus fairy-removal populations ( $-0.01 \pm 0.1 \text{ mm day}^{-1} \pm \text{SEM}$ ) on low-lionfish reefs, whereas the growth rate was  $10.3 \pm 4.30\%$  (mean  $\pm$  SEM) greater in control populations ( $0.01 \pm 0.00 \text{ mm day}^{-1} \pm \text{SEM}$ ) on high-lionfish reefs.

The feeding position of 3 cm blackcap basslet was also affected by a three-way interaction (*competition*  $\times$  *predation*  $\times$  *time* LRT  $p=0.007$ , Fig. C.1). However, in contrast to the pattern of 2 cm blackcap basslet, shifts in feeding position of 3 cm fish did not significantly differ between control and fairy-removal populations on low-lionfish reefs (Fig. C.1A, Table C.3), but did differ between competitor treatments on high-lionfish reefs (*competition*  $\times$  *time* LRT  $p < 0.001$ ) by the fifth week of manipulation (Fig. C.1B, Table C.3). At the end of the experiment, these fish had shifted on average  $40.7 \pm 9.41\%$  ( $\pm$  SEM) further towards the backs of ledges in control versus fairy-removal populations on high-lionfish reefs.

Competition had an effect on the density of 2 cm blackcap basslet (*competition* LRT  $p=0.025$ , Fig. 4.2A and 4.2B). However, this difference in density between competitor treatments was largely driven by one population of blackcap basslet (fairy-removal treatment) on a high-lionfish reef that exhibited an extraordinarily high level of recruitment. Counts of the smallest size class increased from one to 104 fish between baseline and Week 1 censuses, and over 80 fish were maintained in this population over the following weeks. The next largest count of any size class of either basslet species during the entire experiment was 40 fish within a single population.

Lionfish did not alter any of the effects of competition on fairy basslet (Tables C.2 and C.4). The effects of competition on the feeding positions of 2 and 3 cm fairy basslet were consistent, regardless of lionfish treatment (*competition*  $\times$  *time* LRT  $p<0.001$  and *competition* LRT  $p=0.002$ , respectively). Similarly, competition was the only variable that affected the growth rate of small fairy basslet (*competition* LRT  $p<0.001$ ).

#### 4.3.2 Lionfish behavior

Lionfish visited focal basslet populations during 15% of the filmed time (7.59 out of 50.7 hours), and were observed hunting significantly more than any other behavior, with the exception of resting (Table C.6). The proportion of time lionfish were observed did not significantly differ among basslet treatments nor among ledge positions (Table C.6). Further, lionfish spent similar amounts of time hunting along all ledge positions (Table C.6). Lionfish were observed hunting both basslet species, but the respective amounts of time could not be accurately quantified from video footage, given the small size of prey ( $<5$  cm TL).

## 4.4 DISCUSSION

This study clearly indicates that an invasive marine predator altered competition between native prey fishes: lionfish differentially affected fairy basslet, which tipped the balance of competition from symmetrical to asymmetrical in favor of blackcap basslet. Lionfish consumed juvenile (2 cm) fairy basslet in local populations, thereby reducing the effects of competition on blackcap basslet as evidenced by a positive indirect effect on the feeding position and growth rate of juveniles. Specifically, predation on fairy basslet by lionfish was sufficient to cause corresponding shifts in feeding position towards the fronts of ledges and increases in growth rates of juvenile blackcap basslet that were comparable to the response of these fish in populations where fairy basslet had been experimentally removed (Fig. 4.3).

Native predators of basslets are typically found at the backs of ledges (Webster 2004), whereas invasive lionfish were observed hunting along the entire lengths of ledges. While this leads to an expectation of lionfish affecting all size classes of prey across all feeding positions, lionfish consumed substantial amounts of only the smallest individuals positioned furthest toward the backs of ledges. This discrepancy could be explained by size-selective predation whereby lionfish target smaller fish more frequently, similar to other marine piscivores which are known to have particularly large effects on the early life stages of demersal fishes (Hixon 1991, 2015, Myers and Cadigan 1993, Almany and Webster 2006). Success rates of lionfish attacks could also be greatest at the backs of reef ledges where levels of ambient light are the lowest and piscivores would likely have a visual advantage over prey fishes (Hixon 1991, McFarland 1991).

Invasive predators are expected to have comparable effects on congeneric prey species that are taxonomically and functionally similar (Diamond and Case 1986, Ricciardi and Atkinson 2004, Thomsen et al. 2011). Additionally, invasive lionfish are typically considered to be generalist predators (Morris and Akins 2009, Muñoz et al. 2011, Côté et al. 2013b), yet lionfish

reduced the density of only fairy basslet in this study. This effect of predation occurred regardless of the presence of the competitor species, and despite local populations often consisting of blackcap basslet that were equal or greater in density than fairy basslet. Therefore, lionfish did not exhibit switching behavior (Murdoch 1969, Roughgarden and Feldman 1975) and predation was not frequency-dependent. These findings are consistent with previous studies that found the addition of invasive lionfish to reefs results in increased predation on fairy basslet (Ingeman and Webster 2015) that can extirpate local populations (Ingeman *in revision*). And, behavioral observations in aquaria of invasive lionfish in response to the simultaneous presence of fairy and blackcap basslets suggest that lionfish have a hunting preference for fairy basslet (Kindinger and Anderson *in revision*).

Characteristic traits and behavior of both predator and prey can influence the probability of a prey item being encountered, attacked, and/or consumed (Hughes 1990, 1993). Individuals that are unique from surrounding group members can be more conspicuous to visually-oriented piscivores (Mathis and Chivers 2003). Fairy basslet are brighter in coloration and more aggressive than blackcap basslet (Kindinger *in revision*), which may enhance the relative detectability of this species to predators. Differences in aggression also suggest that intraspecific competition is likely stronger within fairy versus blackcap basslets (Kindinger *in revision*). Fairy basslet may be outcompeted by conspecifics for refuge space within reef ledges more often than the competitor species. Finally, antipredator recognition and response to invasive lionfish varies among native fishes (Marsh-Hunkin et al. 2013, Black et al. 2014, Kindinger 2015, Anton et al. 2016), and could potentially differ between basslet species.

By consuming a dominant competitor, native predators can indirectly enhance subordinate competitors (Paine 1974, Menge et al. 1994). Invasive predators can also indirectly



facilitate (Schoener 1993) native species by reducing the abundance of a dominant competitor, but there are very few studies that have documented this phenomenon (Rodriguez 2006). An invasive marine crab in California preferentially consumes a competitively dominant clam which results in increased abundances of other native and non-native benthic invertebrates (Grosholz et al. 2000, Grosholz 2005). Off the coast of California, the island fox inhabiting the Channel Islands underwent heavy predation by the newly-colonized golden eagle, releasing populations of a competitively inferior skunk (Roemer et al. 2002). My study has revealed that differential predation of invasive lionfish alters symmetrical competition, which is a newly-demonstrated mechanism by which predation can directly hinder one prey species (juvenile fairy basslet) and indirectly benefit the other prey species (juvenile blackcap basslet).

By altering competition between native species, invasive predators could subsequently influence the relative importance of intraspecific versus interspecific competition. After a time lag, 3 cm blackcap basslet shifted in feeding position further towards the backs of ledges when in the presence of both the competitor and predator species. These results suggest that by modifying interspecific competition, lionfish may indirectly intensify competition within blackcap basslet as 2 cm fish released from competition with fairy basslet encroach on the feeding positions of larger conspecifics. Further research is needed to test whether lionfish alters the relative importance of intraspecific versus interspecific competition (Forrester et al. 2006, Boström-Einarsson et al. 2014) on the local distribution and demography of basslets.

Overall, this study provides strong evidence that an invasive predator can alter interspecific competition in a marine system, where differential predation tips the balance of competition between native prey species from symmetrical to asymmetrical effects on juveniles. My study also demonstrates that an invasive predator can have negative direct and positive

indirect effects on native prey, further broadening our mechanistic understanding of the interactive effects of predation and competition in the context of invasive species. Conceptual frameworks of invasions consistently highlight the need to incorporate both direct and indirect effects when predicting overall impact (Parker et al. 1999, Ehrenfeld 2010, Simberloff 2011, Ricciardi et al. 2013). Yet indirect processes remain a neglected concept in empirical studies (White et al. 2006) and unexpected consequences can arise following the strategic reduction or eradication of invasive consumers (Murphy and Bradfield 1992, Bergstrom et al. 2009, Simberloff 2009, Kessler 2011). Therefore, demonstrating complex interactions between invasive and native species can greatly inform and enhance management and conservation initiatives (Zavaleta et al. 2001, Byers et al. 2002).

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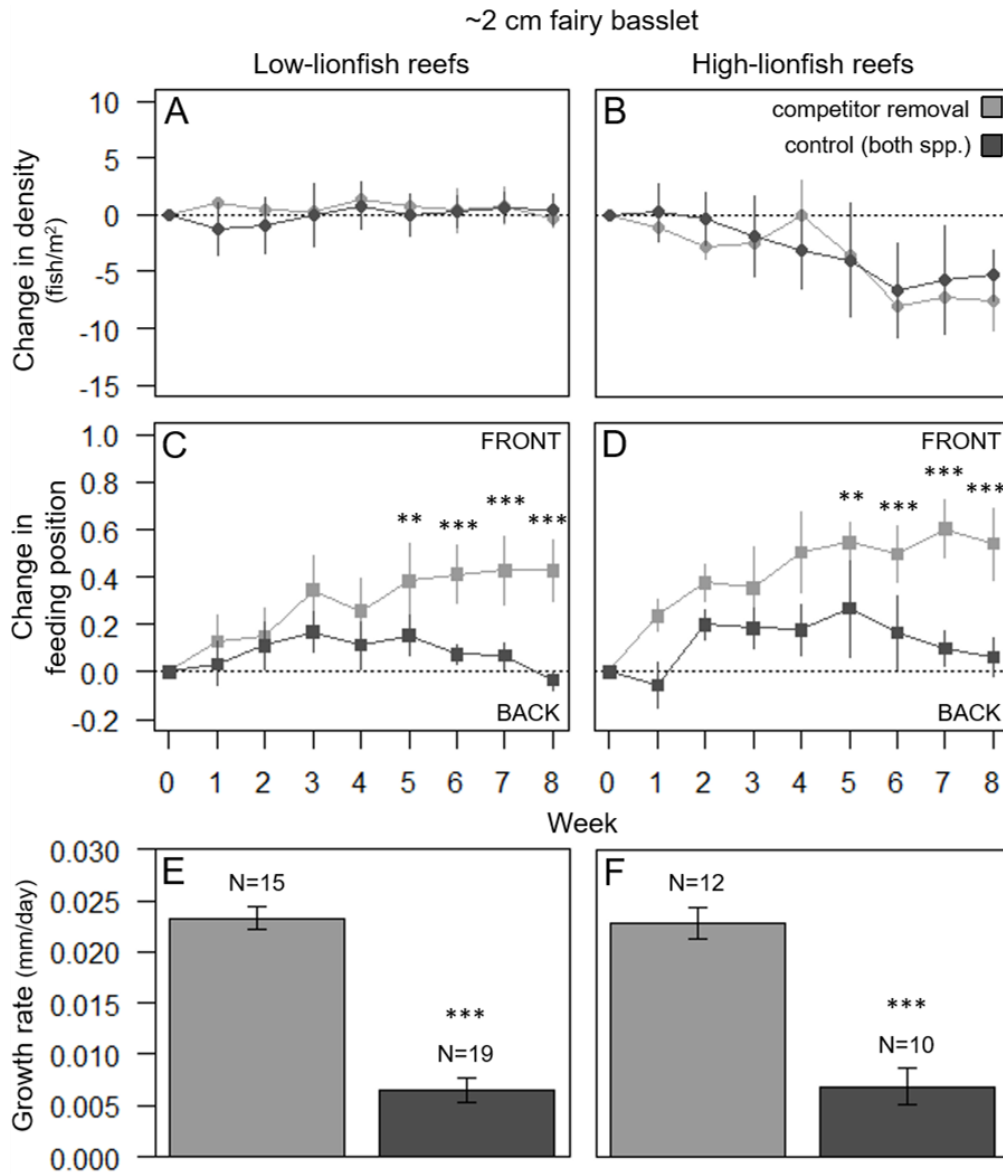
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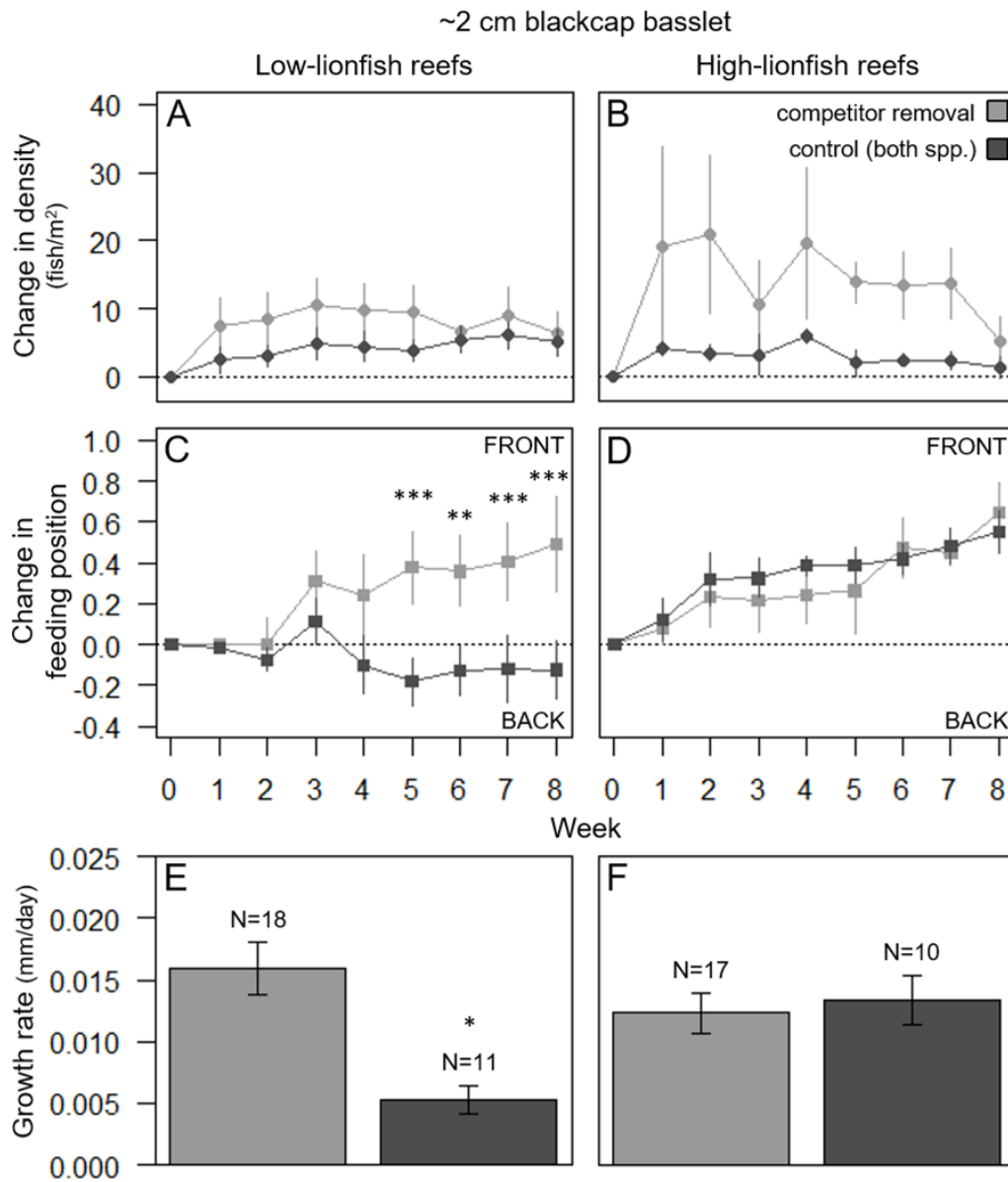
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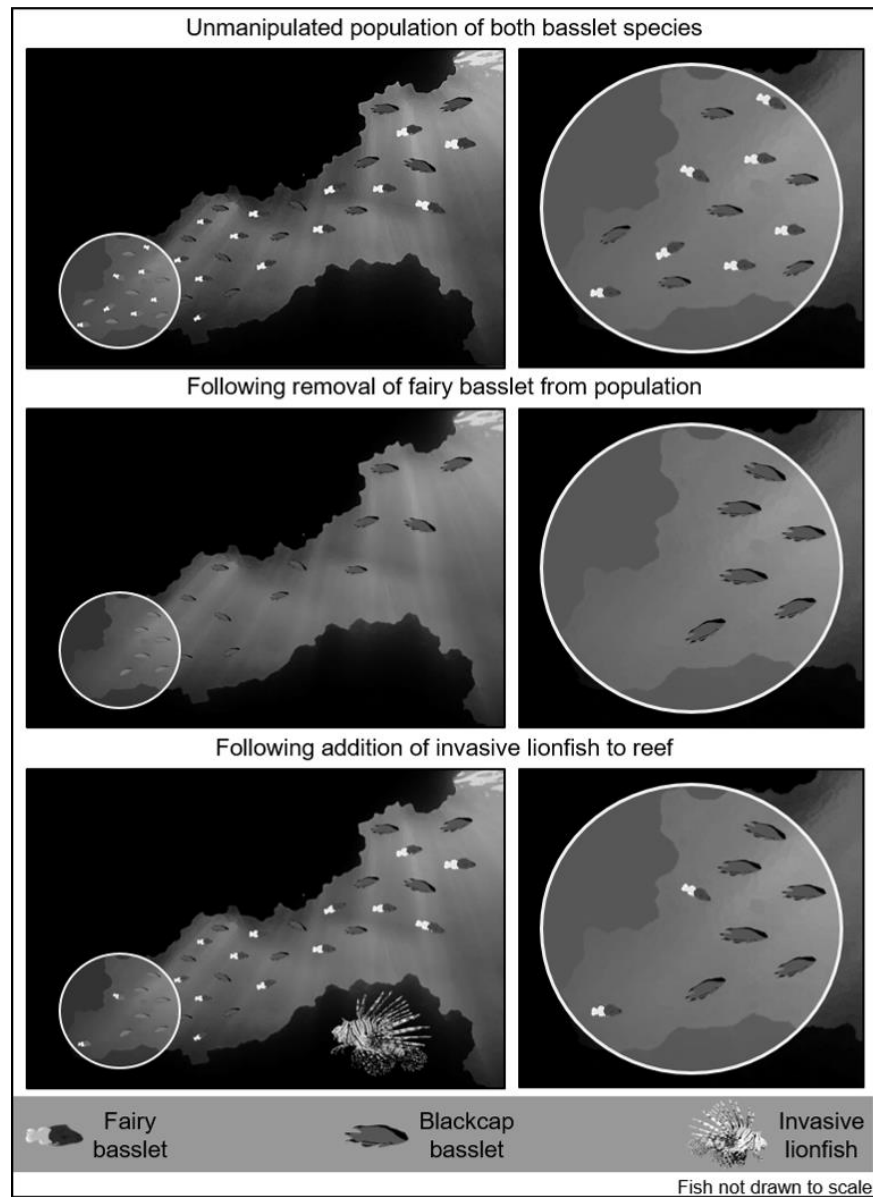


**Fig. 4.1** Change in density (A, B) and feeding position (C, D) of 2 cm fairy basslet through time (week) and growth rates of ~2 cm individuals (E,F; sample sizes indicated above bars) in a cross-factored manipulative experiment ( $n=3$  populations per treatment) consisting of local populations with blackcap basslet removed and unmanipulated control populations (lighter and darker shading, respectively) within low- and high-lionfish reefs (left and right plots, respectively). Error bars are standard error of the mean. The significance of fixed effects were calculated using likelihood-ratio tests, which revealed no significant effect of lionfish on any of the response variables (see Table C.2 for results). Therefore, significance indicated in each plot represents differences between basslet treatments (competition) when lionfish treatments were pooled:  $*p < 0.05$ ,  $**p < 0.01$ ,  $***p < 0.001$ . When there was evidence of a significant interaction with *time* (change in feeding position), p-values indicated in plots C and D are from linear combinations and were adjusted ( $p_{\text{cor}}$ ) to achieve an approximate family-wise error rate of 5%.





**Fig. 4.2** Change in density (A, B) and feeding position (C, D) of 2 cm blackcap basslet through time (week) and growth rates of ~2 cm individuals (E, F; sample sizes indicated above bars) in a cross-factored manipulative experiment ( $n=3$  populations per treatment) consisting of local populations with fairy basslet removed and unmanipulated control populations (lighter and darker shading, respectively) within low- and high-lionfish reefs (left and right plots, respectively). Error bars are standard error of the mean. The significance of fixed effects were calculated using likelihood-ratio tests (see Table C.3 for results). When there was evidence of a significant three-way interaction among competition, predation, and time, subsequent models were fit to test for the effects of competition and time on the response in low- and high-lionfish reefs (separately). When there was evidence of a significant two-way interaction, p-values from linear contrasts were adjusted to achieve an approximate family-wise error rate of 5%, with respective significance indicated in each plot: \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ .



**Fig. 4.3** Overview of how invasive lionfish alters symmetrical competition between native fairy and blackcap basslets via differential predation. Basslets are typically distributed in local populations based on a size hierarchy, whereby larger basslets occupy prime feeding locations at the fronts of ledges and smaller fishes are found closer to the backs of ledges (A, C, E). In the absence of the invasive predator (A), interspecific competition inhibits the feeding position and growth rates of juveniles of both basslet species equally (B). Following the experimental removal of fairy basslet (C), juvenile blackcap basslet move closer to the fronts of ledges and grow faster (D). Following the addition of invasive lionfish to reefs (E), juvenile fairy basslet are reduced in abundance such that juvenile blackcap basslet shift closer to the fronts of ledges and exhibit increased growth rates (F). Therefore, the effect of invasive lionfish on interspecific competition is comparable to the effect of experimentally removing fairy basslet from populations (C-F).

**Chapter 5 – Preference of invasive lionfish and native grouper between congeneric prey fishes**

Tye L. Kindinger and Emily R. Anderson

Marine Ecology Progress Series  
*In press*

## ABSTRACT

To gain insight about how an invasive predator may influence native prey, we performed a series of experiments in aquaria to characterize and compare the prey preferences of the invasive red lionfish (*Pterois volitans*) and an ecologically-similar native mesopredator, the graysby grouper (*Cephalopholis cruentata*). Preference for native congeneric fishes, the fairy and blackcap basslets (*Gramma loreto* and *G. melacara*, respectively) were tested. We observed behavior of predators in response to two individual prey consisting of cross-factored combinations of species (fairy and blackcap basslets) and size (small and large). Upon initial exposure to prey, lionfish first hunted fairy basslet and graysby first hunted blackcap basslet, with both predators initially preferring large over small fish. Overall behavior (quantified from the entire duration of observation) indicated both predators lacked a preference between basslet species based on total number of strikes and hunting time. Despite essentially identical size ranges of predators studied, graysby overall preferred large basslet across all graysby sizes, whereas the overall preference of lionfish between prey size varied with lionfish size. Importantly, the initial preferences of predators were likely least affected by the unnatural setting in aquaria. By preferentially consuming the less-preferred prey species of native graysby or by increasing predation on larger basslets, invasive lionfish may enhance coexistence between basslet species or among basslet sizes within local populations structured according to a size hierarchy, respectively. Alternatively, increased consumption of basslets may deplete local basslet populations, especially if lionfish exhibit prey switching behavior.

## 5.1 INTRODUCTION

Invasive predators typically have effects on native prey that are more severe than the effects of native predators (Salo et al. 2007), which can cause substantial declines in native species (Pitt & Witmer 2007). These predators often have generalized diets and in extreme cases, can drive native species to local or global extinction (Clavero & García-Berthou 2005). Therefore, accurately predicting the effects of invasive predators on native prey populations and communities is important for informing management and conservation strategies.

A key mechanism underlying predatory effects is prey preference. Predators may have a preferred prey which is disproportionately consumed, or they may exhibit prey switching behavior (*sensu* Murdoch 1969) where the predator switches to other available prey once the preferred prey becomes rare. Further, the combination of native and invasive predation may result in enhanced depletion of a single prey species if both predators have a preferred prey in common. If predators differ in prey preference, predation may also be enhanced as the invasive predator consumes the less-preferred prey of the native predator. Switching behavior exhibited by an invasive predator could ultimately lead to the extinction of native prey once they become sequentially preferred (e.g., Savidge 1987). Overall, understanding the prey preference of an invasive predator and comparing it to that of a native predator can reveal potential mechanisms underlying the overall effects of an invasion on native communities.

By performing a series of experiments, we characterized the prey preference of an invasive marine predator, the Pacific red lionfish (*Pterois volitans*), and compared this preference to that of an ecologically-similar mesopredator that is native throughout the Atlantic, the graysby grouper (*Cephalopholis cruentata*). Invasive lionfish are commonly found on coral reefs throughout the tropical and subtropical Western Atlantic and greater Caribbean region (Schofield 2010), and like the native graysby, are considered to be generalist predators (e.g.,

Morris & Akins 2009). As a voracious predator, invasive lionfish can cause large reductions in the abundance and richness of small native fishes that scale-up from smaller patch reefs (e.g., Albins & Hixon 2008) to large coral reefs (Albins 2015).

Marine piscivores often preferentially distinguish among prey by species (e.g., Almany et al. 2007) or by size (e.g., Floeter & Temming 2003). We hypothesized that native graysby and invasive lionfish have similar prey preferences, because they are both generalist mesopredators. We predicted that neither predator would display a strong preference between two congeneric prey species (*Gramma loreto* and *G. melacara*), but would both exhibit shifts in preference from smaller- to larger-sized prey with increasing predator size, because graysby and lionfish are gape-limited predators.

## 5.2 METHODS

### 5.2.1 Study area and fish collection

We conducted this study during August 2014 at the Cape Eleuthera Institute on Eleuthera, the Bahamas where we investigated the preference of predators for two native coral-reef fishes, the fairy and blackcap basslets (*Gramma loreto* and *G. melacara*, respectively). These congeners are popular aquarium fishes that differ in appearance primarily by coloration (Fig. D.1) and are commonly found under ledges (rock overhangs) throughout Caribbean reefs (Böhlke & Randall 1963, Starck et al. 1978). SCUBA divers collected basslets from reefs in the Exuma Sound at maximum depths of 15 m with small aquarium hand nets and the fish anesthetic quinaldine. We collected graysby and lionfish from shallow patch reefs (<5 m deep) in Rock Sound with the respective use of hand fishing lines while snorkeling and hand nets on SCUBA. We collected 15 lionfish ranging in size from 10.2 - 20.9 cm total length (TL) and 15 graysby

with a size range of 10.0 - 20.3 cm TL. All fish were maintained in outdoor tanks with continuous flow-through saltwater systems and fed daily; predators were fed live silverside fish and basslets were fed live brine shrimp (*Artemia* sp.).

### 5.2.2 *Experimental design*

We conducted all experimental trials in 50-gallon acrylic aquarium tanks (91.5 x 38 x 51 cm) with continuous flow-through seawater systems. Food was withheld from predators 24 hours prior to observation to ensure predator response to the presence of prey. Tanks were divided in half with a removable central barrier of solid aluminum (Fig. 5.1). We released a single predator into one side of the tank and placed two basslets in the other side. Basslets were held in identical small glass containers (~500 ml) with mesh covers (one basslet per container) positioned in each corner of the tank. With these prey containers, predators were able to receive both visual and chemical cues from basslets, but could neither make physical contact nor consume any basslets.

To determine whether the preference of predators for basslets was driven by basslet species (fairy and blackcap) or basslet size (small: 1.7-2.5 cm TL and large: 3.5-5.2 cm TL) we presented pairs of basslets in cross-factored combinations of the two variables, resulting in the following treatments: (1) small fairy and large fairy, (2) small blackcap and large blackcap, (3) small fairy and small blackcap, (4) large fairy and large blackcap, (5) small fairy and large blackcap, and (6) large fairy and small blackcap. In addition to randomizing the order of basslet treatments presented to each predator, we also randomized which corner of the tank basslets were placed every time a treatment was presented.

Once the predator and basslets were in their respective sides of the tank, we allowed them to acclimate for 20 minutes, after which we removed the central barrier and observed the predator's behavior for 10 minutes. Observations were performed either in-person (74 lionfish trials; 73 graysby trials) or filmed with a digital video camera (16 lionfish trials; 17 graysby trials) positioned outside of the tank. During each 10-minute trial, we recorded (1) which basslet the predator hunted (defined below) first (initial hunting preference); (2) the number of times the predator's mouth made physical contact with each glass container (number of strikes); and (3) the amount of time the predator hunted each basslet (hunting time). We defined the hunting behavior of lionfish as occurring when an individual directly faced a basslet with flared pectoral fins and/or blew pulsed jets of water towards a basslet (Cure et al. 2012). We characterized graysby hunting behavior as occurring when an individual positioned itself near a basslet (<10 cm in this experiment) while directly facing the basslet (Webster 2004).

At the conclusion of the 10-minute trial, we separated the predator from the basslets and placed the central barrier back in the tank. A new combination of basslets were placed in the glass containers, and all fish were allowed to acclimate for 20 minutes before removing the barrier and observing predator response for another 10 minutes. This procedure was repeated until all six basslet treatments had been presented to each predator in random order.

### *5.2.3 Statistical analyses*

When testing for significant differences in predator response between fairy versus blackcap basslets, we analyzed only the four treatments where predators were presented with two different basslet species (lionfish: n=11, graysby: n=11). Similarly, we analyzed the four treatments where we presented predators with two basslets differing in size (small versus large)



when comparing predator response between basslet sizes (lionfish:  $n=13$ , graysby:  $n=12$ ). If a predator did not display any predatory behavior during any of the four treatments described in the treatment groupings above, then the individual was dropped from that respective group prior to analysis (resulting in the final sample sizes reported above).

To test whether initial hunting preferences between basslet species (fairy and blackcap) and basslet sizes (small and large) significantly differed between predators (lionfish and graysby) and/or among predator sizes (continuous variables), we fit Generalized Estimation Equations (GEEs) with binomial distributions and exchangeable correlation structures. GEEs are an extension to the generalized linear model approach that allow for correlations between observations from the same subject, thus allowing us to account for repeated measures. We fit a full model with an interaction between predators and predator size, and then compared the model fit to that of the reduced additive model by calculating quasi-likelihood values under the independence model criterion (QIC; Pan 2001). If the initial hunting preference significantly varied between predators, we then performed a post-hoc McNemar test with a continuity correction for lionfish and graysby (separately) to test whether each predator had a significant initial preference.

We fit full GEEs with Poisson distributions and exchangeable correlation structures to test whether the number of strikes and hunting time of predators significantly depended on a three-way interaction among the type of predator, predator size, and basslet species. We compared the full and reduced additive GEEs with QIC. If the three-way interaction was significant, we fit GEEs for lionfish and graysby separately to determine whether each predator's response significantly differed among predator size and/or basslet species (or an interaction between the two). Again, final models (full versus reduced) were selected for each predator

based on QIC values. We repeated this entire process, but with basslet size instead of basslet species as an explanatory variable in all the GEEs. All statistical analyses were conducted using *R* version 3.1.2 (*R* Core Team 2014) with the associated packages *geepack* (Halekoh et al. 2006) and *MESS* (Ekstrom 2014).

### 5.3 RESULTS

Invasive lionfish and native graysby exhibited clear initial hunting preferences for basslet species that significantly differed between predators (Fig. 5.2A-B, GEE, Wald  $\chi^2=25.5$ ,  $p<0.0001$ ), yet did not significantly differ among predator sizes (GEE, Wald  $\chi^2=1.49$ ,  $p=0.22$ ). Upon initial exposure to both basslet species, lionfish first hunted fairy basslet significantly more often than blackcap basslet (McNemar test  $\chi^2 = 96.01$ ,  $p < 0.0001$ ), whereas graysby initially hunted blackcap basslet (McNemar test;  $\chi^2 = 62.02$ ,  $p < 0.0001$ ). However, these initial preferences were not maintained for the remainder of the observational periods. Across all predator sizes observed, there was no significant difference in the number of strikes or hunting time directed at each basslet species exhibited by either predator (Table D.2).

When testing the initial hunting preference between basslet sizes, we found that despite the full GEE model having a lower QIC value than the reduced model (Table D.1), the interaction between the predator species and predator size was not significant (GEE, Wald  $\chi^2=2.60$ ,  $p=0.11$ ). Initial preference between basslet sizes did not significantly differ between predator species (GEE, Wald  $\chi^2=2.57$ ,  $p=0.11$ ) nor across predator sizes (GEE, Wald  $\chi^2=1.01$ ,  $p=0.31$ ). Both lionfish and graysby had a significant initial preference for large basslet (Fig. 5.2C-D, McNemar tests;  $\chi^2 = 16.1$  and  $29.0$ , respectively;  $p<0.0001$  for both predators). This preference for large basslet remained consistent for graysby in terms of both the overall number

of strikes (Fig. 5.3A, GEE, Wald  $\chi^2=13.19$ ,  $p<0.0003$ ) and hunting time (Fig. 5.3B, GEE, Wald  $\chi^2=10.24$ ,  $p=0.0014$ ). This preference was also maintained across all sizes of graysby tested (number of strikes: GEE, Wald  $\chi^2=0.65$ ,  $p=0.4202$ ; hunting time: GEE, Wald  $\chi^2=0.01$ ,  $p=0.9433$ ).

In contrast, both the overall number of strikes and hunting time of lionfish depended on a significant interaction between the size of lionfish and basslet size (Fig. 5.4, number of strikes: GEE, Wald  $\chi^2=8.42$ ,  $p=0.0037$ ; hunting time: GEE, Wald  $\chi^2=11.53$ ,  $p<0.0007$ ). Predatory behavior directed at small basslet was greatest among smaller-sized lionfish sizes, and gradually decreased with increasing lionfish size (Fig. 5.4A and 5.4C). We found the opposite trend in response to large basslet, with increasing levels of predatory response as lionfish size increased (Fig. 5.4B and 5.4D).

## 5.4 DISCUSSION

The distinctiveness hypothesis postulates that invasive predators are expected to have similar effects on prey species that are taxonomically and functionally similar (e.g., Ricciardi & Atkinson 2004). Contrary to this prediction, we have provided evidence of an invasive marine predator having strong prey preferences that depend on both the species and size of prey upon initial exposure to a pair of congeneric coral-reeffishes. Lionfish first hunted fairy basslet more often than blackcap basslet, and initially preferred large over small fishes. In contrast, native graysby first hunted blackcap basslet, yet were consistent with lionfish in exhibiting an initial preference for large fish. Following these initial preferences, overall predatory behavior quantified from the entire duration of observations revealed that both the invasive and native predators hunted and struck about equally at both basslet species. In terms of overall preference

between prey size, only the preference of invasive lionfish varied with predator size. Native graysby preferred large fishes across all predator sizes, yet smaller lionfish preferred small basslets and larger lionfish preferred large basslets.

We also observed additional differences in behavior between predators in response to basslets. Graysby typically performed strikes at basslets in quick succession, striking the glass containers up to as many as nine times in three seconds. In contrast, there was a minimum of two seconds between individual lionfish strikes. We also observed lionfish more often than graysby switching between which basslet was hunted within a single trial. A review of the trials we recorded with a digital camera revealed that lionfish switched which basslet was hunted a total of 31 times, whereas graysby switched only six times. More than half of the observed switches by lionfish seemed associated with basslet movement, where immediately following the movement of a basslet in the glass container, lionfish switched and began hunting that basslet. None of the switches between basslets by graysby were associated with basslet movement.

Both in the experimental setting of this study and on natural reefs, recognition of basslet species by lionfish and graysby likely involves the use of visual and/or olfactory cues from prey (or combinations of both). Most reef-fish have acute color vision (McFarland 1991), so these predators may be able to interpret the differences in coloration between fairy and blackcap basslets. Preferences for a prey species could also be explained by varying activity levels between basslets. Anecdotally, fairy basslet appeared to be more active in the glass containers compared to blackcap basslet in this study, and our observations of lionfish often switching which basslet was being hunted seemingly in response to basslet movement further supports this hypothesis. Kindinger (*in review*) revealed that fairy basslet were more aggressive than blackcap basslet, which may indicate fairy basslet are also more conspicuous in a natural setting.

The behavior of predators observed in this study suggest that invasive lionfish may have a slightly broader range of effects on basslets than native graysby, given that lionfish are seemingly more likely to hunt both small and large basslets, and even may exhibit switching behavior. However, the initial preferences of predators are of particular importance, because they were the observations that were least likely to reflect the unnatural setting used in this study. Predators in aquaria were unable to consume prey fishes, and the glass containers with basslets seemed to deter predators. Once a predator struck at the glass, there were often few subsequent strikes for the remainder of a trial, although predators did continue to display hunting behavior. Therefore, if the initial observations of behavior are indicative of the true preferences of these predators, then the addition of invasive lionfish on reefs may promote coexistence between basslets by consuming the less-preferred species of the native predator. In contrast, invasive lionfish may enhance overall predation of larger basslets.

The combination of invasive and native predation likely results in complex interactions with basslets. Basslets are found distributed among ledge positions in local populations based on a size hierarchy (Webster & Hixon 2000, Kindinger *in revision*). Under ledges, individuals compete both within and between species for feeding position, whereby larger individuals maintain coveted positions towards the fronts of ledges where the ability to obtain planktonic food is greatest. If both the invasive and native predators preferentially consume these larger fishes, the ability of smaller basslets to shift closer toward coveted feeding positions may increase. Interspecific competition between basslet species (Kindinger *in revision*) also may be altered by invasive lionfish via increased consumption of fairy basslet.

Alternatively, invasive lionfish may enhance predation of native basslets to the point where competition no longer exists within local populations. Indeed, previous field studies

indicate that fairy basslet are faced with increased predation from the addition of lionfish to native reefs (Ingeman & Webster 2015), and invasive lionfish can even drive local populations of fairy basslet to extirpation (Ingeman *in review*). In addition to these effects on fairy basslet, invasive lionfish may substantially affect both basslet species via elevated consumption rates of larger individuals. Over time, this increased consumption of larger size classes of prey could cause shifts in the overall size distribution of basslets, or potentially even influence population growth rates via preferential targeting of adult basslets that are reproductively mature. Additionally, the enhanced depletion of prey fishes could also have potential indirect effects on native predators (including graysby) via competition for food.

Our study demonstrates aspects of prey preference that are different and similar between invasive and native predators. As a result, invasive lionfish may at one extreme enhance coexistence by preferentially consuming the less-preferred prey species of the native predator or by enhancing preferential predation on larger, competitively-dominant basslets. At the other extreme, increased consumption of basslets by invasive lionfish may deplete local basslet populations, especially if lionfish exhibit switching behavior following the reduction of preferred prey. Determining how the combination of invasive and native predation will ultimately affect native prey populations and communities is imperative for accurately predicting the extent of impact from an invasion, which can inform management and conservation initiatives.

## 5.5 ACKNOWLEDGMENTS

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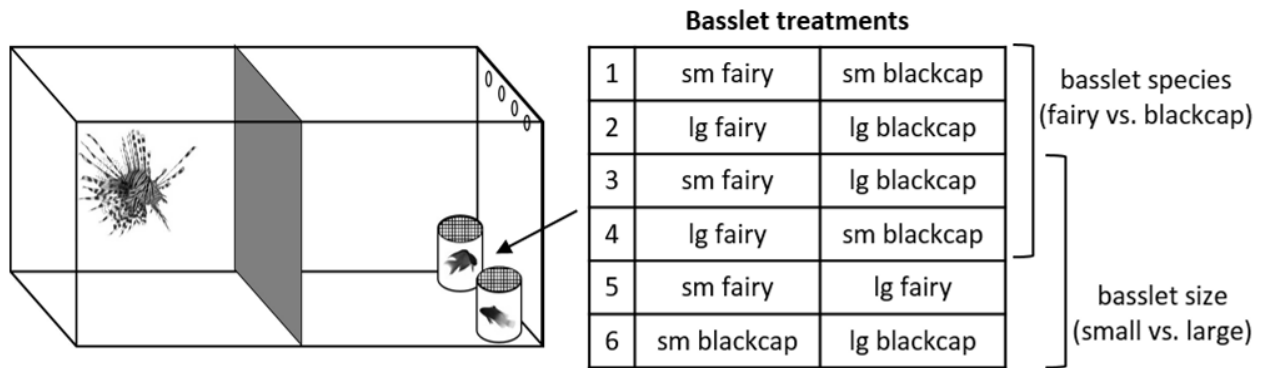
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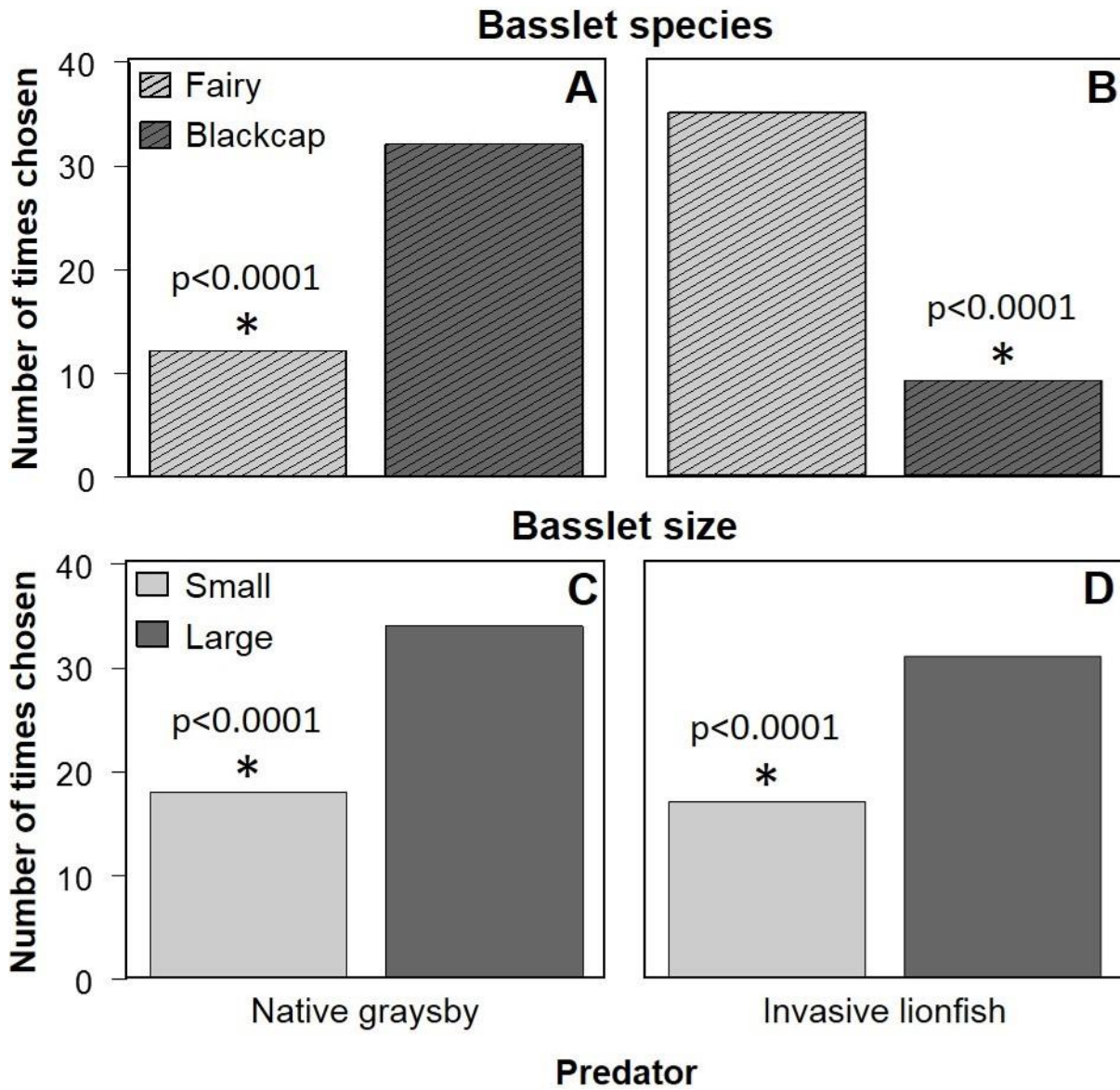
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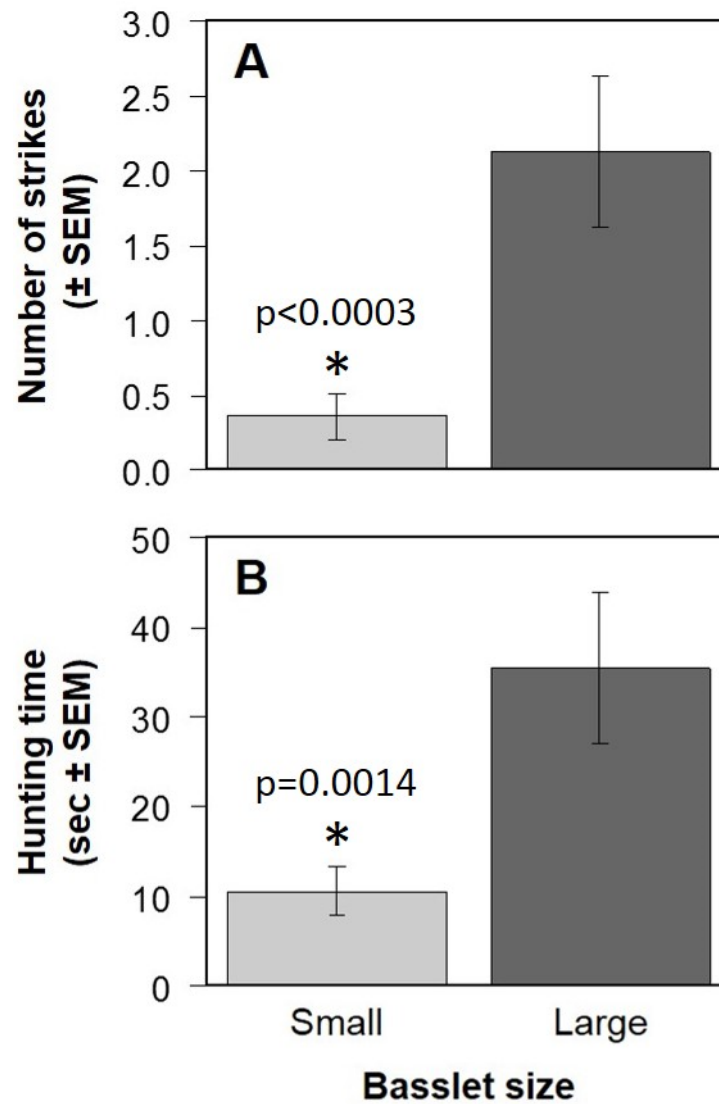
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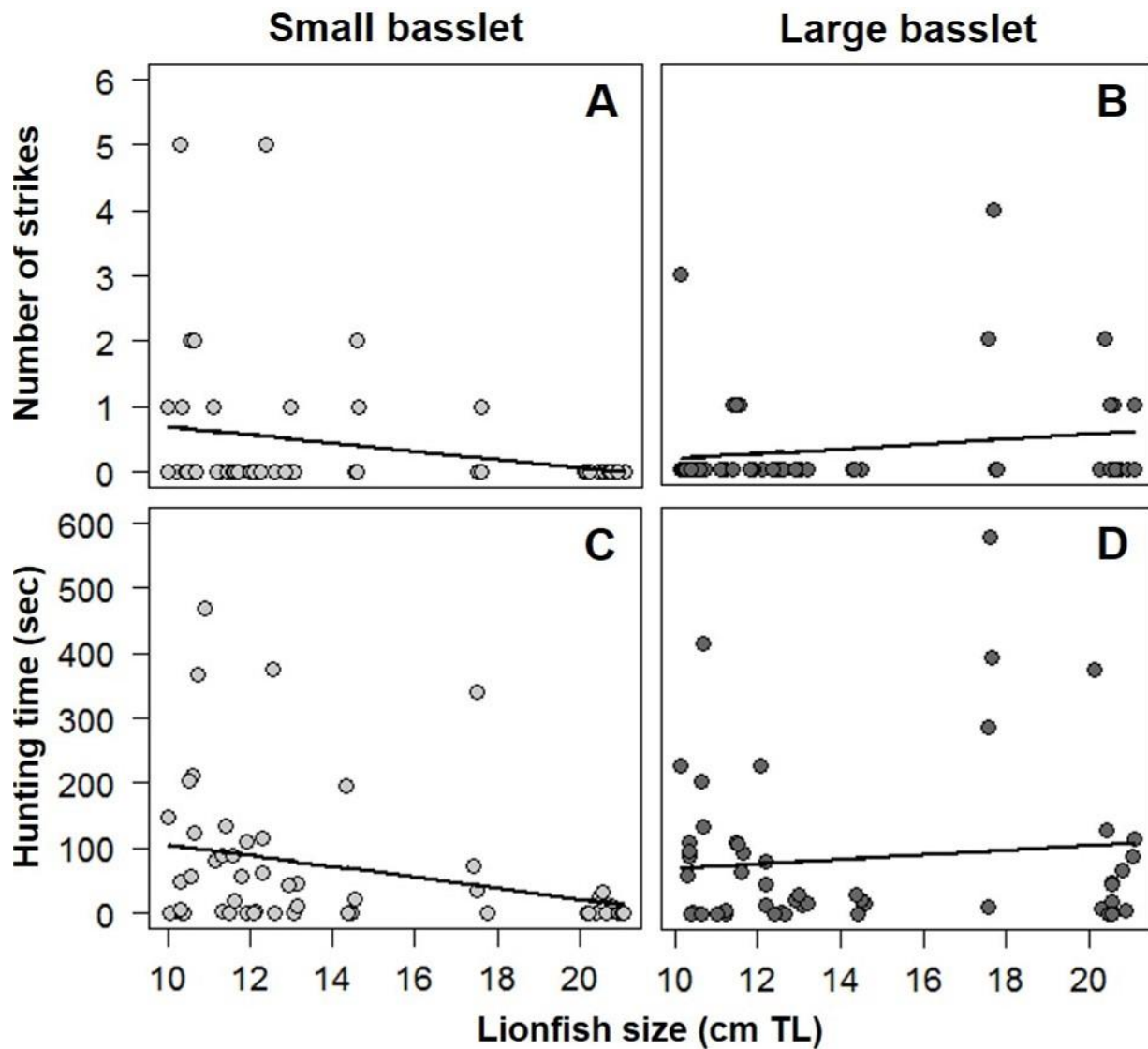
**Fig. 5.1** Experimental tank setup (left), consisting of a 50-gallon acrylic aquarium tank, divided by a removable aluminum central barrier separating basslets (in ~500 ml glass containers with mesh covers) from a predator (lionfish shown here). After a 20-minute acclimation period, the central barrier was removed and predator behavior was observed in response to randomized combinations of individual basslets randomly placed in glass containers. Basslet treatments (right) consisted of basslet species (fairy and blackcap) cross-factored with basslet size (small: 1.7-2.5 cm TL and large: 3.5-5.2 cm TL) to determine whether the preference of predators was driven by either variable.



**Fig. 5.2** Initial hunting preference of (A, C) native graysby and (B, D) invasive lionfish between (A, B) fairy versus blackcap basslets (n=11 graysby, n=11 lionfish) and (B, D) small versus large basslets (n=12 graysby, n=13 lionfish). Bars represent the total number of times that each predator initially hunted each basslet during treatments consisting of two different basslet species (n=4 per individual predator) and two different basslet sizes (n=4 per individual predator).



**Fig. 5.3** Mean ( $\pm$ SEM) number of strikes (A) and mean amount of time spent hunting (B) by native grayshy ( $n=12$ ) in response to small versus large basslets during treatments consisting of two different basslet sizes ( $n=4$  per individual predator).



**Fig. 5.4** Number of strikes (A, B) and amount of time spent hunting (C, D) by invasive lionfish ( $n=13$ ) throughout a range of lionfish sizes (cm total length) in response to small (A, C) and large (B, D) basslets during treatments consisting of two different basslet sizes ( $n=4$  per individual predator). Regression lines are models with significant interactions between lionfish size and basslet size.

**Chapter 6 – Consumptive and non-consumptive effects of an invasive marine predator  
on native coral-reef herbivores**

Tye L. Kindinger and Mark A. Albins

Biological Invasions  
*In revision*

## ABSTRACT

Invasive predators typically have larger effects on native prey populations than native predators, yet the potential roles of their consumptive versus non-consumptive effects (CEs versus NCEs) in structuring invaded systems remains unclear. Invasive lionfish (*Pterois volitans*) may have ecosystem-level effects by altering native fish grazing on benthic algae that could otherwise displace corals. Lionfish could reduce grazing by decreasing the abundance of herbivorous fishes (CEs), and/or the predation risk posed by lionfish could alter grazing behavior of fishes (NCEs). To test for these CEs, we manipulated lionfish densities on large reefs in The Bahamas and surveyed fish populations throughout June 2009-2011. In July 2011, NCEs of lionfish were measured by observing fish grazing behavior on algal-covered substrata placed in microhabitats varying in lionfish presence at different spatial scales, and quantifying any resulting algal loss. Lionfish reduced small herbivorous fish density by the end of the 2010 summer recruitment season. Grazing by small and large fishes was reduced on high-lionfish-density reefs, and small fish grazing further decreased when in the immediate presence of lionfish within-reefs. Lionfish had a negative indirect effect on algal loss, with 66-80% less algae removed from substrata in high-lionfish-density reefs. Parrotfishes were likely driving the response of herbivorous fishes to both CEs and NCEs of lionfish. Because the CEs of lionfish affect only small herbivorous fishes, but their NCEs affect both small and large fish grazing, we hypothesize that the NCEs of lionfish currently have a larger role in diminishing the ecosystem function of native herbivorous fishes.

## 6.1 INTRODUCTION

Predators can affect prey population dynamics both through direct consumption (i.e., consumptive effects [CEs]; (Taylor 1984, Sih et al. 1985, Murdoch et al. 2013) and alteration of prey behavior, morphology, or life history traits (i.e., non-consumptive effects [NCEs]; (Peacor & Werner 1997, Lima 1998). NCEs are induced when prey are faced with a tradeoff between predation risk and resource acquisition, habitat use and movement, or mating (Dill 1987, Lima & Dill 1990, Sih & Wooster 1994), and can be as strong, or stronger than, CEs on prey demography (Peacor & Werner 2001, Preisser et al. 2005). Invasive predators typically have effects on native prey populations that are larger than the effects of native predators (Salo et al. 2007, Paolucci et al. 2013), yet the role of CEs versus NCEs of invasive predators in structuring invaded communities and ecosystems remains unclear.

Negative impacts of invasive predators are most commonly attributed to CEs (Ruiz et al. 1999, Strayer et al. 2006), because these predators often cause large declines in native species (Grosholz 2002, Snyder & Evans 2006, Pitt & Witmer 2007, Cucherousset & Olden 2011, Gallardo et al. 2016) that can even reach local or global extinction (Clavero & García-Berthou 2005, Medina et al. 2011, Pringle 2011, Woinarski et al. 2015). However, the prevalence and importance of NCEs are seldom considered. The existence of NCEs hinges on the ability of prey to both perceive and respond to predation risk (Lima & Steury 2005, Berger et al. 2010). Therefore, a lack of evolutionary history between native prey and invasive predators reduces the expectation of NCEs (Sih et al. 2010), and studies that fail to corroborate NCEs of invasive predators (e.g. Pearl et al. 2003, Smith et al. 2008, Gomez-Mestre and Díaz-Paniagua 2011) typically infer that native prey are naïve (Diamond & Case 1986, Cox & Lima 2006, Banks & Dickman 2007). However, a growing number of studies illustrate the importance of considering NCEs in addition to the CEs of invasive predators in order to accurately assess both the acute



and chronic effects of invasions. For example, (Freeman & Byers 2006) demonstrated that an invasive crab induces shell thickening in a native mussel in regions of New England where the predator has invaded, and fails to induce this defense mechanism in regions where the predator has not yet invaded. And, some native species of freshwater zooplankton exhibit shifts in vertical distribution in the presence or cues of an invasive predatory cladoceran (Bourdeau et al. 2011).

The ongoing invasion of Western Atlantic and Caribbean coral reefs by Pacific red lionfish (*Pterois volitans*; Schofield 2009, 2010) constitutes one of the rare occurrences of a successful invasion by a marine fish (Côté et al. 2013a, Côté & Bruno 2015). Lionfish are novel predators in the Atlantic both in their appearance (coloration and morphology) and use of unique hunting strategies, including herding prey with widely-fanned pectoral fins (Côté & Maljković 2010, Green et al. 2011, Cure et al. 2012) and blowing directed jets of water at prey (Albins & Lyons 2012). The lionfish invasion has been recognized as a major conservation issue in a global assessment (Sutherland et al. 2010) due to the ability of this predator to cause large reductions in native fish abundance and biomass on smaller patch reefs (Albins & Hixon 2008, Albins 2013, Green et al. 2014, Benkwitt 2015) and large coral reefs (Albins 2015). These studies consistently assume that such declines in native fishes are caused by consumption of invasive lionfish, given that lionfish are considered generalist predators that hunt (Côté & Maljković 2010, Green et al. 2011, Cure et al. 2012) and consume (Morris and Akins 2009; Muñoz et al. 2011; Côté et al. 2013b) an extensive variety of small native fishes, with high consumption rates (Albins & Hixon 2008, Côté & Maljković 2010).

While the CEs of invasive lionfish on small native fishes have been well-documented, no prior studies have considered the potential role of their NCEs on a broader size range of fishes.

Without considering these potential NCEs, the documented effects of invasive lionfish on native systems could be greatly underestimated. Albins and Hixon (2013) postulated invasive lionfish could have ecosystem-level effects on invaded coral reefs similar to those caused by overfishing of native parrotfishes and other herbivores (Mumby et al. 2006, Mumby & Steneck 2008), whereby a reduction in grazing of algae indirectly enhances the ability of algae to outcompete and/or interfere with corals. Therefore, we tested for both CEs and NCEs of invasive lionfish on this important ecosystem function of native herbivorous fishes for maintaining coral-dominated reefs.

Invasive lionfish could reduce native fish grazing on reefs by depleting the abundance of grazers (CEs). Small herbivorous fishes have frequently been found in the stomachs of invasive lionfish (Albins & Hixon 2008, Morris & Akins 2009, Côté & Maljković 2010, Green et al. 2011, Muñoz et al. 2011, Cure et al. 2012, Layman & Allgeier 2012, Albins 2013, 2015, Côté et al. 2013b), including parrotfishes which are the dominant grazers on Caribbean coral reefs (Carpenter 1986, Steneck 1994) with large individuals being especially effective at removing noticeable quantities of algae (Mumby et al. 2006). The predation risk posed by invasive lionfish could potentially influence the grazing behavior of large herbivorous fishes in addition to smaller, prey-sized individuals (NCEs).

## **6.2 METHODS**

We selected 10 large (1400-4000 m<sup>2</sup>), isolated coral reefs located on the Great Bahama Bank near Lee Stocking Island, Bahamas, which ranged in depth from 2 to 11 m and were paired by similarity in habitat type. In June 2009, we performed baseline surveys of the fish community at each reef using SCUBA (survey methods below), and then manipulated invasive lionfish

densities as part of a long-term experiment (Albins 2015). We haphazardly assigned reefs in each pair to low- or high-lionfish-density treatments. Lionfish were removed from low-lionfish-density reefs using hand nets and pole spears, and we released live lionfish onto high-lionfish-density reefs. Artificially augmented lionfish densities were never greater than the highest baseline density ( $0.43 \text{ lionfish/m}^2$ ) observed across the system prior to manipulation. Every 3-5 months thereafter, a pair of SCUBA divers maintained lionfish treatments at all experimental reefs.

### *6.2.1 Reef fish surveys and analyses*

Visual surveys of reef fishes were conducted by a pair of SCUBA divers throughout (seafloor to surface) two permanent square plots ( $10 \times 10 \text{ m}$ ) and four permanent strip transects ( $2 \times 25 \text{ m}$ ), for a total area of  $400 \text{ m}^2$  per reef (Albins 2015). We positioned square plots to include areas of the reef with the highest apparent relief, and strip transects were placed randomly across the remaining hard substrate, with the intent of including all important high-relief habitat features. Divers conducted censuses of each sampling unit whereby each fish was identified to the species-level and total length (TL) was visually estimated to the nearest cm. Paired reefs (low- and high-lionfish-densities) were surveyed within 24 hours by the same set of observers, and all reefs were surveyed by coauthor, M. Albins. Every 3-5 months thereafter, we resurveyed the fish community at all experimental reefs.

We quantified CEs of invasive lionfish on native herbivorous fish populations throughout the two-year experiment by comparing the change in density and biomass of small and large herbivorous fishes between lionfish-density treatments. *Small* fish were  $\leq 10 \text{ cm TL}$ , which encompasses the majority of prey fish sizes reported in invasive lionfish gut-content studies for

the size range of lionfish (2-35 cm TL) observed on our experimental reefs (Morris & Akins 2009, Muñoz et al. 2011). Responses of fish >10 cm TL were consistent, regardless of whether individuals were binned into medium (11-20 cm TL) and large (>20 cm TL) size classes, so hereafter we refer to all fish >10 cm TL as *large*. To determine the relative response of different subguilds of herbivorous fishes, we also calculated the change in small and large fish density and biomass by fish family: (1) *parrotfishes* (Labridae); (2) *surgeonfishes* (Acanthuridae); (3) *angelfishes* (Pomacanthidae); and (4) *damselfishes* (Pomacentridae). We used published length-weight conversions to calculate fish biomass; parameters of closely related species were used when conversions were not available (Online Resource 1). We calculated changes in fish density and biomass at every survey interval by subtracting the baseline value (prior to initial lionfish manipulation) for each sub-sample (plots and transects) from the corresponding value of each subsequent survey.

To test for an effect of invasive lionfish through time on changes in density and/or biomass of each group of native fishes (described above), we fitted linear mixed effects models (LMMs) with *lionfish*-density treatment and *time* as categorical fixed effects, and *sub-sample* nested within *reef* as random effects (Pinheiro & Bates 2000, Bolker et al. 2009, Zuur et al. 2009). *Time* was a categorical variable because we had no a priori reason to assume any linear relationships with response variables. Full models included weighted terms allowing variances to differ among reefs and AR1 structures to account for temporal autocorrelation (Zuur et al. 2009). We fitted full and reduced models (with versus without weighted terms and/or AR1 structures) using restricted maximum likelihood (REML) and compared full and reduced models using Akaike's Information Criterion (AIC) and likelihood ratio tests (LRTs). Visual

examination of residuals of the best-fit models indicated that the assumptions of normality, homogeneity, and independence were all met.

To assess the magnitude of fixed effects, we refit each model using maximum likelihood estimation (ML) and applied LRTs (Zuur et al. 2009). Fixed effects that were not significant were sequentially dropped from models. The resulting best-fit models in terms of variance structure, temporal correlation, and fixed effects were refit using REML in order to estimate the fixed-effects parameters and associated effect sizes. If LRTs indicated the *lionfish*  $\times$  *time* interaction was significant, we made simultaneous inferences about the marginal effects of the lionfish treatment at each survey period, and adjusted the associated p-values to maintain an approximately 5% family-wise error rate (Hothorn et al. 2008).

Regardless of whether the *lionfish*  $\times$  *time* interaction was significant, we estimated expected values and standard error of the means (SEMs) for all response variables from low- and high-lionfish-density treatments during each survey period. We also fit LMMs to compare the baseline levels of each response variable between lionfish-density treatments using a similar procedure to the one outlined above, but with density and biomass of each group of small and large fishes (described above) as the response (rather than the change in these variables). Additionally, we fit LMMs to assess whether small ( $\leq 10$  cm) and large ( $> 10$  cm) native *mesopredators* (Table E.1) that are potentially ecologically-similar to invasive lionfish differed between the reefs assigned to each lionfish-density treatment at the baseline survey (mesopredator density and biomass) and at each subsequent survey period (change in mesopredator density and biomass).

### 6.2.2 Fish grazing surveys and analyses

To quantify NCEs of invasive lionfish on native herbivores, we observed the grazing behavior of herbivorous fishes at each of the 10 experimental reefs over 10 consecutive days in July 2011, observing paired reefs on adjacent days. Each day, we collected 20 haphazardly selected pieces of algal-covered coral rubble (0.43-0.94 m<sup>2</sup> surface area) from a non-experimental reef containing an extensive area of dead *Acropora cervicornis* coral rubble inhabited by a high density of three-spot damselfish (*Stegastes planifrons*). This territorial fish maintains higher standing stocks of farmed palatable seaweeds (Brawley & Adey 1977) via interspecific aggression in response to intruding herbivores (Gibson et al. 2001).

Each piece of algal substratum was carefully placed into a plastic bag filled with seawater, photographed out of water onboard a boat, returned to its plastic bag, and transported in a cooler of seawater to a nearby experimental reef. At high-lionfish-density reefs, we randomly assigned paired substrata to two similar, but separate microhabitats (e.g., next to a coral head, on a ledge, etc.) that differed only in the presence (<0.25 m away) versus absence (>3 m away) of lionfish at the time of observation. At low-lionfish-density reefs, we placed algal substrata in paired microhabitats that were similar to those used at high-lionfish-density reefs, except lionfish were always absent during observation. All replicates were therefore placed in types of microhabitats frequented by lionfish, regardless of actual lionfish presence. Overall, we observed grazing of translocated algal-covered substrata at three levels of lionfish presence: (1) low-lionfish-density reef with lionfish absent from the observed microhabitat (n=100); (2) high-lionfish-density reef with lionfish absent from the microhabitat (n=50); and (3) high-lionfish-density reef with lionfish present in the microhabitat (n=50); hereafter referred to as *low-absent*, *high-absent*, and *high-present* treatments, respectively. These treatments were designed to provide insight on the spatial scale at which lionfish presence affects herbivorous fish behavior

by allowing simultaneous comparisons of grazing behavior between (1) low- and high-lionfish-densities at the reef-scale while controlling for lionfish presence at the within-reef scale (i.e., low-absent vs. high-absent treatments) and (2) lionfish presence-absence at the within-reef scale while controlling for lionfish density at the reef-scale (i.e., high-absent vs. high-present treatments).

At each experimental reef, we monitored four of the translocated algal substrata -- one pair in the morning (0900-1200) and one pair in the afternoon (1400-1600) -- for 60 minutes each using automated underwater video cameras placed approximately 3 m away. Meanwhile, we observed the remaining 16 algal substrata with SCUBA (8 replicates per diver) one at a time for 20 minutes each, with observations divided evenly throughout the day (2 pairs in the morning and 2 pairs in the afternoon per diver). All observations were therefore performed during the day when the probability of lionfish predation is greatly reduced (Green et al. 2011; Cure et al. 2012) and all lionfish observed were inactive. We identified the species of each fish that visited these substrata, visually estimated its TL to the nearest cm, and counted the number of times it took a bite of algae. Each fish was considered to be a unique individual once it entered the diver's field of view (approximately 2 m surrounding the focal rock), and continuing until the time it left the field of view and could no longer be visually tracked. At the end of each observation period, the algal substratum was carefully returned to its plastic bag full of fresh seawater and kept underwater until all 20 replicates had been observed. We then rephotographed each replicate onboard the boat.

Grazing behavior observed at each replicate algal substratum comprised the following response variables: (1) visitation rate (number of fish/minute); (2) percent visitation rate (percent fish/minute); (3) bite rate (number of bites/minute); and (4) individual bite rate (mean number of

bites per fish/minute). The percent visitation rate and individual bite rate allowed us to account for any potential differences in herbivorous fish densities between low- and high-lionfish-density reefs. Percent visitation rates were calculated by dividing the total number of fish observed grazing (per minute) by the total number of herbivorous fish counted at each reef during the reef fish surveys conducted just prior (June 2011) to the grazing observations (July 2011). For all the herbivorous fish that grazed on each experimental substrate, the number of bites each fish took during individual grazing bouts was averaged to measure the individual bite rate. We also used the before and after photographs of each substrate to estimate the percent loss of algal cover from observed grazing. We quantified percent cover from photographs using the image processing program, ImageJ.

Parrotfishes accounted for 69.2% of the herbivorous fishes that grazed on the experimental substrate. Therefore, the response (same variables as above) of this fish family was also analyzed by fish size class (*small* and *large*, with *large* encompassing the response among fishes >10 cm TL, which remained consistent regardless of further size binning into medium (11-20 cm TL) and large (>20 cm TL) size classes). The remaining fish families (surgeonfishes, angelfishes, and damselfishes) were not further divided by size class, because such extensive division of each response variable would have resulted in highly zero-inflated data. The percent loss of algae from substrata was not analyzed by fish size class nor by fish family, because individual contributions of each fish to the overall algal loss could not be distinguished.

We fitted LMMs using a similar procedure as the one described above to account for the nested design of the fish grazing surveys when comparing grazing behavior of herbivorous fish among lionfish treatments. Random effects consisted of paired microhabitats nested within paired reefs. In addition to *lionfish* treatment, all full models included the initial algal percent



cover (*algae*) of each replicate substratum as a fixed factor in order to account for any influence this parameter could have on grazing behavior, as well as an *algae*  $\times$  *lionfish* interaction. With the exception of the percent loss in algal cover model, we log-transformed all rate response variables and allowed variances to differ among reefs with weighted terms to meet all assumptions of normality, homogeneity, and independence. When lionfish treatment was significant in the model based on LRTs, we performed multiple comparisons of the response at every combination of lionfish treatments using Tukey's Honestly Significant Difference (HSD) method.

All statistical analyses of both reef fish surveys and fish grazing observations were conducted using the statistical software *R* version 3.1.2 (*R* Core Team 2014) with the associated packages, *nlme* (version 3.1-118; Pinheiro et al. 2014) and *multcomp* (version 1.3-7; Hothorn et al. 2008).

## 6.3 RESULTS

### 6.3.1 Consumptive effects of lionfish on native herbivorous fish populations

The baseline density and biomass of all groups and size classes of fishes did not significantly differ prior to lionfish-density manipulation (Table E.3). Following manipulation, lionfish reduced the density of small but not large herbivorous fishes (Table 6.1, Fig. 6.1), and this effect varied over time (*lionfish*  $\times$  *time* interaction: LRT  $P = 0.002$ ). While densities of small herbivorous fishes were always lower on high-lionfish-density reefs than low-lionfish-density-reefs (Fig. 6.1A), densities differed only in August 2010 ( $-0.61 \pm 0.17$  fish  $\cdot$  m<sup>2</sup>  $\pm$  SEM, LMM  $P_{\text{cor}} = 0.014$ ). Lionfish did not have an effect on the biomass of herbivorous fishes (Table 6.1). The response of parrotfishes was similar to the overall herbivorous fish community response

(Table 6.1, Fig. 6.1) in that the density of small parrotfishes was generally lower on high-lionfish-density reefs than low-lionfish-density reefs. While parrotfish density fluctuated over time (LRT  $P = 0.017$ , Fig. 6.1C) negative effect of lionfish were detected only in August 2010 ( $-0.37 \pm 0.14 \text{ fish} \cdot \text{m}^{-2} \pm \text{SEM}$ , LMM  $P_{\text{cor}} = 0.048$ ). Lionfish did not have an effect on any other individual herbivorous fish families (Table E.2).

Throughout the experiment, lionfish densities at high-lionfish-density reefs were consistently an order of magnitude greater than at low-lionfish-density reefs (mean  $\pm$  SEM:  $0.031 \pm 0.004$  and  $0.002 \pm 0.0009$ , respectively). Densities were calculated from lionfish counts conducted prior to lionfish manipulations performed during each survey period. The density and biomass of both small and large native mesopredators did not significantly differ between reefs assigned to low- and high-lionfish-density treatments (Table E.2).

### 6.3.2 *Non-consumptive effects of lionfish on grazing by native herbivorous fishes*

When herbivorous families were pooled, lionfish had a negative effect on both small and large fish grazing behavior in all response variables measured (Table 6.2). Small herbivorous fishes decreased grazing in response to lionfish at high-lionfish-density reefs (low-absent vs. high-absent and high-present lionfish treatments), and decreased grazing even further in the presence of lionfish at the within-reef scale (high-absent vs. high-present lionfish treatments, Table E.4, Fig. 6.2). Lionfish also caused a decline in large fish grazing at the between-reef scale that was maintained regardless of lionfish presence within-reefs (Table E.4, Fig. 6.2). Lionfish did not have a significant effect on the grazing behavior of individual fish families, with the exception of parrotfishes (Tables 6.2 and E.5). The response of both small and large parrotfishes decreased with increasing presence of lionfish, yet lionfish caused a reduction in all

response variables (Table 6.2) that significantly differed only at the between-reef scale (Table E.4, Fig. 6.3). In addition to lionfish treatment, the amount of available *algae* affected the individual bite rates of large herbivorous fishes and large parrotfishes (Table 6.2), with increases of  $0.98 \pm 0.01$  and  $0.97 \pm 0.01$  bites·fish<sup>-1</sup>·min<sup>-1</sup>, respectively, with each percent increase in initial algal cover.

The rate of algal loss from observed fish grazing increased with increasing initial algal percent cover and varied with lionfish abundance at the between-reef scale (*algae* × *lionfish* interaction: LRT  $P=0.002$ , Fig. 6.4). On low-lionfish-density reefs, the amount of algae removed from substrata (*algal loss*) increased by  $0.56 \pm 0.08$  % per one percent increase in initial algal cover. This relationship was diminished on high-lionfish-density reefs (low-absent vs. high-absent lionfish treatments: LMM  $P = 0.020$ ) with 66% less algae removed ( $0.19 \pm 0.13$  % per percent increase in initial algal cover). 80% less algae was removed in high-present ( $0.11 \pm 0.12$  % per percent increase in initial algal cover) versus low-absent lionfish treatments, yet this algal loss was not greater than the loss observed in the high-absent lionfish treatment (LMM  $P = 0.615$ ). While not every species of herbivorous fish identified during the reef fish surveys was observed during the fish grazing surveys (Table E.6), the algal-covered substrata we used in this study were still sufficient for capturing substantial grazing behavior on our experimental reefs; over 75% of the substrata (151 of 200 replicates) were grazed by an herbivorous fish at least once.

## 6.4 DISCUSSION

At this point in the invasion, our study indicates that the CEs of lionfish affect small, but not large native herbivorous fishes, while their NCEs affect both small and large native

herbivorous fishes. Parrotfishes (the dominant grazers on Caribbean coral reefs) appeared to drive the response of the overall native herbivorous fish community to both the CEs and NCEs of lionfish. The ability of parrotfishes to remove algae from coral reefs is strongly dependent not only on their abundance, but also individual body and jaw size (Hoey & Bellwood 2008). Therefore, in terms of the amount of algae removed on coral reefs via fish grazing, we hypothesize that the NCEs of invasive lionfish have greater effects on the ecosystem function of native herbivorous fishes than their CEs.

Over the course of our two-year study, we observed an expected seasonal trend in small herbivorous fish density, with increases in density occurring throughout the summer months when fish recruitment exceeds mortality, followed by declines in density during the winter months when mortality exceeds recruitment and individuals leave the size class with growth. Changes in density of small herbivorous fishes did not differ through time between low- and high-lionfish-density reefs, with the exception of the end of the 2010 summer recruitment season. These findings are consistent with previous studies which demonstrate invasive lionfish reduced the abundance of small native fish populations by the end of summer (Albins & Hixon 2008, Albins 2013, 2015, Green et al. 2014, Benkwitt 2015).

Prior behavioral observations (Maljković et al. 2008; Green et al. 2011; Cure et al. 2012) and gut-content studies provide clear evidence that invasive lionfish consume small native herbivorous fishes (e.g. Morris and Akins 2009; Côté and Maljković 2010; Layman and Allgeier 2012; Côté et al. 2013b). Therefore, we assume that the reduction in small herbivorous fish density observed in this study was indicative of direct CEs of invasive lionfish. The density of herbivorous fishes did not consistently differ between lionfish treatments through time, which further bolsters the assumption of CEs of lionfish. If NCEs of invasive lionfish were influencing

the abundance of herbivorous fishes on reefs, then these fishes would be expected to exhibit lower abundances on high- versus low-lionfish-density reefs consistently through time.

However, it is possible that the effect of lionfish presence (lionfish NCEs) on the foraging behavior of herbivorous fishes in our study likely represents associated costs of antipredator behavior (Peckarsky et al. 1993, Ruxton & Lima 1997, Brown & Kotler 2004, Creel et al. 2007, Pangle et al. 2007). In turn, this may have contributed to the decline in density of small herbivorous fishes that we observed on high-lionfish-density reefs. In addition, recruitment of coral-reef fishes can be influenced by the presence of predators and/or conspecifics (i.e., priority effects, Shulman et al. 1983, Almany 2003, 2004, Shulman 2015). Thus lionfish may have influenced the recruitment of native herbivorous fishes on experimental reefs, either directly via their presence as a potential predator and/or indirectly by altering the abundance of conspecifics or other native fishes through time.

Herbivorous fishes decrease grazing behavior in response to predation risk (Madin et al. 2010), resulting in characteristic grazing halos surrounding coral reefs (Randall 1965, Hay et al. 1983, Madin et al. 2011). Despite lionfish being a novel predator, we have shown that (Preisser et al. 2005) the presence of invasive lionfish resulted in NCEs on both small and large herbivorous fishes: fewer fish grazed (visitation rate) and individuals that did graze took fewer bites (individual bite rate), which resulted in an overall decrease in grazing intensity (bite rate). Decreased visitation rates could be explained by lower densities of herbivorous fishes on high-lionfish-density reefs, yet when we accounted for lionfish CEs (percent visitation rate), we still found lower visitation rates. Additional decreases in grazing by small herbivorous fishes (but not large herbivorous fishes) when lionfish were present (versus absent) within-reefs may also suggest that the spatial scale of sensory data used in risk-based decision making likely varies

with body size, and/or ontogenetic shifts in response to cues (Ferrari et al. 2010) of a gape-limited predator, whereby the level of perceived risk necessary to warrant a behavioral response may increase with herbivorous fish body size.

Lönnstedt & McCormick (2013) demonstrated that a Pacific prey species (*Chromis viridis*) fails to respond to visual and/or chemical cues of lionfish (*P. volitans*) collected from the native range. Studies to date that document the ability of Atlantic prey to recognize and/or appropriately respond to the presence of invasive lionfish as a potential predator suggest antipredator response may be species-dependent (Marsh-Hunkin et al. 2013, Black et al. 2014, Kindinger 2015, Anton et al. 2016). Our study clearly demonstrates that both juvenile and adult native parrotfishes reduce their grazing activity when in the presence of invasive lionfish, which is consistent with previous observations of grazing by juveniles of a native parrotfish when in the presence of invasive lionfish in aquaria (Eaton et al. 2016).

Differences in the antipredator responses of prey fishes between the native and invaded ranges of lionfish could be explained by the relative predation pressure of lionfish in each range. Population densities of lionfish are far greater in their invaded range, reaching over 390 fish/hectare versus 26.3 fish/hectare in their native range (Green & Côté 2009, Kulbicki et al. 2012). Therefore, the rate of encounter between lionfish and prey fishes is likely to be much higher in the invaded range. As a result, the extent in which survival outweighs the costs of antipredator behavior in response to lionfish is likely greater in Atlantic prey.

Throughout the invaded range, native prey that experience initial heavy predation by an invasive predator are expected to shift toward adaptive antipredator behavior (Sih et al. 2010). Studies consistently demonstrate that herbivorous fishes (especially parrotfishes) are among the native species on which invasive lionfish have the greatest effects (Albins & Hixon 2008, Albins

2013, Green et al. 2014, Benkwitt 2015), and thus may have an increased likelihood of adapting antipredator response to lionfish relatively sooner than fishes that are less affected. Some herbivorous fishes, such as parrotfishes, often forage in groups (Itzkowitz 1977, Ogden & Lobel 1978, Wolf 1985), which could further facilitate transmission of antipredator response among group individuals via social learning (Mathis et al. 1996).

Differences in antipredator behavior among native prey in response to invasive lionfish could also be explained by variance among species in the ability to recognize and respond appropriately to this novel predator. Aquatic prey may use general or specific cues when detecting predators (Petranka et al. 1987, Chivers & Smith 1998, Kats & Dill 1998, Brown 2003). General cues include signals from damaged conspecifics or heterospecifics, or the presence of any novel object larger than a minimum size threshold (Dill 1974, Sih 1986). Prey that rely upon general cues are more likely to exhibit an antipredator response to a novel predator (Sih et al. 2010), but are also more likely to unnecessarily respond to stimuli from non-threatening sources (e.g., Langerhans & DeWitt 2002). In our study, herbivorous fishes responded to invasive lionfish throughout the day when lionfish are relatively inactive and do not pose an actual predation threat (Côté & Maljković 2010, Green et al. 2011, Cure et al. 2012), which suggests these fishes may use general cues.

Field observations of juvenile parrotfishes conducted during the day by Anton et al. (2016) indicated native individuals that approached invasive lionfish reached distances that were closer than those of individuals that swam near native predators. The authors conclude that this behavior suggests prey naiveté, but these findings could also suggest that parrotfishes in the invaded range have adapted an appropriate response to inactive lionfish in terms of parrotfish movement within reefs. Alternatively, antipredator response of native parrotfishes to invasive

lionfish could consist of only altered grazing activity. Additional observations need to be conducted at dawn and dusk to observe both the movement and grazing behavior of native parrotfishes in the presence of invasive lionfish that are actively hunting. Further research is also needed to determine the types of cues (chemical and/or visual) of lionfish that cause (or fail to cause) a response in parrotfishes, and test which types of behaviors parrotfishes alter in response to these cues.

Albins & Hixon (2013) postulated invasive lionfish could have indirect effects on native benthic communities similar to those caused by overfishing of parrotfishes and other herbivores (Mumby et al. 2006, Mumby & Steneck 2008). Our study further supports the potential for this lionfish trophic cascade by demonstrating that lionfish have a negative indirect effect on algal loss via reduced fish grazing, which corresponded with herbivorous fish grazing behavior (likely driven by parrotfishes). Less algae was removed at high-lionfish-density reefs when grazing was reduced by both small and large herbivorous fishes. However, reduced grazing of small herbivorous fishes alone when lionfish were present within-reef failed to produce a corresponding reduction in the amount of algae removed. Therefore, we infer that the pattern in algal loss was largely driven by large herbivorous fish behavior, especially since larger parrotfishes have the biomechanical means to remove substantial quantities of algae (Hoey & Bellwood 2008). Additional testing is needed to determine whether this reduced grazing on substrata caused by the presence of lionfish is maintained at larger spatial scales and occurs on the natural reef landscape.

Further testing of CEs and NCEs of invasive predators on native prey at larger temporal and spatial scales will greatly inform our understanding of the effects of invasive predators on native communities and ecosystems. Over longer time periods, we predict that if invasive



lionfish continue to cause increased prey mortality in addition to any potential survival and fitness costs related to antipredator behavior (Peckarsky et al. 1993, Ruxton & Lima 1997, Brown & Kotler 2004, Creel et al. 2007, Pangle et al. 2007), then native herbivorous fish populations could further decline in density and experience shifts in size and age structure. This could ultimately result in even greater reductions in fish grazing of algae throughout invaded ecosystems.

We have demonstrated the importance of considering and rigorously testing for NCEs in addition to CEs of invasive predators when assessing the effects of invasions. Understanding the roles of CEs and NCEs of invasive predators on native prey can also provide crucial insight for detecting novel indirect effects and trophic cascades that could potentially have ecosystem-level consequences. Further testing of these interactions between invasive predators and native prey at larger scales will greatly enhance our ability to accurately predict both acute and chronic impacts of invasions.

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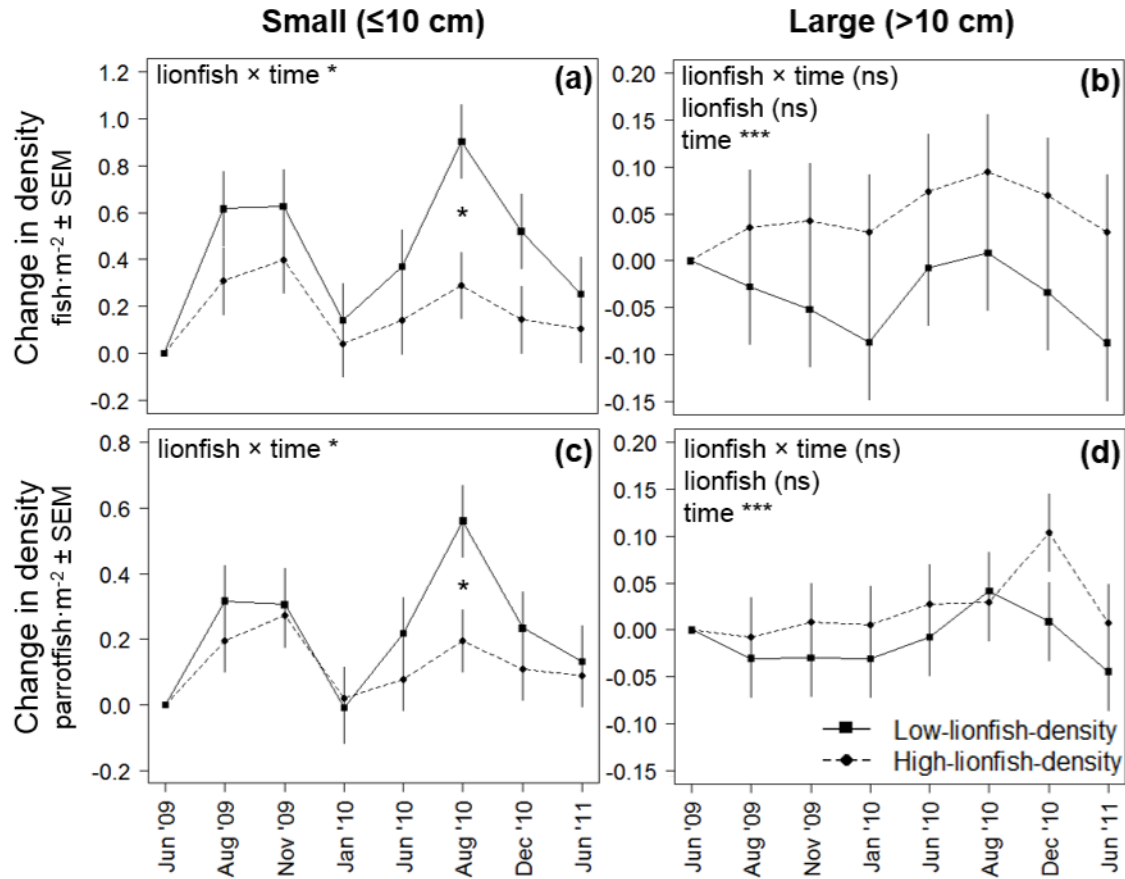


**Table 6.1** Results of hypothesis tests for the effect of lionfish-density-treatment (“lionfish”, *Pterois volitans*) and time on the density and biomass of small ( $\leq 10$  cm TL) and large ( $> 10$  cm TL) herbivorous fish of all families combined and parrotfishes observed during reef surveys. The significance of fixed effects was calculated using likelihood-ratio tests (LRT) comparing nested models fit by Maximum Likelihood Estimation. If the lionfish  $\times$  time interaction was significant, p-values from linear combinations were adjusted ( $p_{adj}$ ) to achieve an approximate family-wise error rate of 5%.

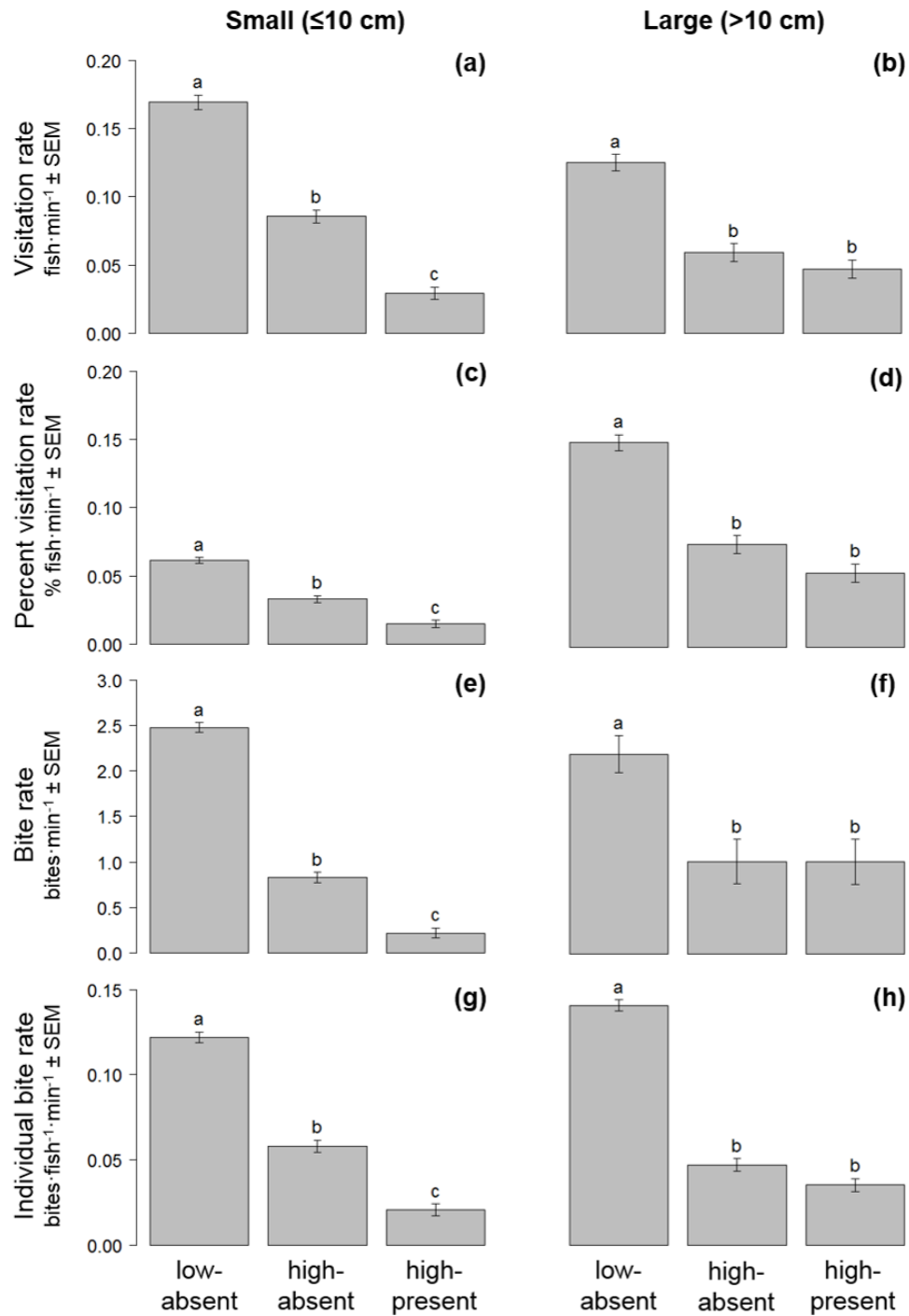
Group	Size class	Response variable	Fixed effect	LRT p	Survey period	$p_{adj}$
All herbivorous fishes	Small	Density	<b>lionfish <math>\times</math> time</b>	<b>0.002</b>	Aug 2009	0.348
					Nov 2009	0.593
					Jan 2010	0.976
					Jun 2010	0.585
					<b>Aug 2010</b>	<b>0.014</b>
					Dec 2010	0.203
					Jun 2011	0.865
	Large	Biomass	lionfish $\times$ time	0.053		
			lionfish	0.211		
			<b>time</b>	<b>&lt;0.001</b>		
		Density	lionfish $\times$ time	0.798		
			lionfish	0.218		
			<b>time</b>	<b>&lt;0.001</b>		
		Biomass	lionfish $\times$ time	0.875		
			lionfish	0.396		
			<b>time</b>	<b>&lt;0.001</b>		
Parrotfishes (Labridae)	Small	Density	<b>lionfish <math>\times</math> time</b>	<b>0.017</b>	Aug 2009	0.857
					Nov 2009	0.999
					Jan 2010	0.999
					Jun 2010	0.770
					<b>Aug 2010</b>	<b>0.048</b>
					Dec 2010	0.843
					Jun 2011	0.999
	Large	Biomass	lionfish $\times$ time	0.118		
			lionfish	0.344		
			time	0.113		
		Density	lionfish $\times$ time	0.248		
			lionfish	0.461		
			<b>time</b>	<b>&lt;0.001</b>		
		Biomass	lionfish $\times$ time	0.140		
			lionfish	0.662		
			<b>time</b>	<b>&lt;0.001</b>		

**Table 6.2** Results of likelihood ratio tests of lionfish treatment (“lionfish”) and initial algal percent cover (“algae”) on small ( $\leq 10$  cm TL) and large ( $> 10$  cm TL) herbivorous fishes.

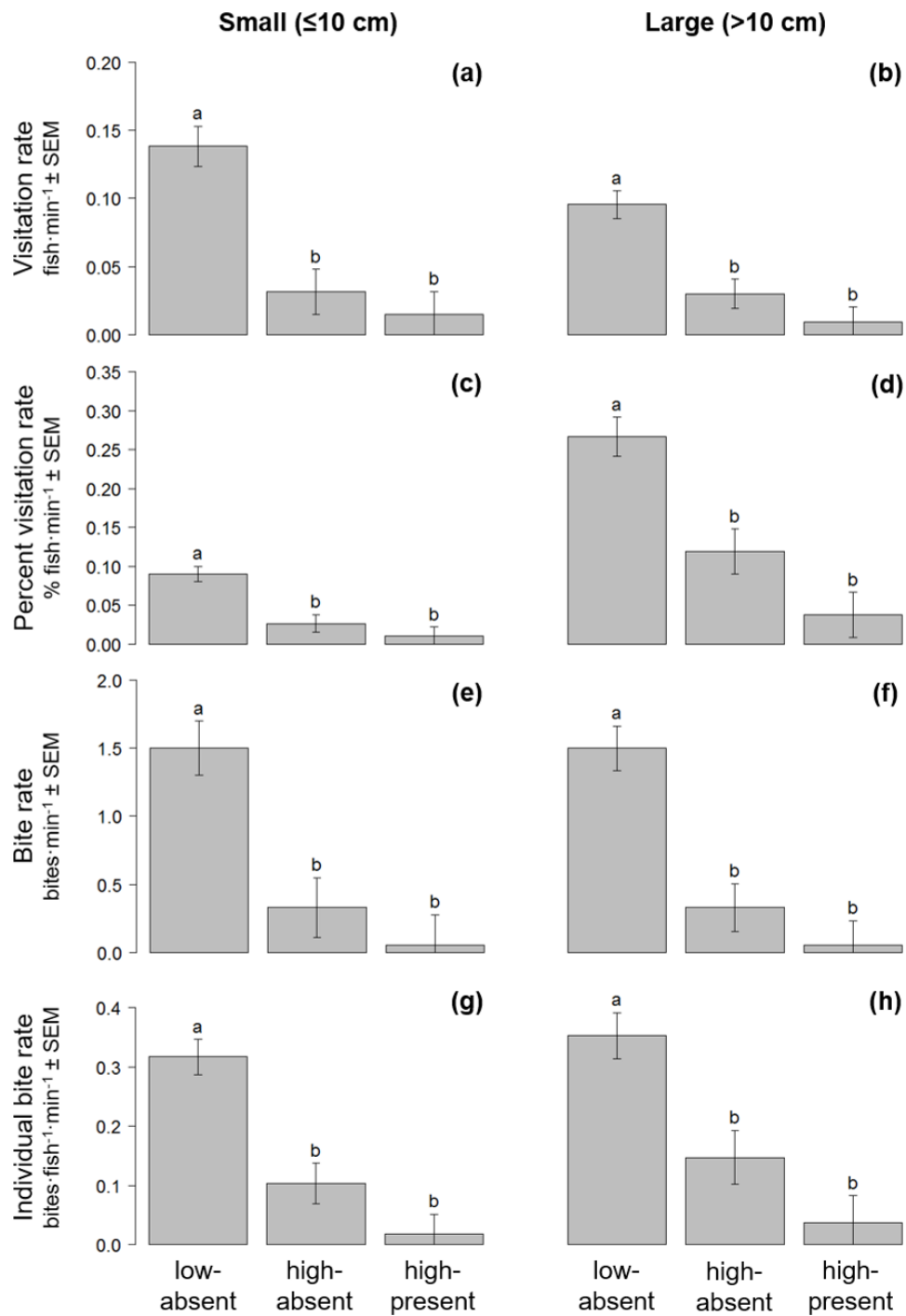
Group	Size class	Response variable	Fixed effect	LRT p
All herbivorous fishes	Small	Visitation rate	algae $\times$ lionfish	0.641
			algae	0.411
			<b>lionfish</b>	<b>&lt;0.001</b>
		Percent visitation rate	algae $\times$ lionfish	0.590
			algae	0.387
			<b>lionfish</b>	<b>&lt;0.001</b>
		Bite rate	algae $\times$ lionfish	0.585
			algae	0.348
			<b>lionfish</b>	<b>&lt;0.001</b>
	Large	Visitation rate	algae $\times$ lionfish	0.518
			algae	0.698
			<b>lionfish</b>	<b>&lt;0.001</b>
		Percent visitation rate	algae $\times$ lionfish	0.591
			algae	0.994
			<b>lionfish</b>	<b>&lt;0.001</b>
		Bite rate	algae $\times$ lionfish	0.442
			algae	0.840
			<b>lionfish</b>	<b>&lt;0.001</b>
Parrotfishes (Labridae)	Small	Visitation rate	algae $\times$ lionfish	0.530
			algae	0.240
			<b>lionfish</b>	<b>&lt;0.001</b>
		Percent visitation rate	algae $\times$ lionfish	0.441
			algae	<b>0.042</b>
			<b>lionfish</b>	<b>&lt;0.001</b>
		Bite rate	algae $\times$ lionfish	0.811
			algae	0.796
			<b>lionfish</b>	<b>&lt;0.001</b>
	Large	Visitation rate	algae $\times$ lionfish	0.892
			algae	0.789
			<b>lionfish</b>	<b>&lt;0.001</b>
		Percent visitation rate	algae $\times$ lionfish	0.957
			algae	0.911
			<b>lionfish</b>	<b>&lt;0.001</b>
		Bite rate	algae $\times$ lionfish	0.953
			algae	0.994
			<b>lionfish</b>	<b>&lt;0.001</b>
	Small	Visitation rate	algae $\times$ lionfish	0.581
			algae	0.367
			<b>lionfish</b>	<b>&lt;0.001</b>
		Percent visitation rate	algae $\times$ lionfish	0.599
			algae	0.408
			<b>lionfish</b>	<b>&lt;0.001</b>
		Bite rate	algae $\times$ lionfish	0.516
			algae	0.135
			<b>lionfish</b>	<b>&lt;0.001</b>
	Large	Individual bite rate	algae $\times$ lionfish	0.220
			<b>algae</b>	<b>0.002</b>
			<b>lionfish</b>	<b>&lt;0.001</b>



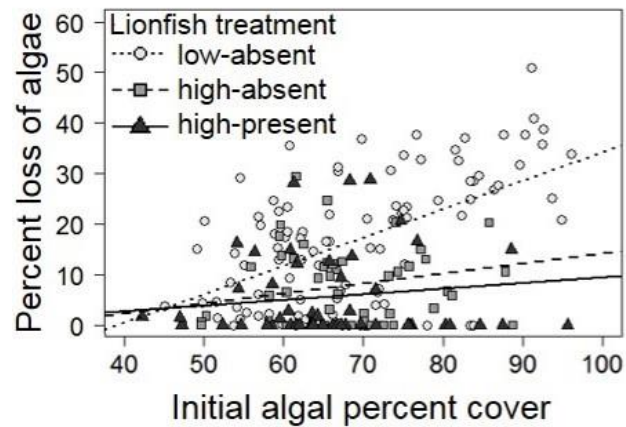
**Fig. 6.1** Change in density of (a, c) small and (b, d) large herbivorous fish of (a, b) all families combined and (c, d) parrotfishes at low- and high-lionfish-density reefs ( $n = 5$  reefs each). Means and SEMs were estimated from the full linear mixed effects models with the lionfish  $\times$  time interaction term. Results of likelihood ratio tests for the fixed effects are shown at the top left of each plot. When the lionfish  $\times$  time interaction was significant, the marginal effects of lionfish treatment were examined at each survey date; adjusted p-values to obtain an approximate family-wise error rate of 5% are indicated for each date. Significance: ns:  $p > 0.05$ , \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ .



**Fig. 6.2** Response of (a, c, e, g) small and (b, d, f, h) large herbivorous fishes of all families combined observed during grazing surveys in each lionfish treatment: low-absent ( $n = 100$ ), high-absent ( $n=50$ ), and high-present ( $n=50$ ). Estimated mean values and SEMs were calculated from the final nested models fit by Restricted Maximum Likelihood. Letters within each plot indicate significant differences in response among lionfish treatments from the final models, with matching letters signifying a  $p$ -value  $> 0.05$ .



**Fig. 6.3** Response of (a, c, e, g) small and (b, d, f, h) large parrotfishes observed during grazing surveys in each lionfish treatment: low-absent ( $n = 100$ ), high-absent ( $n=50$ ), and high-present ( $n=50$ ). Estimated mean values and SEMs were calculated from the final nested models fit by Restricted Maximum Likelihood. Letters within each plot indicate significant differences in response among lionfish treatments from the final models, with matching letters signifying a  $p$ -value  $> 0.05$ .



**Fig. 6.4** Percent loss in algal cover due to grazing by herbivorous fishes during grazing surveys as a function of initial algal cover on translocated substrata. The result of a likelihood-ratio test indicated a significant initial algae  $\times$  lionfish treatment interaction ( $p=0.002$ ). Symbols represent the percent algal loss of each rock observed in low-absent ( $n=100$ ), high-absent ( $n=50$ ), and high-present ( $n=50$ ) lionfish treatments. Corresponding lines for each lionfish treatment were calculated (estimated intercepts and slopes) from the full nested model fit by Restricted Maximum Likelihood.

## **Chapter 7 – General Conclusions**

The research described in this dissertation demonstrates that an invasive predator alters native community interactions in a marine system both directly and indirectly. This work includes the first experimental evidence of invasive lionfish indirectly affecting native organisms on Atlantic coral reefs. Indirect effects of biotic invasions are seldom considered across all systems (White et al. 2006), despite the potential consequences these types of interactions can have throughout ecosystems (Parker et al. 1999, White et al. 2006, Ehrenfeld 2010, Simberloff 2011, Ricciardi et al. 2013).

The model bottle study conducted in Chapter 2 revealed that the behavior of native threespot damselfish in response to invasive lionfish did not differ from the minimal response exhibited toward the empty bottle control. Therefore, the territories of this aggressive damselfish are unlikely to indirectly serve as refugia from lionfish predation for native recruit fishes. I further speculated that if damselfish effectively provide refugia for native fishes by excluding native predators from their territories but fail to deter invasive lionfish, then lionfish could potentially exploit damselfish territories as possible sources of prey.

Positioning of fairy and blackcap basslets within local populations under reef ledges described in Chapter 3, was consistent with an overall size hierarchy, with larger fish progressively closer to the outer edges of ledges. The combination of behavioral observations and a manipulative experiment revealed that fairy basslet were more aggressive than blackcap basslet, yet competition had symmetrical effects on the juveniles of both species. Interference between species drove juvenile basslets further back under ledges where feeding and growth rates of individuals were reduced.

By simultaneously manipulating the presence of invasive lionfish in addition to the competitor basslet species, the overall results of this cross-factored experiment, reported in Chapter 4, provided clear evidence of invasive lionfish altering the outcome of interspecific competition between native prey species. Lionfish reduced the density of juvenile fairy basslet, thereby reducing the effects of competition on blackcap basslet, as evidenced by corresponding shifts in position towards coveted ledge positions and increases in growth rates of juvenile blackcap basslet that were comparable to the response of these fish in populations where fairy basslet had been experimentally removed. Therefore, differential predation of invasive lionfish tipped the balance of competition between native prey species from symmetrical to asymmetrical effects on juveniles.

Behavioral observation of invasive and native predators in a controlled setting described in Chapter 5, demonstrated aspects of prey preference that were either different or similar between invasive and native predators. Upon initial exposure to prey fishes, invasive lionfish first hunted fairy basslet whereas native graysby hunted blackcap basslet first, and both predators initially preferred large over small fish. These initial preferences of predators were least affected by the unnatural setting within aquaria compared to any subsequent behaviors, and were thus likely to reflect true preferences. The combination of these invasive and native predators could at one extreme enhance coexistence within and between basslets, or at the other extreme, deplete local basslet populations via increased overall predation.

The field experiment conducted in Chapter 6 revealed that invasive lionfish caused a decline in the density of small (but not large) herbivorous fishes on reefs. Grazing behavior of small herbivorous fishes was also reduced on high-lionfish-density reefs, and decreased even further in the presence of lionfish within-reefs. Lionfish presence at the reef-scale also caused a



decline in grazing of large fish that was maintained regardless of lionfish presence within reefs. These reductions in grazing resulted in 66-80% less algae removed from substrata placed in microhabitats within high-lionfish-density reefs. Parrotfishes likely drove the response of the overall herbivorous fish community (density and grazing behavior) to lionfish. Because the consumptive effects of lionfish affected only small herbivorous fishes, but their non-consumptive effects affected both small and large fish grazing, these results suggest that the non-consumptive effects of invasive lionfish are likely to have a larger role in diminishing the ecosystem function of native herbivorous fishes.

In summary, this dissertation demonstrates that throughout native coral reefs, invasive lionfish (1) are not chased by native territorial damselfish, thereby removing a potential refuge for new recruits of native reef fishes; (2) alters the outcome of interspecific competition between native basslets via differential predation which tips the balance of competition from symmetrical to asymmetrical; and (3) has both consumptive and non-consumptive effects on native herbivorous fishes, that can reduce grazing and indirectly benefit benthic algae. Together, this research reveals that the addition of an invasive predator can induce both direct and indirect interactions that can be either negative or positive in native communities.

Few studies have demonstrated that invasive predators can indirectly facilitate (*sensu* Schoener 1993) native species (Rodriguez 2006). Testing for these types of positive interactions and incorporating them into conceptual frameworks is important for accurately predicting the effects of invasions, as well as the outcomes of management and restoration efforts. Indeed, unexpected consequences can arise following the strategic reduction or eradication of populations of invasive consumers, often due to undocumented positive interactions between

invasive and native organisms (e.g., Murphy and Bradfield 1992, Bergstrom et al. 2009, Simberloff 2009, Kessler 2011).

Trophic cascades driven by invasive species is another neglected concept throughout invasion literature (White et al. 2006). The indirect effects demonstrated in this dissertation indicate that by altering the abundance and/or behavior of native prey, invasive lionfish are likely to subsequently influence lower trophic levels. Specifically, invasive lionfish could potentially drive shifts in the local abundance and diversity of zooplankton by modifying the outcome of interspecific competition between native basslets, which could ultimately have further cascading effects on the structure of local phytoplankton communities. Perhaps of even greater concern (Albins and Hixon 2013) is the seemingly strong likelihood of invasive lionfish driving a lionfish-parrotfishes-algae trophic cascade that could alter competition between algae and corals. Reduced stocks of herbivorous fishes from overfishing can generate a similar trophic cascade that impairs coral resilience (Mumby 2006, Mumby and Steneck 2008), preventing recovery from acute disturbances, such as hurricanes or bleaching events, which can ultimately lead to reef degradation (Hughes 1994).

In conclusion, the research described in this dissertation emphasizes the need for consistency between conceptual expectations versus empirical testing of the effects of a novel predator throughout invaded systems. In particular, it is apparent that invasive predators typically have strong, negative effects on native prey (Clavero and García-Berthou 2005, Clout and Russell 2011, Cucherousset and Olden 2011), but additional testing is needed to determine whether these effects further cascade throughout entire communities and ecosystems. Importantly, this research will broaden our mechanistic understanding of predation in the context

of invasive species, as well as greatly inform management and conservation initiatives as humans continue to induce environmental change at a global scale.

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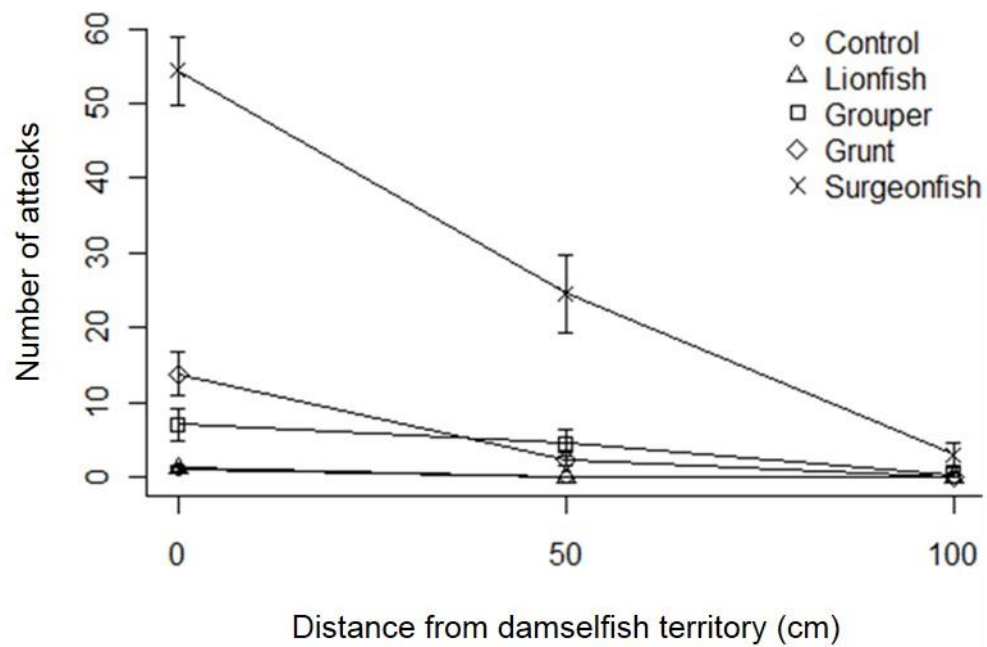
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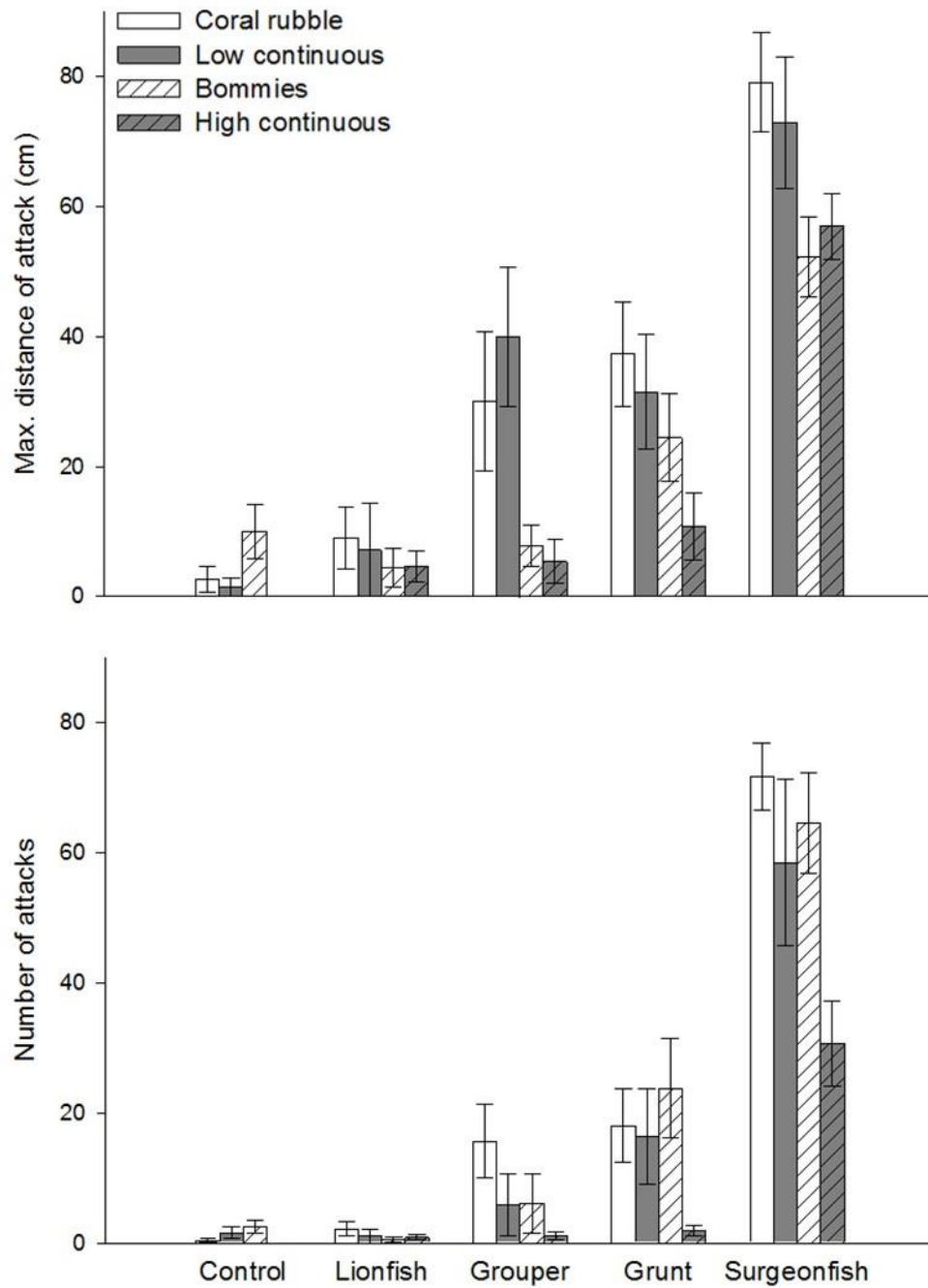
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**Appendix A – Chapter 2 Supplementary Materials**



**Fig. A.1** Mean number of damselfish attacks ( $\pm$ SEM) as each model-bottle treatment was placed closer to the center of the damselfish territory (distance = 0 cm) in 50 cm increments. Mean number of damselfish attacks did not clearly differ among all fish treatments until they were placed in the center of territories.



**Fig. A.2** Mean damselfish response ( $\pm$ SEM) among model-bottle treatments in each of the four microhabitats occupied by damselfish territories (in order of increasing rugosity): dead coral rubble, low-relief continuous reef, coral bommies, and high-relief continuous reef. Non-shaded and shaded bars are habitats observed in the Bahamas and the Cayman Islands, respectively. Solid bars are low-relief habitats with low rugosity, and bars with diagonal patterning are high-relief habitats with higher levels of rugosity.

**Appendix B – Chapter 3 Supplementary Materials**

**Table B.1** Habitat parameters of ledges and initial densities of fairy and blackcap basslet in focal populations used for behavioral observations (A) and a manipulative experiment (B).

**A. Observations of basslet behavior (July-August 2013)**

Reef name	Reef area (m <sup>2</sup> )	Ledge ID #	Ledge depth (m)	Ledge surface area (m <sup>2</sup> )	Initial fairy (fish/m <sup>2</sup> )	Initial blackcap (fish/m <sup>2</sup> )
T08	533	64	15.5	0.90	13.3	11.1
		65	15.2	4.36	2.75	0.92
		83	14.6	9.99	2.30	1.20
Twin	322	3	13.1	2.10	4.29	0.95
		49	11.9	1.92	4.17	0.52
		74	11.9	7.92	4.17	0.21

**B. Manipulative experiment (June-August 2014)**

Reef name	Reef area (m <sup>2</sup> )	Ledge ID #	Ledge depth (m)	Ledge surface area (m <sup>2</sup> )	Initial fairy (fish/m <sup>2</sup> )	Initial blackcap (fish/m <sup>2</sup> )	Ledge treatment
Cathedral	1023	8	14.3	1.27	7.11	3.95	Control
		24	14.9	1.69	2.37	2.37	Fairy-removal
		4	13.4	1.22	4.94	1.65	Blackcap-removal
M02	344	14	15.5	1.90	12.6	11.1	Control
		15	15.5	1.92	6.27	1.04	Fairy-removal
		16	15.8	2.07	2.42	2.90	Blackcap-removal
T08	533	23	14.6	2.38	3.78	0.84	Control
		44	14.6	2.15	5.58	0.93	Fairy-removal
		65	15.2	4.36	6.74	0.88	Blackcap-removal

**Table B.2** Results of likelihood ratio tests (LRTs) of the hypothesized relationship between the relative frequency of chases between basslet species (fairy and blackcap) and the *size* class of fish (2-5 cm), *role* of fish (aggressor versus recipient), and/or *time of day* (dawn, midday, dusk) within local populations of both species (n=6 populations). All significant correlations and corresponding p-values are in bold.

Basslet species	Fixed effect	LRT p
Fairy	size $\times$ role $\times$ time of day	0.137
	role $\times$ time of day	0.624
	size $\times$ time of day	0.088
	size $\times$ role	0.161
	size	0.104
	time of day	0.553
	<b>role</b>	<b>0.002</b>
Blackcap	size $\times$ role $\times$ time of day	0.969
	role $\times$ time of day	0.209
	size $\times$ time of day	0.948
	size $\times$ role	0.611
	size	0.566
	time of day	0.182
	<b>role</b>	<b>0.034</b>



**Table B.3** Results of likelihood ratio tests (LRTs) of the hypothesized relationship between the number of chases in which fairy and blackcap basslets chased (aggressor) and were chased (recipient) by each species (*rec species* and *agg species*, respectively) in populations of both basslets (n=6 populations), given the size class of focal fishes (2-5 cm, *agg size* and *rec size*) and/or *time of day* (dawn, midday, dusk). In the instance when the interaction between *rec size* and *agg species* was significant, p-values from linear combinations testing the relationship of *agg species* with each *rec size* were adjusted to achieve an approximate family-wise error rate of 95 %. All significant correlations and p-values are in bold.

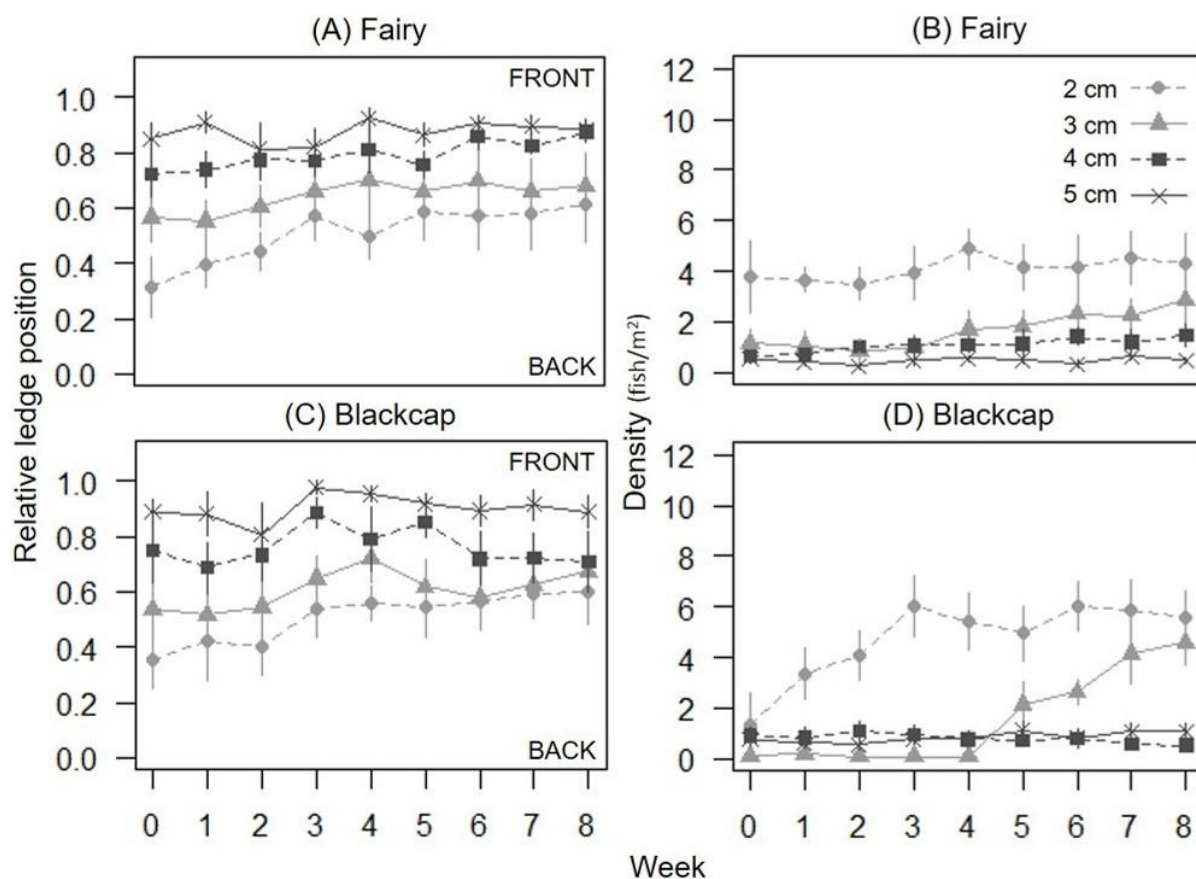
Basslet role	Basslet species	Fixed effect	LRT p	Contrasts	p <sub>cor</sub>
Aggressor	Fairy	agg size × rec species × time of day	0.747		
		agg size × time of day	0.597		
		rec species × time of day	0.834		
		agg size × rec species	0.807		
		agg size	0.472		
		rec species	0.311		
		time of day	0.232		
	Blackcap	agg size × rec species × time of day	0.259		
		agg size × time of day	0.410		
		rec species × time of day	0.922		
		agg size × rec species	0.393		
		agg size	0.791		
		<b>rec species</b>	<b>0.003</b>		
		time of day	0.299		
Recipient	Fairy	rec size × agg species × time of day	0.468		
		rec size × time of day	0.196		
		agg species × time of day	0.916		
		<b>rec size × agg species</b>	<b>&lt;0.001</b>	<b>2 cm</b>	<b>&lt;0.001</b>
				<b>3 cm</b>	<b>&lt;0.001</b>
				<b>4 cm</b>	<b>&lt;0.001</b>
				5 cm	0.549
		time of day	0.253		
	Blackcap	rec size × agg species × time of day	0.457		
		rec size × time of day	0.350		
		agg species × time of day	0.735		
		rec size × agg species	0.907		
		rec size	0.060		
		agg species	0.681		
		time of day	0.302		

**Table B.4** Results of likelihood ratio tests (LRTs) of the hypothesized relationship between the feeding rate of 2.0-2.5 cm individuals in local populations of both species (n=6 populations) and the continuous variable, *ledge position*, and/or categorical variables, *time of day* (dawn, midday, and dusk) and basslet *species* (fairy and blackcap). When interactions with *time of day* were significant, p-values from linear combinations between dawn, midday, and dusk were adjusted ( $p_{\text{cor}}$ ) to achieve an approximate family-wise error rate of 5%. All significant correlations and corresponding p-values are in bold.

Fixed effect	LRT p	Contrasts	$p_{\text{cor}}$
ledge position $\times$ time of day $\times$ species	0.880		
time of day $\times$ species	0.568		
<b>ledge position <math>\times</math> species</b>	<b>0.050</b>		
<b>ledge position <math>\times</math> time of day</b>	<b>&lt;0.007</b>	dawn vs. midday	0.117
		<b>dawn vs. dusk</b>	<b>&lt;0.001</b>
		<b>midday vs. dusk</b>	<b>0.033</b>

**Table B.5** Results of likelihood ratio tests (LRTs) of the hypothesized effect of the potential competitor (*comp*) and/or *time* on the change in ledge position and density of 4 and 5 cm basslets in a manipulative experiment. Response of basslets were compared between populations with the potential competitor removed versus unmanipulated populations of both species (n=3 populations per treatment). Variables with significant effects and corresponding p-values are in bold.

Basslet species	Response variable	Basslet size	Fixed effect	LRT p
Fairy	Change in ledge position	4 cm	comp × time	0.648
			comp	0.345
			time	0.637
		5 cm	comp × time	0.245
			comp	0.761
			time	0.380
	Change in density	4 cm	comp × time	0.753
			comp	0.431
			time	0.101
		5 cm	comp × time	0.073
Blackcap	Change in ledge position	4 cm	comp	0.164
			<b>time</b>	<b>0.039</b>
			time	0.310
		5 cm	comp × time	0.280
			comp	0.577
			time	0.316
	Change in density	4 cm	comp × time	0.178
			comp	0.316
			time	0.262
		5 cm	comp × time	0.222
			comp	0.400
			time	0.358
	Change in density	4 cm	comp × time	0.072
			comp	0.790
			time	0.699



**Fig. B.1** Ledge position (left plots) and density (right plots) of 2-5 cm fairy basslet (A and B) and blackcap basslet (C and D) through time (week) during the manipulative experiment. Size classes of basslets are indicated by combinations of symbols and shading (see legend), and error bars are standard error of the mean.

**Appendix C – Chapter 4 Supplementary Materials**

**Table C.1** Habitat parameters of reefs and ledges used in the manipulative experiment in which invasive predation (lionfish treatment) was cross-factored with competition (basslet treatment). Reefs were paired by similar types of habitat and randomly assigned a low- or high-lionfish treatment. Independent local populations of both basslet species under isolated ledges within each reef were assigned a basslet treatment (n=3 populations per treatment: unmanipulated control, fairy removal, and blackcap removal). Mean densities (fish/m<sup>2</sup>) of invasive lionfish and native basslet species (fairy and blackcap) were calculated by averaging weekly densities across the eight-week experiment.

REEF MEASUREMENTS				LEDGE MEASUREMENTS					
Pair	Lionfish treatment (reef name)	Area (m <sup>2</sup> )	Mean lionfish	ID #	Depth (m)	Area (m <sup>2</sup> )	Mean fairy	Mean blackcap	Basslet treatment
A	Low (Cathedral)	1023	<<0.001	8	14.3	1.27	12.6 ± 1.17	10.2 ± 1.98	Control
				24	14.9	1.69	3.16 ± 0.93	9.01 ± 1.23	Fairy rem.
				4	13.4	1.22	6.40 ± 0.27	0.27 ± 0.19	Black rem.
	High (Shack)	807	0.002	25	14.3	1.02	11.1 ± 1.48	4.82 ± 0.62	Control
				7	11.9	2.00	0.39 ± 0.18	4.67 ± 1.23	Fairy rem.
				22	12.8	0.56	4.37 ± 0.52	0.20 ± 0.20	Black rem.
B	Low (M02)	344	0.001	14	15.5	1.90	9.01 ± 1.04	10.1 ± 1.05	Control
				15	15.5	1.92	2.44 ± 0.5	5.40 ± 0.86	Fairy rem.
				16	15.8	2.07	4.57 ± 0.40	0.85 ± 0.28	Black rem.
	High (M01)	639	0.016	5	15.8	2.54	8.50 ± 0.71	6.66 ± 1.11	Control
				17	17.1	1.68	3.04 ± 0.52	17.6 ± 2.56	Fairy rem.
				6	17.1	1.08	12.1 ± 0.91	4.65 ± 1.16	Black rem.
C	Low (T08)	533	0.002	23	14.6	2.38	3.41 ± 0.28	2.52 ± 0.53	Control
				44	14.6	2.15	3.05 ± 0.59	17.6 ± 2.31	Fairy rem.
				65	15.2	4.36	6.97 ± 0.16	0.23 ± 0.14	Black rem.
	High (T09)	358	0.019	43	16.2	1.40	4.92 ± 1.28	6.27 ± 1.52	Control
				3	17.4	2.14	1.35 ± 0.55	32.8 ± 5.12	Fairy rem.
				2	17.1	0.72	11.4 ± 0.89	7.87 ± 2.37	Black rem.

**Table C.2** Results of likelihood ratio tests (LRTs) indicating the significance of the fixed effects, competition (*comp*, blackcap-removal versus unmanipulated control populations), predation (*pred*, low- versus high-lionfish reefs), and *time* (weeks) on the change in density and feeding position of 2 and 3 cm fairy basslet, and the significance of competition and predation effects on the growth rates of ~2 cm individuals. If there was evidence of a significant interaction with *time*, p-values associated with linear contrasts were adjusted ( $p_{\text{cor}}$ ) to achieve an approximate family-wise error rate of 5%. Variables with significant effects and respective p-values are in bold.

Response variable	Size (cm)	Fixed effect	LRT p	Linear contrast	$p_{\text{cor}}$
Change in density	2	comp×pred×time	0.247		
		comp×pred	0.494		
		comp×time	0.476		
		<b>pred×time</b>	<b>0.012</b>	wk 1	0.413
				wk 2	0.893
				wk 3	0.665
				wk 4	0.608
				wk 5	0.159
	3	comp	0.798	<b>wk 6</b>	<b>&lt;0.001</b>
		comp×pred×time	0.412	<b>wk 7</b>	<b>0.002</b>
		comp×pred	0.354	<b>wk 8</b>	<b>0.008</b>
		comp×time	0.727		
		pred×time	0.277		
		comp	0.838		
Change in feeding position	2	pred	0.160		
		<b>time</b>	<b>0.001</b>		
		comp×pred×time	0.525		
		comp×pred	0.499		
		<b>comp×time</b>	<b>&lt;0.001</b>	wk 1	0.475
				wk 2	0.744
				wk 3	0.059
				wk 4	0.073
	3	pred×time	0.067	<b>wk 5</b>	<b>0.009</b>
		pred	0.356	<b>wk 6</b>	<b>&lt;0.001</b>
		comp×pred×time	0.783	<b>wk 7</b>	<b>&lt;0.001</b>
		comp×pred	0.674	<b>wk 8</b>	<b>&lt;0.001</b>
		comp×time	0.051		
		pred×time	0.988		
Growth rate	~2	<b>comp</b>	<b>0.002</b>		
		pred	0.632		
		time	0.143		
		comp×pred	0.473		
		<b>comp</b>	<b>&lt;0.001</b>		
		pred	0.911		

**Table C.3** Results of likelihood ratio tests (LRTs) indicating the significance of the fixed effects, competition (*comp*, fairy-removal versus unmanipulated control populations), predation (*pred*, low- versus high-lionfish reefs), and *time* (weeks) on the change in density and feeding position of 2 and 3 cm blackcap basslet, and the significance of competition and predation effects on the growth rates of ~2 cm individuals. If there was evidence of a significant three-way interaction, post-hoc models were fit to test for an effect of competition on the response in the absence (no *pred*) and presence (*pred*) of lionfish. If two-way interactions involving *time* were significant, p-values associated with linear contrasts were adjusted ( $p_{\text{cor}}$ ) to achieve an approximate family-wise error rate of 5%. Variables with significant effects are in bold.

Response variable	Size (cm)	Fixed effect	LRT p	Post-hoc model	Post-hoc fixed effect	Post-hoc LRT p	Linear contrast	$p_{\text{cor}}$
Change in density	2	comp×pred×time	0.870					
		comp×pred	0.179					
		comp×time	0.246					
		pred×time	0.118					
		<b>comp</b>	<b>0.025</b>					
		pred	0.505					
		time	0.503					
	3	comp×pred×time	0.329					
		comp×pred	0.149					
		comp×time	0.770					
		pred×time	0.544					
		comp	0.263					
		pred	0.620					
Change in feeding position	2	<b>comp×pred×time</b>	<b>0.012</b>	No pred	<b>comp×time</b>	<b>0.043</b>	wk 1	0.254
							wk 2	0.997
							wk 3	0.643
							wk 4	0.088
							<b>wk 5</b>	<b>&lt;0.001</b>
							<b>wk 6</b>	<b>0.003</b>
							<b>wk 7</b>	<b>&lt;0.001</b>
							<b>wk 8</b>	<b>&lt;0.001</b>
				Pred	comp×time	0.658		
					comp	0.201		
					<b>time</b>	<b>&lt;0.001</b>		
	3	<b>comp×pred×time</b>	<b>0.007</b>	No pred	comp×time	0.578		
					comp	0.083		
					<b>time</b>	<b>0.050</b>		
				Pred	<b>comp×time</b>	<b>&lt;0.001</b>	wk 1	0.299
							wk 2	0.995
							wk 3	1.000
							wk 4	1.000
							<b>wk 5</b>	<b>0.032</b>
Growth rate	~2	comp×pred	<b>0.049</b>				<b>no pred</b>	<b>0.046</b>
							pred	0.680



**Table C.4** Results of likelihood ratio tests (LRTs) indicating the significance of the fixed effects, competition (*comp*, blackcap-removal versus unmanipulated control populations), predation (*pred*, low- versus high-lionfish reefs), and *time* (weeks) on the change in feeding position and density of 4 and 5 cm fairy basslet. Variables with significant effects and respective p-values are in bold.

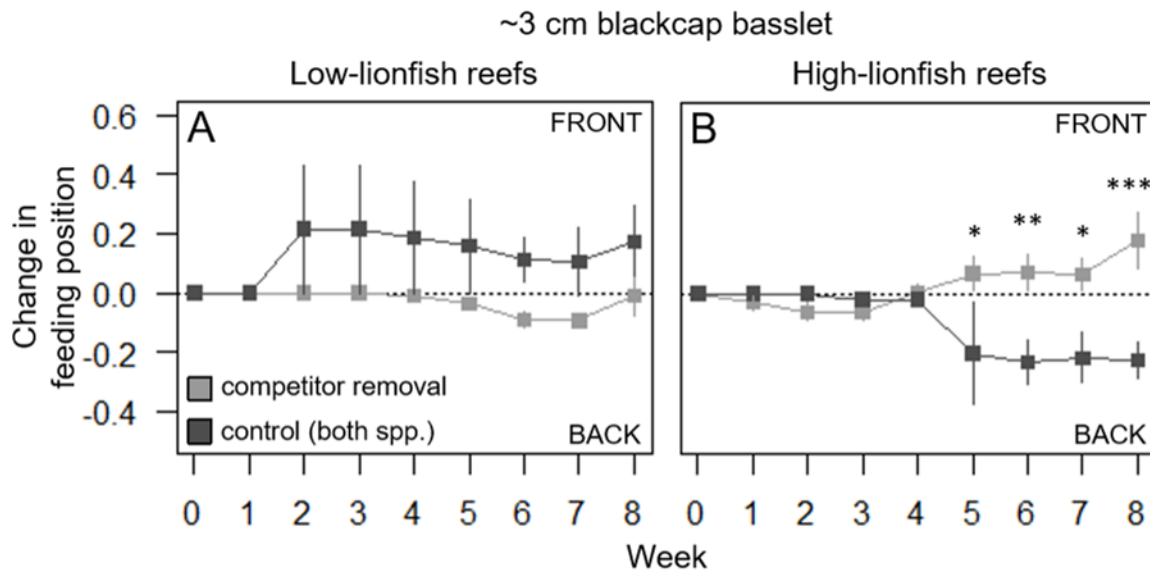
Response variable	Size (cm)	Fixed effect	LRT p
Change in feeding position	4	comp×pred×time	0.959
		comp×pred	0.629
		comp×time	0.510
		pred×time	0.055
		comp	0.296
		pred	0.695
		<b>time</b>	<b>&lt;0.001</b>
	5	comp×pred×time	0.649
		comp×pred	0.986
		comp×time	0.116
		pred×time	0.954
		comp	0.132
		pred	0.524
		time	0.221
Change in density	4	comp×pred×time	0.118
		comp×pred	0.097
		comp×time	0.540
		pred×time	0.599
		comp	0.459
		pred	0.370
		time	0.920
	5	comp×pred×time	0.148
		comp×pred	0.765
		comp×time	0.082
		pred×time	0.804
		comp	0.600
		pred	0.822
		time	0.797

**Table C.5** Results of likelihood ratio tests (LRTs) indicating the significance of the fixed effects, competition (*comp*, fairy-removal versus unmanipulated control populations), predation (*pred*, low- versus high-lionfish reefs), and *time* (weeks) on the change in feeding position and density of 4 and 5 cm blackcap basslet. Variables with significant effects and respective p-values are in bold.

Response variable	Size (cm)	Fixed effect	LRT p
Change in feeding position	4	comp×pred×time	0.501
		comp×pred	0.940
		comp×time	0.053
		pred×time	0.709
		comp	0.080
		pred	0.827
		time	0.139
	5	comp×pred×time	0.778
		comp×pred	0.623
		comp×time	0.652
		pred×time	0.306
		comp	0.347
		pred	0.274
		time	0.260
Change in density	4	comp × pred × time	0.842
		comp × pred	0.633
		comp × time	0.785
		pred × time	0.120
		comp	0.618
		pred	0.071
		<b>time</b>	<b>0.003</b>
	5	comp × pred × time	0.499
		comp × pred	0.728
		comp × time	0.906
		pred × time	0.089
		comp	0.432
		pred	0.571
		<b>time</b>	<b>0.005</b>

**Table C.6** Results of likelihood ratio tests (LRTs) indicating the significance of relationships between the proportion of time lionfish were observed visiting focal populations of basslets (2 videos of 3 populations in 3 reefs: total n=18) and the fixed effects, lionfish behavior (*lion.behav*: resting, hovering, swimming, hunting) and basslet treatment (*bass.trt*: control, fairy removal, blackcap removal). Significant relationships between the response variables, proportion of time lionfish were observed and proportion of time lionfish were hunting, and the fixed effects, ledge position of lionfish (*ledge.pos*) and basslet treatment, were also tested. When pairwise comparisons were appropriate, Tukey's HSD was used to calculate corrected p-values ( $p_{cor}$ ). Variables with significant effects and respective p-values are in bold.

Response variable	Fixed effect	LRT p	Multiple comparisons	$p_{cor}$
Proportion of time observed	<i>lion.behav</i> × <i>bass.trt</i>	0.124		
	<b><i>lion.behav</i></b>	<b>&lt;0.008</b>	rest vs. hover	0.335
			rest vs. swim	0.949
			rest vs. hunt	0.068
			hover vs. swim	0.666
			<b>hover vs.hunt</b>	<b>&lt;0.001</b>
			<b>swim vs. hunt</b>	<b>0.015</b>
	<i>bass.trt</i>	1.000		
Proportion of time hunting	<i>ledge.pos</i> × <i>bass.trt</i>	0.089		
	<i>ledge.pos</i>	0.656		
	<i>bass.trt</i>	1.000		



**Fig. C.1** Change in feeding position of 3 cm blackcap basslet through time (week) in a cross-factored manipulative experiment ( $n=3$  populations per treatment) consisting of local populations with fairy basslet removed and unmanipulated control populations (lighter and darker shading, respectively) within low- and high-lionfish reefs (left and right plots, respectively). Error bars are standard error of the mean. Likelihood ratio tests indicated a significant three-way interaction among competition, predation, and time ( $p=0.007$ ). Subsequent models were fit to test for the effects of competition and time on the response in low- and high-lionfish reefs (separately). When there was evidence of a significant two-way interaction (plot B),  $p$ -values from linear contrasts were adjusted to achieve an approximate family-wise error rate of 5%, with respective significance indicated in each plot: \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ .

**Appendix D – Chapter 5 Supplementary Materials**

**Table D.1** Quasi-Akaike Information Criterion (QIC) values of full and reduced Generalized Estimating Equation (GEE) models, where full models include all interactions among explanatory variables and reduced models are additive models. QIC values in bold and asterisked (\*) are the lower QIC values between the full and reduced models of each response variable.

Response variable	Full GEE model	QIC values	
		Full model	Additive model
Initial preference <i>basslet species</i>	~ Predator size x Predator species	103.324	<b>101.286*</b>
Initial preference <i>basslet size</i>	~ Predator size x Predator species	<b>134.34*</b>	135.98
Number of strikes <i>basslet species</i>	~ Predator size x Predator species x Basslet size	<b>320.07*</b>	321.91
Number of strikes <i>basslet size</i>	~ Predator size x Predator species x Basslet size	<b>271.72*</b>	303.74
Lionfish strikes <i>basslet size</i>	~ Lionfish size x Basslet size	<b>148.41*</b>	159.61
Graysby strikes <i>basslet size</i>	~ Graysby size x Basslet size	123.05	<b>122.21*</b>
Hunting time <i>basslet species</i>	~ Predator size x Predator species x Basslet size	<b>-69559.80*</b>	-68693.87
Hunting time <i>basslet size</i>	~ Predator size x Predator species x Basslet size	<b>-65091.26*</b>	-63650.07
Lionfish hunting time <i>basslet size</i>	~ Lionfish size x Basslet size	<b>-54905.07*</b>	-53933.97
Graysby hunting time <i>basslet size</i>	~ Graysby size x Basslet size	<b>-10183.24*</b>	-10142.15

**Table D.2** Results of full Generalized Estimating Equation (GEE) models of the number of strikes and hunting time of predators (graysby and lionfish) in response to two different basslet species (fairy and blackcap). Full models were selected for both response variables based on Quasi-Akaike Information Criterion (QIC) values (see Table D.1).

Response variable	Explanatory variable (from full model)	Wald $\chi^2$	p-value
Number of strikes	Predator size	0.780	0.380
	Basslet species	0.420	0.520
	Predator species	0.230	0.640
	Predator size x Basslet species	0.740	0.390
	Predator size x Predator species	0.720	0.400
	Basslet species x Predator species	0.560	0.460
	Predator size x Basslet species x Predator species	0.500	0.480
Hunting time	Predator size	0.35	0.556
	Basslet species	0.77	0.379
	Predator species	2.96	0.085
	Predator size x Basslet species	0.24	0.622
	Predator size x Predator species	0.18	0.672
	Basslet species x Predator species	2.92	0.088
	Predator size x Basslet species x Predator species	1.89	0.170



**Fig. D.1** Two native prey fishes used in experiment (left to right): fairy basslet (*Gramma loreto*) and blackcap basslet (*Gramma melacara*). Photo credits: Emily R. Anderson left and unknown (Google Images) right.



**Appendix E – Chapter 6 Supplementary Materials**

**Table E.1** Length-weight conversion parameters used to calculate fish biomass. Conversion equation used:  $W = a \cdot (L \cdot c)^b$  (W = weight in g, L = total length in cm). When original 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. If information was not available for a species, we used a closely related or similarly shaped substitute species, as indicated. We also incorporated a length conversion multiplier  $c$  based on length-length conversion factors from the FishBase database when sources reported conversions from standard or fork lengths.

Group	Species	Substitute species	a	b	Reference
Parrotfishes (Labridae)	<i>Cryptotomus roseus</i>		0.05034	3.18177	1
	<i>Scarus coeruleus</i>	<i>S. iserti</i>	0.01580	3.05150	2
	<i>Scarus iserti</i>		0.01580	3.05150	2
	<i>Scarus taeniopterus</i>		0.03351	2.70847	1
	<i>Scarus vetula</i>		0.03330	2.71018	1
	<i>Sparisoma atomarium</i>		0.01214	3.02654	1
	<i>Sparisoma aurofrenatum</i>		0.00472	3.42689	1
	<i>Sparisoma chrysopteron</i>		0.01540	3.04230	2
	<i>Sparisoma radians</i>		0.01790	3.03480	2
	<i>Sparisoma rubripinne</i>		0.01448	3.06236	1
	<i>Sparisoma viride</i>		0.02237	2.92434	1
Surgeonfishes (Acanthuridae)	<i>Acanthurus bahianus</i>		0.03480	2.68940	2
	<i>Acanthurus chirurgus</i>		0.02820	2.81370	2
	<i>Acanthurus coeruleus</i>		0.03756	2.83271	1
Angelfishes (Pomacanthidae)	<i>Holocanthus ciliaris</i>		0.03395	2.89815	1
	<i>Holocanthus tricolor</i>		0.04311	2.85585	1
	<i>Pomacanthus arcuatus</i>		0.03420	2.96972	1
	<i>Pomacanthus paru</i>		0.02042	3.12525	1
Damsel fishes (Pomacentridae)	<i>Abudefduf saxatilis</i>		0.02033	3.14238	1
	<i>Stegastes adustus</i>		0.03274	2.89605	1
	<i>Stegastes dienaecus</i>		0.03231	2.89955	1
	<i>Stegastes leucostictus</i>	<i>S. dienaecus</i>	0.02770	2.87110	2
	<i>Stegastes partitus</i>		0.01606	3.15370	1
	<i>Stegastes planifrons</i>		0.03275	2.85660	1
	<i>Stegastes variabilis</i>		0.02886	2.83952	1
Mesopredators	<i>Cephalopholis cruentatus</i>		0.03902	2.80000	3
	<i>Cephalopholis fulva</i>		0.01949	2.92862	1
	<i>Epinephelus guttatus</i>		0.01015	3.22400	1
	<i>Epinephelus striatus</i>		0.01108	3.11249	1

Online Resource 1 references:

1. Bohnsack, J. A., D. E. Harper, and S. F. Center. 1988. Length-weight relationships of selected marine reef fishes from the southeastern United States and the Caribbean. National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southeast Fisheries Center, Miami, Florida, USA.
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3. González-Gándara, C., E. Pérez-Díaz, L. Santos-Rodríguez, and J. Arias-González. 2003. Length-weight relationships of coral reef fishes from the Alacran Reef, Yucatan, Mexico. *Naga* 26:14–16.

**Table E.2** Results of likelihood ratio tests for the effect of lionfish-density-treatment (“lionfish”) and time on the density and biomass of small ( $\leq 10$  cm TL) and large ( $> 10$  cm TL) fishes.

Group	Size class	Response variable	Fixed effect	LRT p
Surgeonfishes (Acanthuridae)	Small	Density	lionfish $\times$ time	0.291
			lionfish	0.180
			time	0.057
		Biomass	lionfish $\times$ time	0.264
			lionfish	0.405
			time	0.224
	Large	Density	lionfish $\times$ time	0.785
			lionfish	0.461
			time	0.054
		Biomass	lionfish $\times$ time	0.549
			lionfish	0.486
			<b>time</b>	<b>0.011</b>
Angelfishes (Pomacanthidae)	Small	Density	lionfish $\times$ time	0.090
			lionfish	0.191
			<b>time</b>	<b>0.002</b>
		Biomass	lionfish $\times$ time	0.820
			lionfish	0.258
			<b>time</b>	<b>&lt;0.001</b>
	Large	Density	lionfish $\times$ time	0.574
			lionfish	0.714
			<b>time</b>	<b>0.006</b>
		Biomass	lionfish $\times$ time	0.619
			lionfish	0.842
			time	0.053
Damsel­fishes (Pomacentridae)	Small	Density	lionfish $\times$ time	0.111
			lionfish	0.126
			<b>time</b>	<b>&lt;0.001</b>
		Biomass	lionfish $\times$ time	0.165
			lionfish	0.321
			<b>time</b>	<b>&lt;0.001</b>
	Large	Density	lionfish $\times$ time	0.320
			lionfish	0.276
			time	0.116
		Biomass	lionfish $\times$ time	0.728
			lionfish	0.109
			time	0.311
Mesopredators	Small	Density	lionfish $\times$ time	0.265
			lionfish	0.697
			time	0.282
		Biomass	lionfish $\times$ time	0.644
			lionfish	0.401
			time	0.320
	Large	Density	lionfish $\times$ time	0.094
			lionfish	0.414
			time	0.113
		Biomass	lionfish $\times$ time	0.423
			lionfish	0.649
			time	0.535

**Table E.3** Estimates and results from likelihood ratio tests of full mixed-effects models for differences in density and biomass between reefs assigned to lionfish-density-treatments prior to lionfish manipulation.

Group	Size class	Response variable	Estimated difference $\pm$ SEM	p
All herbivorous fishes	Small	Density	$0.02 \pm 0.14$	0.911
		Biomass	$12.3 \pm 117$	0.919
	Large	Density	$0.06 \pm 0.02$	0.053
		Biomass	$1001 \pm 781$	0.236
Parrotfishes (Labridae)	Small	Density	$-0.00 \pm 0.08$	0.973
		Biomass	$-8.18 \pm 77.5$	0.919
	Large	Density	$0.01 \pm 0.03$	0.729
		Biomass	$417 \pm 507$	0.434
Surgeonfishes (Acanthuridae)	Small	Density	$-0.00 \pm 0.01$	0.553
		Biomass	$3.18 \pm 18.3$	0.866
	Large	Density	$0.01 \pm 0.02$	0.432
		Biomass	$-304 \pm 399$	0.469
Angelfishes (Pomacanthidae)	Small	Density	$-0.00 \pm 0.01$	0.100
		Biomass	$-2.89 \pm 1.97$	0.180
	Large	Density	$-0.00 \pm 0.01$	0.541
		Biomass	$-129 \pm 443$	0.778
Damsel fishes (Pomacentridae)	Small	Density	$0.03 \pm 0.08$	0.747
		Biomass	$28.3 \pm 40.3$	0.503
	Large	Density	$0.09 \pm 0.06$	0.181
		Biomass	$532 \pm 348$	0.165
Mesopredators	Small	Density	$-0.00 \pm 0.01$	0.803
		Biomass	$0.61 \pm 3.68$	0.853
	Large	Density	$-0.00 \pm 0.01$	0.707
		Biomass	$-106 \pm 199$	0.609

**Table E.4** Results of multiple comparisons (Tukey's HSD) of small ( $\leq 10$  cm TL) and large ( $> 10$  cm TL) herbivorous fishes among lionfish treatments (low-absent, high-absent, high-present).

Group	Size class	Response variable	Treatment comparison	Estimated difference $\pm$ SEM	LMM p
All herbivorous fishes	Small	Visitation rate	lo-abs v. hi-abs	<b><math>0.81 \pm 0.24</math></b>	<b>0.001</b>
			lo-abs v. hi-prs	<b><math>1.37 \pm 0.23</math></b>	<b>&lt;0.001</b>
			hi-abs v. hi-prs	<b><math>0.56 \pm 0.23</math></b>	<b>0.039</b>
		Percent visitation rate	lo-abs v. hi-abs	<b><math>0.37 \pm 0.13</math></b>	<b>0.047</b>
			lo-abs v. hi-prs	<b><math>0.83 \pm 0.17</math></b>	<b>&lt;0.001</b>
			hi-abs v. hi-prs	<b><math>0.45 \pm 0.18</math></b>	<b>0.029</b>
		Bite rate	lo-abs v. hi-abs	<b><math>1.29 \pm 0.43</math></b>	<b>0.004</b>
			lo-abs v. hi-prs	<b><math>2.49 \pm 0.40</math></b>	<b>&lt;0.001</b>
			hi-abs v. hi-prs	<b><math>1.20 \pm 0.43</math></b>	<b>0.015</b>
		Individual bite rate	lo-abs v. hi-abs	<b><math>0.74 \pm 0.31</math></b>	<b>0.049</b>
			lo-abs v. hi-prs	<b><math>1.78 \pm 0.32</math></b>	<b>&lt;0.001</b>
			hi-abs v. hi-prs	<b><math>1.03 \pm 0.37</math></b>	<b>0.013</b>
	Large	Visitation rate	lo-abs v. hi-abs	<b><math>0.93 \pm 0.22</math></b>	<b>&lt;0.001</b>
			lo-abs v. hi-prs	<b><math>1.23 \pm 0.21</math></b>	<b>&lt;0.001</b>
			hi-abs v. hi-prs	$0.30 \pm 0.22$	0.343
		Percent visitation rate	lo-abs v. hi-abs	<b><math>0.87 \pm 0.21</math></b>	<b>&lt;0.001</b>
			lo-abs v. hi-prs	<b><math>1.21 \pm 0.23</math></b>	<b>&lt;0.001</b>
			hi-abs v. hi-prs	$0.35 \pm 0.23$	0.286
		Bite rate	lo-abs v. hi-abs	<b><math>1.40 \pm 0.45</math></b>	<b>&lt;0.002</b>
			lo-abs v. hi-prs	<b><math>2.05 \pm 0.41</math></b>	<b>&lt;0.001</b>
			hi-abs v. hi-prs	$0.65 \pm 0.41$	0.251
		Individual bite rate	lo-abs v. hi-abs	<b><math>1.14 \pm 0.32</math></b>	<b>0.001</b>
			lo-abs v. hi-prs	<b><math>1.45 \pm 0.32</math></b>	<b>&lt;0.001</b>
			hi-abs v. hi-prs	$0.32 \pm 0.34$	0.624
Parrotfishes (Labridae)	Small	Visitation rate	lo-abs v. hi-abs	<b><math>0.99 \pm 0.23</math></b>	<b>&lt;0.001</b>
			lo-abs v. hi-prs	<b><math>1.14 \pm 0.19</math></b>	<b>&lt;0.001</b>
			hi-abs v. hi-prs	$0.15 \pm 0.21$	0.737
		Percent visitation rate	lo-abs v. hi-abs	<b><math>0.85 \pm 0.19</math></b>	<b>&lt;0.001</b>
			lo-abs v. hi-prs	<b><math>0.99 \pm 0.18</math></b>	<b>&lt;0.001</b>
			hi-abs v. hi-prs	$0.14 \pm 0.19$	0.734
		Bite rate	lo-abs v. hi-abs	<b><math>1.71 \pm 0.38</math></b>	<b>&lt;0.001</b>
			lo-abs v. hi-prs	<b><math>2.02 \pm 0.33</math></b>	<b>&lt;0.001</b>
			hi-abs v. hi-prs	$0.31 \pm 0.34$	0.645
		Individual bite rate	lo-abs v. hi-abs	<b><math>0.01 \pm 0.27</math></b>	<b>&lt;0.001</b>
			lo-abs v. hi-prs	<b><math>0.01 \pm 0.27</math></b>	<b>&lt;0.001</b>
			hi-abs v. hi-prs	$0.01 \pm 0.28$	0.447
	Large	Visitation rate	lo-abs v. hi-abs	<b><math>0.91 \pm 0.25</math></b>	<b>&lt;0.001</b>
			lo-abs v. hi-prs	<b><math>1.21 \pm 0.19</math></b>	<b>&lt;0.001</b>
			hi-abs v. hi-prs	$0.31 \pm 0.21$	0.295
		Percent visitation rate	lo-abs v. hi-abs	<b><math>1.17 \pm 0.30</math></b>	<b>&lt;0.001</b>
			lo-abs v. hi-prs	<b><math>1.59 \pm 0.27</math></b>	<b>&lt;0.001</b>
			hi-abs v. hi-prs	$0.42 \pm 0.30$	0.336
		Bite rate	lo-abs v. hi-abs	<b><math>1.31 \pm 0.46</math></b>	<b>&lt;0.001</b>
			lo-abs v. hi-prs	<b><math>1.74 \pm 0.31</math></b>	<b>&lt;0.001</b>
			hi-abs v. hi-prs	$0.43 \pm 0.36$	0.454
		Individual bite rate	lo-abs v. hi-abs	<b><math>1.31 \pm 0.24</math></b>	<b>&lt;0.001</b>
			lo-abs v. hi-prs	<b><math>1.74 \pm 0.31</math></b>	<b>&lt;0.001</b>
			hi-abs v. hi-prs	$0.43 \pm 0.36$	0.454

**Table E.5** Results of hypothesis tests for the effect of lionfish treatment (“lionfish”) and initial algal percent cover (“algae”) on response variables of fish families observed during grazing surveys. The significance of fixed effects was calculated using likelihood-ratio tests (LRT) comparing nested models fit by Maximum Likelihood Estimation.

Group	Response variable	Fixed effect	LRT p
Surgeonfishes (Acanthuridae)	Visitation rate	algae × lionfish	0.899
		<b>algae</b>	<b>0.005</b>
		lionfish	0.170
	Percent visitation rate	algae × lionfish	0.752
		<b>algae</b>	<b>0.001</b>
		lionfish	0.163
	Bite rate	algae × lionfish	0.882
		<b>algae</b>	<b>0.002</b>
		lionfish	0.088
	Individual bite rate	algae × lionfish	0.829
		<b>algae</b>	<b>0.005</b>
		lionfish	0.111
Angelfishes (Pomacanthidae)	Visitation rate	algae × lionfish	0.484
		algae	0.545
		lionfish	0.628
	Percent visitation rate	algae × lionfish	0.241
		algae	0.788
		lionfish	0.484
	Bite rate	algae × lionfish	0.470
		algae	0.694
		lionfish	0.663
	Individual bite rate	algae × lionfish	0.216
		algae	0.780
		lionfish	0.470
Damsel­fishes (Pomacentridae)	Visitation rate	algae × lionfish	0.885
		algae	0.917
		lionfish	0.221
	Percent visitation rate	algae × lionfish	0.574
		algae	0.929
		lionfish	0.126
	Bite rate	algae × lionfish	0.989
		algae	0.373
		lionfish	0.093
	Individual bite rate	algae × lionfish	0.785
		algae	0.718
		lionfish	0.135

**Table E.6** Presence (\*) and absence (-) of small ( $\leq 10$  cm TL) and large ( $>10$  cm TL) herbivorous fish species observed during grazing surveys (July 2011) in each lionfish treatment (low-absent, high-absent, and/or high-present). Fish species listed were observed during at least one survey period throughout reef fish surveys (June 2009 – June 2011).

Fish family	Species	Small ( $\leq 10$ cm)			Large ( $>10$ cm)		
		low-absent	high-absent	high-present	low-absent	high-absent	high-present
Parrotfishes (Labridae)	<i>Cryptotomus roseus</i>	-	-	-	-	-	-
	<i>Scarus coeruleus</i>	-	-	-	-	-	-
	<i>Scarus vetula</i>	*	-	-	*	*	-
	<i>Sparisoma atomarium</i>	-	-	-	-	-	-
	<i>Sparisoma aurofrenatum</i>	*	*	*	*	*	*
	<i>Sparisoma chrysopteron</i>	-	-	-	*	-	-
	<i>Sparisoma radians</i>	-	-	-	*	-	-
	<i>Sparisoma rubripinne</i>	-	-	-	-	-	-
	<i>Sparisoma viride</i>	*	*	*	*	*	*
Surgeonfishes (Acanthuridae)	<i>Acanthurus bahianus</i>	*	-	*	*	*	-
	<i>Acanthurus chirurgus</i>	-	*	-	*	*	-
	<i>Acanthurus coeruleus</i>	*	*	*	*	*	*
Angelfishes (Pomacanthidae)	<i>Holacanthus ciliaris</i>	*	*	*	*	*	*
	<i>Holacanthus tricolor</i>	-	-	-	-	-	-
	<i>Pomacanthus arcuatus</i>	-	-	-	*	*	*
Damselfishes (Pomacentridae)	<i>Abudefduf saxatilis</i>	-	-	-	-	-	-
	<i>Microspathodon chrysurus</i>	-	-	-	-	-	-
	<i>Stegastes adustus</i>	-	-	-	-	-	-
	<i>Stegastes diencaeus</i>	*	*	*	-	*	*
	<i>Stegastes leucostictus</i>	*	-	*	-	-	-
	<i>Stegastes partitus</i>	*	*	-	-	-	-
	<i>Stegastes planifrons</i>	*	*	-	*	-	-
	<i>Stegastes variabilis</i>	*	*	*	*	*	*