

AN ABSTRACT OF THE DISSERTATION OF

Alexandra Christina Danielle Davis for the degree of Doctor of Philosophy in Zoology presented on December 4, 2018.

Title: Habitat Use and Ecological Interactions of Invasive Lionfish in the Bahamas.

Abstract approved:

Mark A. Hixon

Invasive species are a growing global economic and ecological problem. Invasive Indo-Pacific lionfish (*Pterois* spp.) are known to have extreme negative effects on coral-reef communities in the Bahamas, so understating their distribution within and among reefs, what limits their local movements, and the effects they have on native prey species is crucial for managing the invasion. I studied invasive lionfish off the island of Eleuthera, the Bahamas, at multiple spatial scales. In Chapter 2, I examined their regional distribution and abundance. I used multiple predictive models with a variety of data sources to determine which model was best for predicting lionfish presence/absence and density among reefs. The model with the highest predictive capability included remotely sensed satellite data as well as diver collected microhabitat data for both presence/absence and density of lionfish. The ability to predict lionfish density increased in the model that included native Nassau grouper (a potential predator and competitor of lionfish), but decreased in the lionfish presence/absence model. In Chapter 3, I examined what biotic and abiotic factors

influence lionfish site fidelity at particular reefs. Using dorsal spine clips, and detailed information about coloration, I tracked individual lionfish on reefs over two field seasons. I also collected abundance and size data on native grouper and prey species and conducted detailed habitat surveys focusing on reef structural complexity. I used linear mixed effects models to determine which factors were correlated to three different measures of site fidelity: frequency (number of times lionfish were seen/number of surveys), duration (time between 1st and last sighting of lionfish), and distance (linear distance between sighting locations within a reef). Lionfish density was positively correlated with both frequency and duration, and prey density was negatively correlated with frequency. None of the variables were correlated with average distance moved on the reef. However, lionfish density was correlated with habitat complexity, which suggests that there is both the biotic influence of conspecifics and prey as well as an indirect effect of habitat on lionfish site fidelity. Finally, in Chapter 4, at the individual scale, I explored the potential for lionfish to have consumptive (lethal) and/or non-consumptive (nonlethal) effects on the common native prey *Stegastes partitus*, the bicolor damselfish. I observed the behavior of bicolor damselfish in the presence of either lionfish or native species (including a carnivore and an egg predator) to determine whether bicolor damselfish respond to lionfish similarly to native species. I found that bicolor damselfish do not change their behavior in the presence of lionfish, and even respond less aggressively to lionfish than non-threatening native species. I also measured bicolor fecundity as number and size of egg masses produced. Despite having no behavioral response to lionfish, bicolor damselfish inhabiting reefs with high lionfish densities had lower fecundity.

This pattern may be due to the average adult bicolor being smaller in size, which could be a lagged non-consumptive effect of lionfish. These results show that investigation of invasive species at multiple spatial scales can increase our understanding of their overall effects on native communities. While both habitat and native grouper may have a large effect on the presence and densities of invasive lionfish, lionfish habitat fidelity is more strongly correlated to densities of conspecifics and prey. Additionally, lionfish have non-lethal effects on certain native species that are not apparent if only behavior is examined.

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Habitat Use and Ecological Interactions of Invasive Lionfish in the Bahamas

by
Alexandra Christina Danielle Davis

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APPROVED:

Major Professor, representing Zoology

Head of the Department of Integrative Biology

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.

Alexandra Christina Danielle Davis, Author

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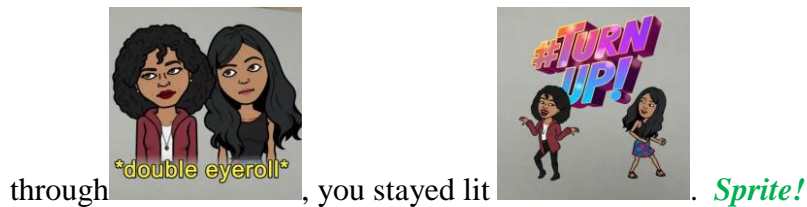
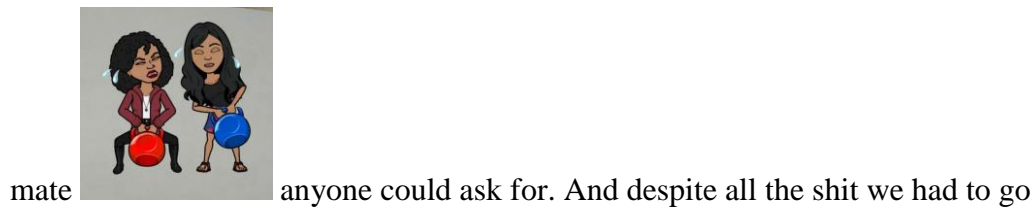
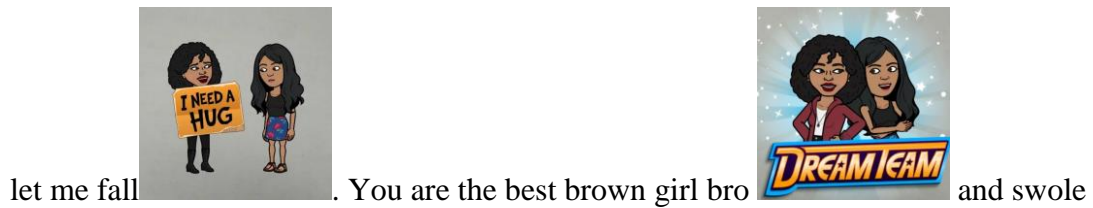
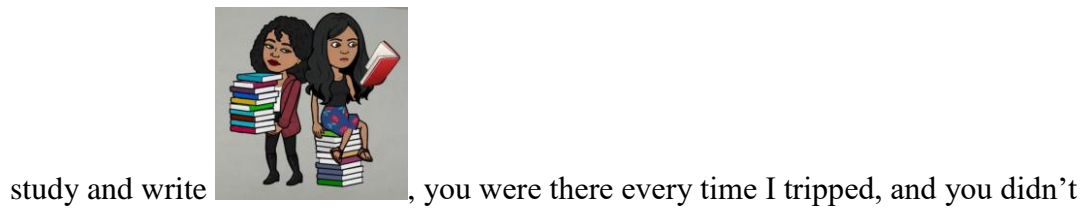
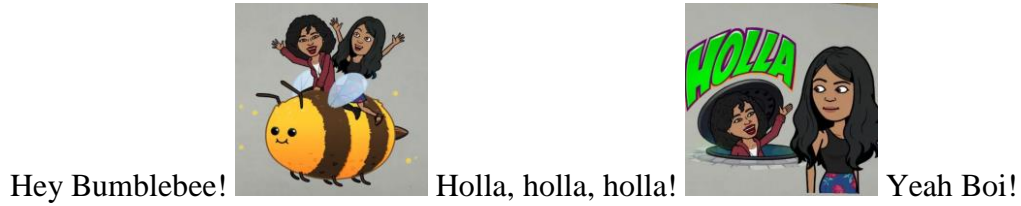
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DEDICATION

This dissertation is dedicated to Brad Chertoff who brought the wonders of the ocean to life in the middle of a desert, and to my grandpa Glen Rolfs who taught me to fish, and to love popcorn.

Habitat Use and Ecological Interactions of Invasive Lionfish in the Bahamas

Chapter 1 – General Introduction

Invasive species have become a global economic and ecological problem because invaders can alter native communities and are responsible for over \$100 billion in environmental damages annually in the US alone (Pimentel et al. 2000). Invaders transmit disease (Pimentel et al. 2000), prey on native species (Bruno et al. 2005), outcompete native species (David et al. 2017), and are one of the leading causes of recent extinctions (Gurevitch and Padilla 2004; Clavero and García-Berthou 2005).

The effects of invasive species can span multiple scales of ecological analysis, as well as varying spatial and temporal scales. Understanding and managing species invasions thus requires ecological information at multiple spatial and temporal scales. Field studies and associated management plans should include (a) accurate mapping of the invasive species over large areas [landscape scale], (b) assessment of the effects of invasive species' on native species [community scale], and (c) quantification of habitat selection and use by invasive species [individual scale]. Different ecological approaches are required at these complementary scales.

Regarding the landscape scales, species distribution models can illuminate broad patterns such as habitat use, range size, and species level movements such as migratory patterns (Franklin 2009). Most species distribution models address single

species responses to the environment (Young and Carr 2015; Young et al. 2016), but they can also be used to predict species richness (Pittman et al. 2007; Pittman and Olds 2015). However, species distribution models typically give a static picture, and can miss the dynamic nature of certain systems (Franklin 2010).

Regarding the community scale, studies of communities examine interactions between species, but are often focused on current assemblages that miss long-term historical or times series data (Jackson and Blois 2015). Community-level studies often have small spatial and temporal extent and focus on patterns of small groups or localized populations.

Regarding the individual scale, behavioral studies provide information about individuals which inform us about resource use and physiological responses to environmental changes (Brooker et al. 2016). Behavioral studies can be expanded to the population level to determine variability in behavior, as well as how relationships between physiology and behavior can inform population management and predict reactions to climate change (Brooker et al. 2016).

As a complicating factor, many ecological processes change based on the spatial and temporal scale of the study (Wiens 1989), and examination of species at multiple scales is important to understand and ultimately manage them (Turner et al. 1989; Rose and Leggett 1990; Graf et al. 2005). For example, diversity changes over time and increases with area, so species interactions when and where only two species are present may not scale-up to a community with 20 or 200 species (Lawton 1996). Additionally, it is impossible to describe species-habitat relationships at a single scale (Wiens 1989).

Marine and coastal systems are among the most highly invaded in the world (Grosholz 2002). The ocean adds another layer of complexity when attempting to manage species invasions, as collecting information in marine systems is inherently more difficult than in most terrestrial settings. One of the most significant obstacles is the availability of benthic maps at an appropriate scale for the study (Grober-Dunsmore et al. 2009).

Indo-Pacific lionfish (*Pterois* spp.) were introduced into the Atlantic in the late 1980s off the coast of Florida (Whitfield et al. 2002), likely due to the aquarium trade (Semmes et al. 2004). Since then, lionfish have spread up the eastern coast of the United States, east to Bermuda (Whitfield et al. 2002), through the greater Caribbean region (Schofield 2010) and all the way down to Brazil (Ferreira et al. 2015) (Figure 1). Lionfish have been extremely successful in their invasion for a variety of reasons. They have no major predators in the invaded range, though there is some evidence that large grouper can provide some biotic resistance to the invasion (Mumby et al. 2011; Diller et al. 2014; Raymond et al. 2015; Ellis and Faletti 2016). Lionfish will eat anything they can get their mouths around (Morris and Akins 2009; Eddy et al. 2016). Stomach contents of lionfish have yielded up to 48 different species of fish and 29 invertebrate species (Morris and Akins 2009; Layman and Allgeier 2012; Valdez-Moreno et al. 2012), and they have been recorded eating fish up to 48% of their total length (Morris and Akins 2009; Pusack 2013). Lionfish may also outcompete native meso-predators, perhaps due to their unique style of hunting in the Atlantic (Albins and Lyons 2012), and they eat the juveniles of many

economically and ecologically important grouper species (Morris and Akins 2009; Muñoz et al. 2011; Côté et al. 2013). Lionfish also have fewer parasites than they do in their native range, and also fewer parasites than native species in the Atlantic (Sikkel et al. 2014; Tuttle et al. 2017). All of these factors combined allow lionfish to grow faster and larger than they do in their native range (Pusack et al. 2016). And though they have comparatively low brood fecundity they have a high rate of batch production (Morris 2009) which allows for overall higher reproductive success than other fishes in the Atlantic (Côté and Smith 2018).

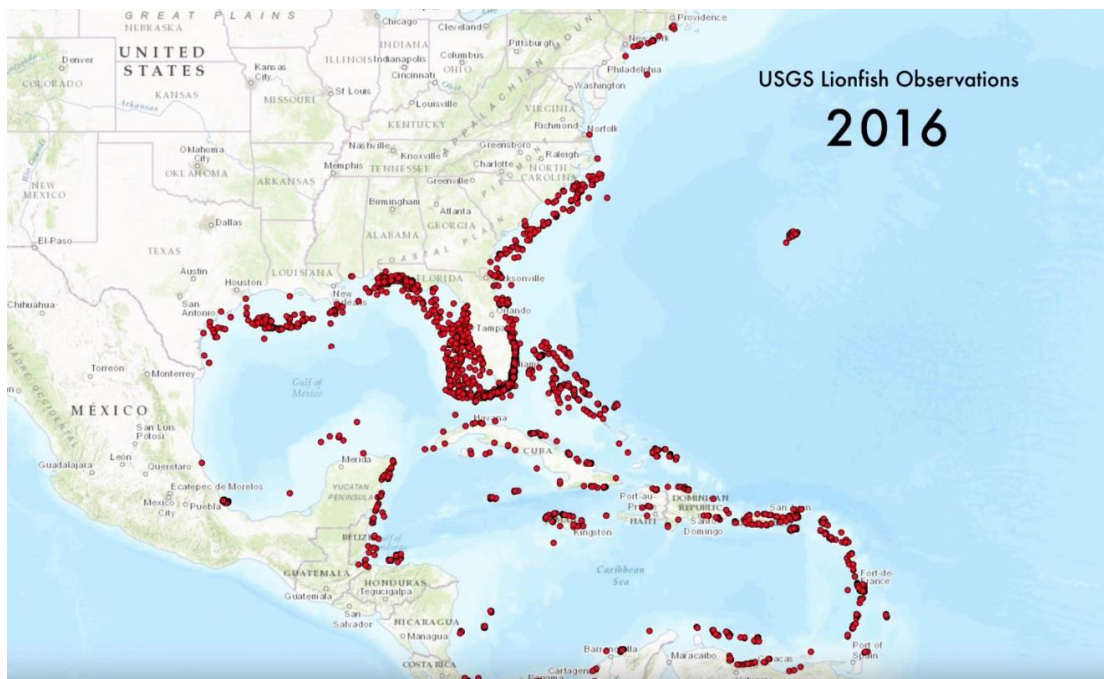


Fig 1.1 Distribution map of invasive lionfish as of 2016. Photo courtesy of USGS.

Current management of the lionfish invasion is limited to divers catching them by hand net or spear, and many local governments have resorted to opening marine reserves to the public for lionfish derbies to help with removal efforts

(Malpica-Cruz et al. 2016; Anderson et al. 2017). Lionfish are also habitat generalists (Cure et al. 2014), and they have been found in estuaries (Jud and Layman 2012; Jud et al. 2015), mangroves (Barbour et al. 2010; Pimiento et al. 2015), and at depths up to 100m (Lesser and Slattery 2011; Andradi-Brown et al. 2017). Therefore, many lionfish occur in habitats that are well beyond the reach of recreational divers. Because control of the invasion is time and labor intensive, understanding the ecology of the lionfish invasion at multiple scales is critical to managing removal efforts effectively.

The major goal of this dissertation is to investigate at multiple scales species-habitat interactions and species-species interactions involving invasive lionfish. All three field-based studies (chapters 2-4) were conducted in the Bahamas on the island of Eleuthera.

In Chapter 2, I examined how physical and biotic factors at different resolutions affect our ability to predict lionfish distribution in their invaded range. Species habitat modeling is becoming more prevalent in marine systems, especially where marine protected areas (MPAs) or other habitat based ecosystem management is practiced (Carr et al. 2011). Because lionfish are habitat generalists, it would be useful for management to know where they are more likely to occur and where their densities are higher for more effective removal efforts. However, data collection can be labor and time intensive depending on the scale of collection.

Remotely sensed data is a good “middle ground” for data resolution (Levin 1992). We can use satellite imagery to produce spatial data on bathymetry, which are more detailed than nautical charts and cover larger areas than traditional, small scale

ecology methods using quadrats and transects. In Chapter 2, I compared the accuracy of species distribution models based on remotely sensed data with those incorporating finer resolution diver-collected habitat and biotic data.

Chapter 3 focuses on how the physical and biotic factors that correlate to lionfish distribution are related to lionfish site fidelity at the individual or reef scale. Lionfish prefer rugose habitat, as do many reef fishes, and they are often found in cracks, caves, and hollowed-out coral heads, where they avoid strong currents (Johnston and Purkis 2013; Cure et al. 2014; Anton et al. 2014). However, habitat structure may not be the only factor that influences lionfish site fidelity. Because lionfish have been shown to consume all prey-size fish from small patch reefs (Benkwitt 2015), perhaps their site fidelity is also linked to prey density. Site fidelity could potentially also be related to other biotic factors, such as individual size, density of conspecifics, or a potential antagonistic relationship between lionfish and native grouper that may interfere with the lionfish's ability to hunt (Mumby et al. 2011; Raymond et al. 2015).

In Chapter 3, I examined how habitat structure (an abiotic factor) and interspecific interactions (biotic factors) were related to lionfish site fidelity. I tracked individual lionfish on 16 reefs over two years, and collected spatially explicit data on locations of lionfish and native groupers, as well as size and density of lionfish, groupers and prey fishes. I quantified site fidelity in three ways: (1) frequency of sightings (total number of sightings / total number of surveys); (2) duration of time on the reef (days between the first and last sighting on the reef); and (3) distance (m)

between sightings. I also collected microhabitat data and quantified human activities on the study reefs that may affect fidelity (Côté et al. 2014).

Chapter 4, “Differential effects of native vs. invasive predators on a common Caribbean reef fish,” is published in *Environmental Biology of Fishes* (Davis 2018). This chapter is a behavioral study of bicolor damselfish (*Stegastes partitus*) to investigate whether lionfish have consumptive and/or non-consumptive effects on one of their common prey species. One hypothesis on why lionfish have been so successful in the invaded range is prey naïveté, or that prey species are not conditioned to recognize lionfish as a predator (Black et al. 2014; Diller et al. 2014; Anton et al. 2016). Previous work by members of the Hixon lab at Oregon State University examined the consumptive effects of lionfish on multiple prey species (Albins 2015; Benkwitt 2015, 2016; Ingeman 2016; Kindinger and Albins 2017; Tuttle 2017), as well as the non-consumptive effects on grazing rates of herbivores (Kindinger and Albins 2017). Previous studies have also documented interactions between lionfish and the threespot damselfish (*Stegastes planifrons*) to determine whether this aggressive territorial fish has a behavioral response to lionfish that might make them less susceptible to consumption, thereby providing a spatial refuge for other prey sized fish (Kindinger 2014). Results from these studies suggested the native prey are naïve to invasive lionfish and this in turn can make them susceptible to predation.

Chapter 4 builds on that previous work by examining whether a less aggressive damselfish would respond similarly to the presence of lionfish as the more aggressive species did. This study also extended that work to examine non-

consumptive effects of lionfish on bicolor damselfish, specifically on their fecundity. This behavioral study used the model-bottle technique described by Myrberg and Thresher (1974) and adapted by Kindinger (2015), which allows observation of a focal “prey” fish without any mortality. In addition, to test how lionfish affected egg production by damselfish, I created artificial nests out of PVC and acetate, and tracked egg production through the study period (see Johnson and Hixon 2011; Hixon et al. 2012). Results show that while bicolor damselfish do not respond behaviorally to lionfish there is evidence that lionfish are reducing the average size of adult bicolors and fecundity.

This dissertation explores at multiple scales the interactions of invasive lionfish with reef habitat and native species. This work provides tangible products to help aid in the management of the lionfish invasion. Overall, this study is an effort to examine the behavior and ecological effects of an invasive species at multiple scales to provide a scientific basis for management and conservation of invaded coral reef ecosystems.

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Chapter 2 – Integrating remote sensing and diver observations to predict the distribution of invasive lionfish on Bahamian coral reefs

Alexandra C. D. Davis

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Abstract The ongoing invasion of coral reefs in the greater Caribbean region by Indo-Pacific lionfish (*Pterois* spp.) poses challenges for managers. Although the dynamics and ecological effects of lionfish invasion have been examined in detail at the scale of individual reefs, relatively little information is available on the patterns of the invasion over larger areas. This study combined species counts and microhabitat observations from SCUBA surveys with satellite derived bathymetry and habitat data to create predictive species distribution maps of lionfish in a 58 km² region along the southern edge of the island of Eleuthera in the Bahamas. Models predicted both lionfish presence/absence and density. The model based on spectral reflectance predicted 71% of presence/absence, discriminating between live reefs and sand flats, but under-predicted lionfish occurrence in areas of roughened hardpan seafloor. A more complex model based on both spectral reflectance and seafloor roughness predicted 76% of presence/absence, and accurately identified lionfish habitat on both live reefs and roughened hardpan seafloor, as well as the absence of lionfish on sand flats. The best fit model for presence/absence combined remotely sensed physical variables, a spectral habitat map, and diver collected microhabitat data predicted 89% of lionfish presence/absence. The best fit models for lionfish density were the microhabitat and biological models, both of which predicted density accurately 74% of the time. These results suggest that physical habitat modeling using remotely sensed bathymetry data may be useful for efforts to establish marine protected areas, conserve native coral-reef ecosystems, and plan targeted lionfish removals.

2.1 Introduction

Invasive Indo-Pacific lionfish (*Pterois* spp.) were introduced to the subtropical western Atlantic late in the last century and have now spread throughout the greater Caribbean (Schofield 2009), including the Gulf of Mexico (Whitfield et al. 2007, Schofield 2010), and into South American coastal waters (Evangelista et al. 2016). Lionfish have been shown to greatly reduce recruitment of ecologically and economically important fish species on reefs (Albins & Hixon 2008, Albins 2015, Ingeman 2016, Kindinger & Albins 2017, Tuttle 2017), including extirpation in some cases (Benkwitt 2013, Ingeman & Webster 2015, Ingeman 2016). Locating and removing lionfish is now a major goal for conservation of coral reefs in the Caribbean (Frazer et al. 2012, de León et al. 2013, Hackerott et al. 2013, Green et al. 2014, Usseglio et al. 2017). However, current management options for controlling lionfish populations are limited to manual search and removal by divers using spears or nets, which are labor intensive and time consuming (Green et al. 2014). More comprehensive regional mapping of lionfish distribution would allow management to prioritize removal efforts.

Species distribution modeling is a useful tool to predict expansion or contraction of species ranges (Rodríguez-Castañeda et al. 2012), and has become widespread in conservation biology and wildlife management (Araújo & Guisan 2006). Species distribution maps, including habitat suitability maps, may be based on predicted presence and absence (Guisan & Thuiller 2005). Many habitats are characterized by physical features that do not change rapidly (McComb et al. 2010). However, biotic interactions may alter species distributions over time and are more

difficult to quantify (Araújo & Guisan 2006). The availability of remotely sensed bathymetry now provides the opportunity to create physical habitat maps for use in marine ecosystems (Pittman et al. 2007, Pittman & Olds 2015, Roelfsema et al. 2018)

Species distribution mapping has also been used for tracking the spread of invasive species and for planning control efforts (Petitpierre et al. 2012). Invasive species can alter or disrupt functioning ecosystems (Pyšek & Richardson 2010) by overconsuming or outcompeting native species for resources, changing nutrient cycling, and overall altering food webs and community structure (Molnar et al. 2008). The rate of spread of invasive species is attributed to a complex combination of factors (Catford et al. 2011), such as native biotic resistance (Kimbrow et al. 2013, Byun & Lee 2017), ecological release (Keane & Crawley 2002, Colautti et al. 2004, Kimbro et al. 2013), and the ecological landscape of the invaded range (Baltz & Moyle 1993, Collinge et al. 2011). Because species interactions and complex community interactions may be more difficult to quantify than physical habitat, using suitable habitat to predict where invasive species occur may be a more practical and general approach.

Based on fine-scale studies of individual reefs (Cure et al. 2014), invasive lionfish (Figure 1) are characterized as habitat generalists (Cure et al. 2014), yet they prefer rugose (rough-textured) seafloors, where they can find cracks and caves in which to shelter during the daytime when not feeding and where currents are strong (Fishelson 1997). Thus, reefs are obviously suitable habitat for lionfish. However, lionfish are not limited to reef structures. Lionfish also occur in seagrass beds (Kulbicki et al. 2012, Benkwitt 2016a), mangroves (Barbour et al. 2010; Pimiento et

al. 2013), river estuaries (Jud & Layman 2012, Kulbicki et al. 2012), and on reef slopes as deep as 100 m (Lesser & Slattery 2011, Nuttall 2014). It is unclear whether lionfish are attracted to reefs because of the high complexity structure, or are responding to some aspects of the biotic community, such as prey abundance, or both. Lionfish may leave small patch reefs at dusk, hunt at night, and return to reefs at dawn, suggesting that they are attracted to reefs as shelter, and not necessarily by the prey assemblage on the reef (Benkwitt 2016a, b). Moreover, large isolated reefs with high complexity, but relatively low prey fish availability, have supported high densities of lionfish for at least weeks (Davis, unpublished data). On the other hand, high densities of large Nassau grouper can interfere with lionfish hunting and may be a deterrent for lionfish to remain on small patch reefs (Pusack 2013, Raymond et al. 2015, and see Ellis and Faletti 2016 for red grouper).

Despite many studies of invasive lionfish in the greater Caribbean region, little is known of the fine-scale regional distribution of lionfish. No studies have yet applied species distribution modeling to describe the spatial pattern of invasive lionfish presence/absence. Available reef maps are typically of very coarse resolution and may not provide information needed at the scale necessary to guide divers to fine-scale locations of lionfish. For example, much of the knowledge of reefs in the Bahamas is obtained from images derived from Google Earth or coarse resolution maps (personal observation). Higher resolution habitat and species distribution maps may therefore be invaluable to conservation efforts in the Bahamas and elsewhere. The goals of this study were:

1. to map the distribution of invasive lionfish based on coarse-scale spectral reflectance and physical habitat features, and evaluate map accuracy as a test of the hypothesis that lionfish will be found in more complex habitats;
2. to map the distribution of lionfish based on fine-scale physical habitat features and a biotic factor, specifically the abundance of Nassau grouper, and evaluate map accuracy as a test of the hypothesis that diver-obtained microhabitat and biological data will improve the model;
3. to understand the relationship between lionfish distribution and abundance of Nassau grouper based on previous work suggesting that grouper exclude lionfish from otherwise suitable physical habitats; and
4. to contribute an improved lionfish habitat suitability map of south Eleuthera, Bahamas, and a method for creating species distribution models that can be replicated to improve habitat suitability maps throughout the invasive range of lionfish.

2.2 Materials and Methods

Lionfish presence/absence and density, the abundance and density of Nassau grouper, and microhabitat features were surveyed at a total of 115 points (random points generated using ArcGIS, and specific reef features chosen non-randomly) from 2013 through 2016 in a 58 km² region on the southern end of the island of Eleuthera in the Bahamas. Remotely sensed spectral and bathymetry data were used to derive a set of physical features of the seafloor. Both physical habitat data and biotic data

(abundance of grouper) were used to develop maps of lionfish presence/absence and density. Deviance explained by the models (defined below) was used to test hypotheses regarding the roles of physical and biotic factors that influence lionfish presence and abundance.

Study area

This study was conducted during the summer months (May-Sept) of 2013-2016 on the southwest end of the island of Eleuthera, the Bahamas (24.829578 N, -76.328444 W) (Figure 1). The system consists mainly of reefs separated by sand and seagrass beds, producing patches with varying degrees of isolation, as well as areas of spur and groove reef on the Exuma Sound side of Cape Eleuthera. The Exuma Sound is exposed to prevailing trade winds and the coastal shelf ranges in depth from 3 to 25 m. Beyond the coastal shelf, the seafloor drops abruptly to 2000 m depth.

Reefs surveyed

Study reefs were first chosen based on two criteria to encompass (1) the natural range of reefs on the shelf, based on knowledge of the area gained from previous studies (Pusack et al. 2014, Ingeman 2016, Kindinger & Anderson 2016), and (2) a naturally occurring range of lionfish densities. From 2013 through 2016, eight to twelve reefs were surveyed annually, some reefs surveyed multiple years, for a total of 23 unique reefs. In 2016, thirteen new reefs were added to the 23 reefs already surveyed. Also in 2016, sampling was done on a set of 90 points distributed

over the 58 km² study area, including all habitat types. Points were selected using the random point generator in ArcGIS (v. 10.2.2).

The resulting sample of 36 study reefs ranged in size from 100 to 1200 m², with an average area of 550 m², and ranged in depth from 4 to 25m. Study reefs also varied in vertical relief and microhabitat structure.

Surveys were conducted throughout the study season (June-September) in each year except 2013, when data were available only for June. All surveys were conducted by a pair of SCUBA divers during daylight hours between 1000 and 1700 hr. Each reef survey typically lasted 1-2 hours, and each random point survey lasted 10-30 minutes.

Fish surveys

Invasive lionfish

Between 2013 and 2016, each of the 36 reefs, including a 10-m diameter buffer of surrounding sand or coral-rubble seafloor, was thoroughly searched for lionfish by divers using dive lights to examine all cracks and crevices. In 2016, a 20m diameter circular plot was surveyed at each of the 90 randomly located points. All lionfish seen were counted, visually sized for total length (TL) to the nearest centimeter, and their locations mapped.

Native fishes

Reef surveys were conducted for large native piscivores (potential predators of lionfish and potential competitors for food, such as groupers and moray eels), and prey sized fish (the known primary forage base of lionfish, Morris & Akins 2009, Valdez-Moreno et al. 2012, Côté, Green, Morris, et al. 2013, Dahl & Patterson 2014, Arredondo-Chávez et al. 2016). All fish were counted and sized to the nearest cm TL visually.

Habitat mapping

Bathymetric data points derived using World View-2/3 satellite images of the southwest coast of Eleuthera, the Bahamas, were obtained from EOMAP GmbH & Co. KG (vertical accuracy 2m grid spacing, horizontal accuracy $\pm 0.5\text{m}$) for the study area. Point data sets were imported into ArcGIS 10.2 and used to create a digital elevation model (DEM) for the 58 km² study area. A variety of habitat variables were generated from the DEM using the *Benthic Terrain Modeler 3.0* plugin for ArcGIS (Wright et al. 2005), including depth, first derivative of slope (curvature), rugosity, and Bathymetric Position Index (BPI), which is a measure of peaks and valleys relative to a designated neighborhood size (Table 1, Figure 2).

At each of the 115 points (including reefs) where lionfish were sampled, I also completed surveys of fine-scale physical habitat, including the location of reef cracks (<2m diameter, i.e., below the resolution of the satellite data), ledges and caves, and surrounding substrate (e.g., sand, hard bottom, seagrass). At the 90 randomly located

points sampled in 2016, substratum was classified in a 20m diameter circular plot. If the random point landed on an isolated reef, then I performed reef area measurements and noted any small cracks, ledges and caves (Figure 2F).

Model design

To test which habitat variables were correlated with the local distribution of lionfish, I ran generalized additive models (GAMs) using the *gam* function in the *R* statistical package for ArcGIS (*R* Developmental Core Team 2015). GAMs are flexible models that can be used with non-linear data (common in ecological studies), allowing the data determine the relationship between the response and explanatory variables (Guisan & Thuiller 2005, Zuur et al. 2009). GAMs can also account for data which do not have constant variance (Guisan & Thuiller 2005).

Habitat complexity variables have been shown to correlate with the local distributions of marine species (Gratwick and Speight 2005, Rilov et al. 2007) and have been used in modeling distributions of marine fishes (Young et al. 2010; Pittman et al. 2007). Therefore, I created a variety of models using four sets of variables as the independent predictors. Remotely-sensed habitat variables included (1) coarse-scale physical habitat from remotely sensed bathymetry, such as depth, slope, aspect, curvature, rugosity, and bathymetric position index (BPI) and (2) seafloor habitat classification layer provided by EOMAP based on seafloor reflectance and spectral characteristics (Table 1), which categorized 4 separate seafloor habitats: coral reef, hard bottom, hard bottom with algae, and unconsolidated sediment. In addition, I included data collected by divers, including (3) fine-scale physical habitat such as

caves and ledges as well as cracks that were smaller than the 2m resolution of the remotely sensed data, and (4) potential biotic interactions, i.e. the presence/ absence or density of grouper.

Model 1 (Figure 3) tested how well the spectrally derived seafloor habitat layer created by EOMAP predicted lionfish occurrence. This layer represented the spatial information available publicly, through Google Earth or World View images. Predictor variables in this model were the four habitat classes: coral reef, hard bottom, hard bottom with algae, and unconsolidated sediment. Response variables were lionfish presence/absence (model 1a) and lionfish density (model 1b).

Predictor variables in model 2 (figure 3) included physical habitat variables derived from remotely sensed bathymetry, i.e., depth, slope, aspect, curvature, rugosity, and bathymetric position index (BPI) as well as the four classes included in the spectrally derived seafloor habitat layer that was used in model 1. Response variables were lionfish presence/absence (model 2a) and lionfish density (model 2b).

Models 3 and 4 included rugosity and BPI and field-based microhabitat data (model 3) or Nassau grouper data (model 4). Response variables were lionfish presence/absence (models 3a, 4a) and lionfish density (models 3b, 4b).

GAM models were fitted in an iterative process in which variables were removed or replaced successively until the best fit model was created. Presence/absence models were fit with a binomial distribution, and density models were fit with a Gaussian distribution.

Model fit was assessed using deviance explained and variable significance. The deviance of a generalized linear model is twice the difference in log-likelihood between the proposed model and a saturated model (a model with as many parameters as there are observations). For a Gaussian family this is the usual residual sum of squares, and the percentage deviance explained is exactly R-squared. For non-Gaussian families, the percentage deviance explained provides an analog of R-squared that can help quantify the goodness of fit of a model. Models were constructed using 70% of the data (n=76). Predictive accuracy of the models was calculated by comparing actual presence/absence and density observations to the predicted distribution from the model using the remaining 30% of data (n= 39).

2.3 Results

The outputs of the models are listed in Table 2.

Lionfish presence/absence

Model 1a: Coral-reef habitat was the only significant variable in the model (*GAM* $p=0.011$), and the deviance explained was 11.2%. This model was based on spectrally derived seafloor habitat and it accurately predicted lionfish presence/absence 71% of the time.

Model 2a: Rugosity was the only significant variable related to lionfish presence and absence (*GAM* $p= 0.003$), and the deviance explained was 37.9%. This model was based on remotely-sensed physical habitat features and accurately predicted lionfish presence/absence 76% of the time.

Model 3a: The model based on coarse-scale physical habitat features and diver-collected fine-scale physical habitat data explained 67.6% of the deviance. Locations with one or two microhabitat features were significantly correlated with lionfish presence (*GAM*, $p = 0.014$ and $\ll 0.001$, respectively), and the broad scale rugosity variable was no longer significant. This model accurately predicted lionfish presence/absence 89% of the time.

Model 4a: The model based on coarse-scale physical habitat features as well as a biotic interaction (density of Nassau grouper) explained 23.1% of the deviance. Rugosity was still a significant factor (*GAM*, $p = 0.038$), as well as the density of Nassau grouper present (*GAM* $p = 0.001$). This model accurately predicted lionfish presence/absence 68% of the time.

Lionfish density

Model 1b: There were no significant variables in this model and the deviance explained was only 6.8 %. This model, based on spectrally derived seafloor habitat, accurately predicted lionfish density 26% of the time.

Model 2b: Rugosity was significantly related to lionfish density (*GAM* $p = 0.010$) and explained 29.4% of the deviance. This model, based on coarse-scale physical habitat features, accurately predicted lionfish density 73% of the time.

Model 3b: Lionfish density was significantly correlated to the number of microhabitat features present (Table 2, *GAM* p ranged from $\ll 0.001$ to 0.040), and

explained 44.5% of the deviance. This model accurately predicted lionfish density 74% of the time.

Model 4b: Rugosity was significantly related to lionfish density (*GAM*, $p = 0.020$), as well as the density of Nassau grouper (Table 2, *GAM* p ranged from $<<0.001$ to 0.005). The deviance explained by this model was 34.6%, and the model accurately predicted lionfish density 74% of the time.

2.4 Discussion

This study demonstrated that lionfish presence/ absence and density can be predicted with varying accuracy (26-76% accuracy) using satellite derived bathymetry with 2m resolution. Adding diver collected microhabitat observations greatly increased the deviance explained by the models for lionfish presence/absence and density by up to 30%. Adding diver collected data on presence and density of Nassau grouper, a native predator, improved the deviance explained by the model for lionfish density by 5% relative to the model based on physical variables only, but decreased the deviance explained of the model for lionfish presence/absence by 14%. Similar to other studies, the use of both presence and absence data creates a more accurate model of species distribution than a model using only one or the other (Brotons et al. 2004). This is especially true for species that have broad habitat ranges and can be tolerant of many environmental conditions, such as lionfish (Barbour et al. 2010, Jud & Layman 2012, Kulbicki et al. 2012, Cure et al. 2014, Loerch et al. 2015). The ability of divers to exhaustively search reefs at most of the sites used in this study

was high, so the overall confidence in the presence/absence observations was high. False absences predicted by the models ranged from 8% with the full physical model to 23% in the microhabitat model. False presences predicted ranged from 4 to 40%, with the microhabitat model having the lowest false presence rate (4%), and the biotic model having the highest (40%). This result suggests that there is a trade-off within the models in their ability to accurately predict presence or absence.

The techniques used in this study are similar to many previous efforts to model species distribution (Brotons et al. 2004, Rodríguez-Castañeda et al. 2012). However, few habitat modeling studies of any marine species have been conducted in the Bahamas (Stoner 2003 for queen conch, Machermer et al. 2012 for parrotfishes). This study provides novel information regarding how lionfish are distributed in the reef ecosystem of Eleuthera. The methods for habitat modeling described here may be used to locate lionfish in other parts of the invaded range.

Broad-scale remotely sensed data provide suitable information for mapping species distributions. These types of data are easily accessed by the public and do not require any special skills to analyze. However, lionfish prefer sub-2m resolution habitat features for “resting” in during daylight hours. This key habitat component was missed by satellite derived remotely sensed data, both because of the top down nature of the images, as well as constraints on resolution. The best fit was provided by model 3a (deviance explained 67.6%, predictive accuracy 89%), which used remotely sensed seafloor habitat and benthic features as well as the diver collected microhabitat data. In this study, divers used a simple classification system based on the presence or absence of certain features, which made collection of the microhabitat

features data easy. Higher resolution remotely sensed imagery might improve detection of microhabitat features, but the success of these techniques likely depends on the depth of the seafloor and would still not be capable of detecting features such as caves.

Nassau density was significantly negatively correlated with both lionfish density and presence/absence, and this biotic variable improved the fit of the lionfish density model (4b) compared to the other physical models of lionfish density (Table 2). One demonstration of this potential negative interaction between fish species is suggested by an area that was predicted to have high lionfish presence based on the physical model (Figure 4 a/d) yet no lionfish were found. However, that survey location had one of the highest densities of Nassau grouper and other large bodied grouper seen in the survey area. Conversely, an analysis of a subset of reefs where prey data were collected showed that lionfish density was positively correlated with reefs that had high prey density and multiple classes of microhabitat features (GLM, $p = 0.0379$). These results suggest that while habitat *is* important for lionfish distribution in their invaded range, potential for negative (via large grouper) or positive (via prey availability) biotic interactions likely influence lionfish fidelity to a reef.

Another biotic factor that may influence lionfish distributions is the presence of large mobile invertebrates such as *Panulirus argus* (Caribbean spiny lobster) and *Diadema antillarum* (longspine urchins). I collected data on these species during my surveys, yet there were not enough reefs with these species present to use as a viable model predictor. Both lobster and urchins occupy cracks and crevices similarly to

lionfish. If the cracks and crevices are important for lionfish on the reef as the models suggest, then high densities of either species may influence lionfish densities, depending upon interspecific interactions. Anecdotally, reefs that had high densities of urchins supported only a few lionfish, and as the urchins left the reef throughout the summer, lionfish density increased (Davis, unpublished data). An experimental approach would be required to confirm this potential interaction.

Ultimately, collecting fish and invertebrate data will always be both labor and time intensive and may not be worth the extra effort. So, was the model including biotic data so much better that the hours of diver observation to collect biotic data was worth the time? Perhaps. Because the biotic data were more important in the density models, additional field observations of native predators may be vital to identify reefs which are vulnerable to long-term lionfish invasions.

This study has important implications for management of the lionfish invasion because it demonstrates that simple models of physical habitat based on satellite-derived bathymetry provide a good approximation of where lionfish may occur. The model that was based purely on spectrally derived seafloor habitat had similar ability to predict lionfish presence/absence as the model based on spectrally derived seafloor habitat as well as other benthic features (71% and 76%, respectively). However, the model that was based purely on spectrally derived seafloor habitat was very accurate at predicting lionfish absence (96%), but not accurate at predicting lionfish presence (31%). In contrast, the model based on spectrally derived seafloor habitat as well as benthic features had 78% accuracy predicting lionfish absence and 70% accuracy predicting lionfish presence. This distinction can be crucial for invasive species

management because an accurate map of potential presence points is important for removal efforts.

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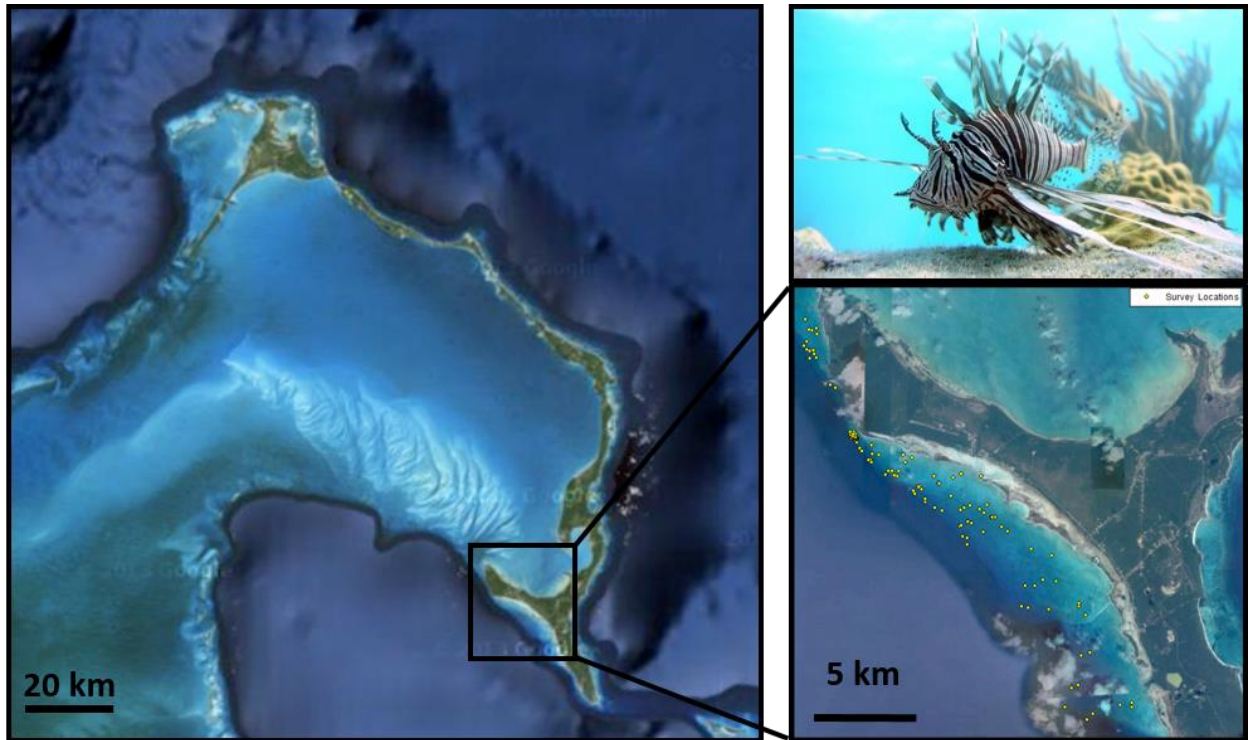


Figure 2.1 Site map of Eleuthera, the Bahamas, the southern edge of the island where all observations were conducted, yellow dots indicate the survey sites, and an invasive lionfish in the invaded range (photo of lionfish by Mark A Albins).

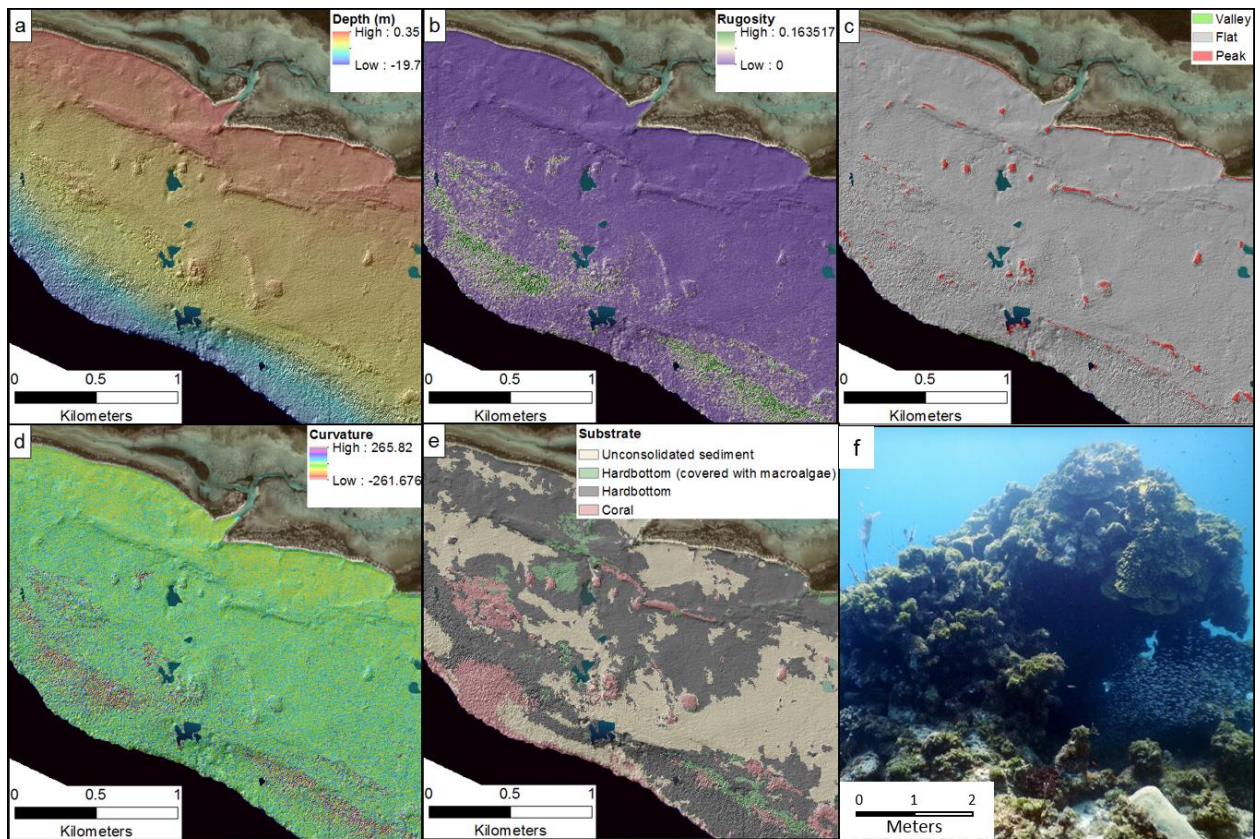


Figure 2.2 Bathymetric variables used in the models. A) rugosity, b) Bathymetry Position Index (BPI), c) curvature, d) depth, e) categorical substrate, and f) photo of one of the study reefs with an overhanging ledge feature.

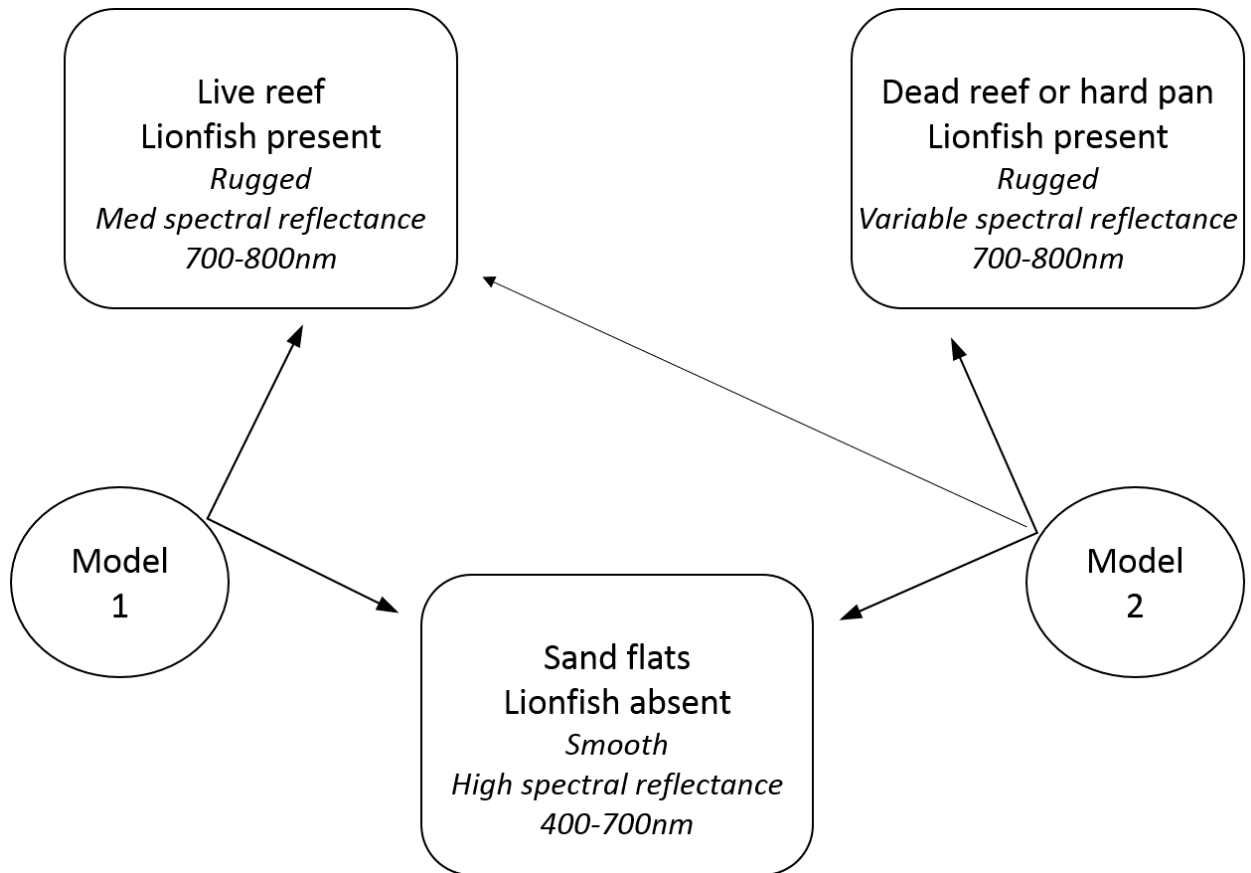


Figure 2.3 Conceptual diagram of three types of habitat that can be classified from remotely sensed imagery. Seafloor ruggedness (rugosity) is calculated as the variation in surface roughness. Spectral reflectance refers to the brightness or albedo of the habitat, and the wavelength (nm) where reflectance is highest. Lionfish presence or absence is predicted based on *a priori* assumptions that lionfish are associated with reef habitat, and observations that lionfish are attracted to structures on the seafloor. Model 1, which uses seafloor habitats classified from spectral reflectance, can distinguish between live reef, hard bottom, and sand but generally classifies only live reef as potential lionfish habitat. Model 2, which also includes measures of ruggedness such as rugosity and bathymetric position, can also distinguish all three habitat types and identifies dead reef or hard bottom areas, as well as live reefs, as potential lionfish habitat.

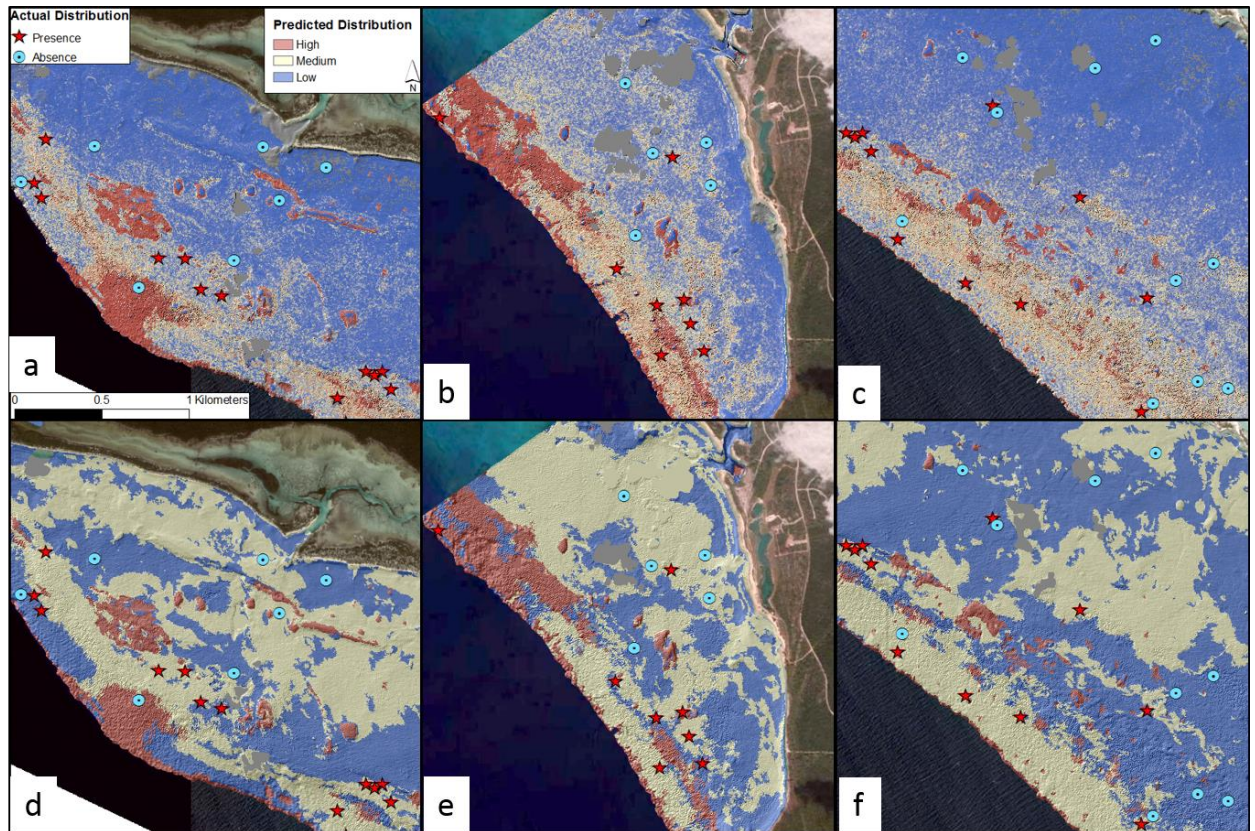


Figure 2.4 Comparison of the predicted distribution of lionfish presence/absence in three locations from model 1b, based on broad scale physical features (panels a, b, c) and model 1a, based only on the spectrally derived seafloor habitat (panels d, e, f). Red areas represent high predicted presence, yellow areas represent medium predicted presence, and blue represent low predicted presence. Red stars represent actual sightings of lionfish (presence) and blue circles represent no lionfish observed (absence). Grey areas represent “no data” due to cloud cover. Comparisons of panels a to d, and of panels b to e, show that the full physical model generates intermediate predictions well, whereas the simple model selects the extremes very well. Panels c and f show that there are some areas where both models either overestimate (c) or underestimate (f) potential lionfish habitat.

Table 2.1 Description of satellite bathymetry products used for habitat classification, and diver obtained microhabitat and biotic observations

Variables derived from satellite bathymetry	Description	Tool used	Variable form used in modeling
Depth	Water depth for each cell, derived from World View satellite images	na	Continuous
Rugosity	Ratio between straight-line distance and the three-dimensional distance	Rugosity tool in BTM	Continuous
Bathymetric position	Measure of a cell's depth relative to its surroundings at a designated scale (used 50m scale)	Broad Scale and Fine Scale BPI tools in BTM	Categorical (3)
Curvature	The degree to which something deviates from a straight line	Curvature tool in BTM	Continuous
Slope	Change in depth	Slope tool in BTM	Continuous
Seafloor habitat layer	Classification of seafloor by EOMAP based on seafloor reflectance and spectral characteristics	na	Categorical (4)
Variables derived from diver observations			
Microhabitat	Caves, ledges, or cracks whose diameter is smaller than 2m at survey location	na	Categorical (4)
Nassau count	Number of Nassau grouper at each survey locations	na	Continuous

Table 2.2 Results from the generalized additive models (GAMs) used to associate target species with habitat and biotic predictors.

Model	Response	Predictors	P value	Total deviance explained (pseudo R ²)	Predictive accuracy
1a: Seafloor habitat layer	Lionfish presence/absence	Unconsolidated sediment	0.338	11.2%	71%
		Coral reef	0.011*		
		Hard bottom	0.202		
		Hard bottom with algae	0.382		
2a: Broad-scale physical	Lionfish presence/absence	Rugosity	0.003**	37.9%	76%
		BPI	0.984		
		Depth	0.678		
		Curvature	0.227		
3a: Fine-scale physical	Lionfish presence/absence	Seafloor habitat (categorical)	0.637, 0.986, 0.816, 0.509	67.6%	89%
		Microhabitat (categorical 0-3)	0.977, 0.014** , < 0.001*** , 0.991		
		Rugosity	0.425		
		BPI	0.995		
4a: Biological	Lionfish presence/absence	Nassau	0.001***	23.1%	68%
		Rugosity	0.031*		
		BPI	0.232		
1b: Seafloor habitat layer	Lionfish density	Unconsolidated sediment	0.900	6.8%	26%
		Coral reef	0.865		
		Hard bottom	0.894		
		Hard bottom with algae	0.893		
2b: Broad-scale physical	Lionfish density	Rugosity	0.010**	29.4%	73%
		BPI	0.989		
		Depth	0.479		
		Curvature	0.194		
3b: Fine-scale physical	Lionfish density	Seafloor habitat (categorical)	0.474, 0.362, 0.468, 0.449	44.5%	74%
		Microhabitat (categorical 0-3)	0.907, 0.040* , << 0.001*** , << 0.001***		
		Rugosity	0.171		
		BPI	0.942		
4b: Biological	Lionfish density	Nassau	0.012*	34.6%	74%
		Rugosity	0.001***		
		BPI	0.985		

Chapter 3 – Abiotic and biotic interactions influencing site fidelity of invasive lionfish on Bahamian coral reefs

Alexandra C D Davis

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submitted

Abstract Site fidelity, the extent to which an animal remains within a restricted home range, is an indication of an animal's interactions with its biotic and abiotic environment. Reef fishes often exhibit very high site fidelity, which may provide consistent access to food and shelter as well as knowledge of the local environment. This study quantified site fidelity of invasive Indo-Pacific lionfish and associated environmental correlates over a two-year period on 16 reefs varying in size, depth, habitat complexity and population density near Eleuthera, the Bahamas. Fidelity was measured by the frequency, duration, and spatial locations of individual lionfish, which were identified individually based on dorsal spine clipping or natural variations in color and morphology. Environmental covariates of site fidelity included density of lionfish, native grouper (potential competitors and predators), and prey-sized fishes, as well as measures of habitat complexity. Lionfish density was the only variable that was significantly positively related to lionfish site fidelity, and lionfish density in turn was positively related to habitat complexity. Site fidelity was negatively related to prey density, but not related to grouper density, habitat complexity, lionfish size, or human activities on the reef. Overall, it appears that biotic interactions with conspecifics and an indirect interaction with habitat complexity are the key factors determining site fidelity in invasive lionfish.

3.1 Introduction

Site fidelity is a measure of an animal's affinity to a particular location and the phenomenon of remaining faithful to specific sites (Schmidt 2004). It has been

measured in various ways, such as the distance between sightings (Marnane 2000), the number of times seen (Defran & Weller 1999, Bond et al. 2012), and the time between sightings (Baracho-Neto et al. 2012). Fidelity is also related to the concept of home range, the area over which an animal or group of animals regularly travels (Burt 1943). Site fidelity is important because it can affect breeding success, and ultimately, population dynamics (Schmidt 2004), can be an indicator of productive feeding grounds (Valenzuela et al. 2009), and may have evolutionary consequences, e.g., by enhancing intraspecific variation (Smith & Green 2005). Site fidelity and home range are often related to an individual's body size, i.e., metabolic scaling (Harestad & Bunnell 1979, Reiss 1988), the patchiness of habitat and distribution of resources such as food and shelter (Green et al. 2012; Beverly et al. 2009), and biotic interactions such as predation and competition (Schmidt 2004), as well as mating (Petersen 1988). Site fidelity and home range measurements are used to gauge movement, implement conservation practices, and protect habitat (Augé et al. 2014, Green et al. 2014, 2015). Smaller coral reef fishes, in particular, are known to have restricted home ranges and likely high site fidelity (reviews by Green et al. 2014, 2015).

Indo-Pacific lionfish (*Pterois* spp.) are invasive species in the greater Caribbean region that are found in a wide variety of habitats and depths (Barbour et al. 2010, Cure et al. 2014, Jud et al. 2015, Andradi-Brown et al. 2017). However, lionfish do have habitat preferences and are unlikely to be found where there are strong currents or little to no physical shelter (Johnston & Purkis 2013, Cure et al. 2014, Anton et al. 2014). Bejarano et al (2015) showed that high topographic relief

supports higher densities of lionfish on deep reef terraces (17-20m) in Little Cayman. Davis (in review) found that rugose reefs with ledges, cracks, and caves are more likely to have lionfish present and can support higher densities of lionfish than less complex reefs.

Knowledge of the extent and patterns of site fidelity is critical to lionfish removal efforts (Frazer et al. 2012). Previous studies varied in spatial scale, location, and results. For example, Jud and Layman (2012) saw little movement of lionfish in rivers and estuaries; the maximum range of lionfish in their study was 28m with no difference among lionfish of different sizes. Conversely, Tamburello and Côté (2015) found that site fidelity on small patch reefs decreased with lionfish size. Lionfish leave patch reefs and hunt at night, returning in the morning, and that behavior changes with the density of conspecifics (Benkwitt 2016). Bachelier et al (2015) used telemetry to track lionfish (210mm-400mm) off the coast of North Carolina, finding that daily movement of lionfish was usually <150m. However, larger fish can travel up to 1.35 km in 15 days (Tamburello & Côté 2015). There is also an increased likelihood of movement with higher lionfish densities (Tamburello & Côté 2015), which may be due to greater intraspecific competition. Greater movement may also occur as prey are depleted on patch reefs (Benkwitt 2016). Detectability of lionfish by divers can be variable, and interactions with humans have been shown to make lionfish wary (Côté et al. 2014). The ability to detect lionfish also varies with lionfish size and reef rugosity (Green et al. 2013).

I hypothesized that site fidelity of invasive lionfish is enhanced by habitat complexity and prey availability, and inhibited by body size (larger fish having larger

home ranges), competition (within and between species), predation risk, and human activities. I tested seven predictions deduced from this hypothesis by comparing lionfish site fidelity among reefs with a variety of associated environmental variables. First, following from previous work, fidelity will be negatively correlated with lionfish body size if larger lionfish move among reefs or at least off reefs for part of the day (Tamburello & Côté 2015). Second, site fidelity will be negatively correlated with lionfish density due to intraspecific competition (Tamburello & Côté 2015). Alternatively, if lionfish have positive social interactions, such as cooperative hunting (Lönnstedt et al. 2014b), then site fidelity will be positively correlated with lionfish density. Third, lionfish site fidelity will be negatively correlated with native grouper density due to interspecific competition and/or predation (Raymond et al. 2015, Ellis & Faletti 2016). Fourth, site fidelity will be positively or negatively correlated with prey density, depending on the movement patterns of lionfish among reefs. If lionfish swim frequently between reefs (i.e. overlapping multi-reef home ranges), then a positive correlation is predicted as lionfish congregate where prey are abundant, i.e., an aggregative response that disperses after prey become rare on a reef (Hixon 1998). If lionfish spend most of their time at a single reef and consume prey faster than prey recruit, then a negative correlation is predicted (Hixon & Beets 1993). Alternatively, prey recruitment rates may exactly match lionfish consumption rates, resulting in no correlation. Fifth, lionfish site fidelity will be positively correlated with habitat complexity (Bejarano et al. 2014). Sixth, site fidelity will be negatively correlated with distance to other reefs because of potential costs of longer-distance movements. Lastly, site fidelity will be negatively correlated with human activities, in this case,

recreational and scientific SCUBA diving, which both remove lionfish and may cause negative non-consumptive effects.

3.2 Materials and Methods

Study site

This study was conducted during the summer months (May-Sept) of 2014 and 2015 in a 25 km² area of large coral patch reefs on the southwest end of the island of Eleuthera, the Bahamas (24.829578 N, -76.328444 W) (Figure 1). The system consists mainly of individual reefs separated by sand and seagrass beds, producing patches with varying degrees of isolation, as well as areas of continuous spur and groove reef on the Exuma Sound side of Cape Eleuthera. The Exuma Sound is exposed to prevailing trade winds and the coastal shelf ranges in depth to 25 m. Reefs ranged in size from 103 to 1155 m² and were isolated by at least 90m from other reefs by sand and seagrass, so that each reef was considered to be statistically independent from other reefs in the study area. A total of 17 unique reefs was sampled: twelve in 2014 and five in 2015. Analyses were limited to reefs that supported at least two lionfish so that possible intraspecific interactions could be examined (n=16 reefs). In addition, four of the reefs surveyed in 2014 were also re-surveyed in 2015 for a final sample size of 20 reef-year combinations, assuming temporal independence (Figure 1, Table S1). Temporal independence was accounted for by including year as a random effect in statistical models (see below). Distance between reefs was measured in meters using Google Earth and ArcGIS.

Lionfish identification

Divers caught lionfish using hand nets and tagged them by clipping a unique combination of dorsal spines (Figure S1). This temporary tagging technique permitted divers to identify and track lionfish movement week-to-week without harming the fish or adding an external tag. An estimated 60% of lionfish present during the first few weeks of the study were captured and clipped (n=38). Lionfish that were not caught or were first sighted after the clipping effort ended were visually identified based on size, coloration, shape and state of the supra-ocular tentacles (Fishelson 2006, Morris & Freshwater 2008), and other natural markings such as stripes, spots on the lateral line and fins, or any noticeable damage to the body. Any lionfish that were not previously identifiable were treated as new individuals (i.e. immigrants).

Fish censuses

Surveys were performed once per week for 9-13 weeks depending on the year. Each reef, including a 10-m diameter buffer of surrounding sand or coral rubble seafloor, was thoroughly searched for lionfish by divers using flashlights to examine all reef cracks and crevices. All lionfish and grouper seen were counted and visually sized for total length (TL) to the nearest centimeter, and their locations within the reef were mapped.

Surveys of prey fish were also conducted on all study reefs. Prey fish were sampled using semi-permanent 2-m wide transects which varied in length from 5 to 10m depending upon patch reef diameter. The number of transects was proportional

to the reef surface area, and transects were positioned to capture the natural diversity of microhabitats identified within each reef (e.g. flat reef, reef edge, sand, etc.). A flashlight was used to search for cryptic fish. Prey size fishes ≤ 10 cm TL were counted and sized visually. Only reef fish ≤ 10 cm TL were surveyed because invasive lionfish mostly consume native fish 10 cm or less in total length (Albins & Hixon 2008, Morris & Akins 2009, Benkwitt 2013, 2015).

Site fidelity

Three measures of lionfish site fidelity at the reef scale were used: (1) frequency of sightings (total number of sightings / total number of surveys, reported as a proportion); (2) duration of time on the reef (days between the first and last sighting on the reef); and (3) distance (m) between sightings.

Habitat complexity

Habitat complexity, which provides reef fishes with both shelter and food sources (Graham & Nash 2013), was quantified in three ways. First, rugosity was measured using the chain and tape technique (Risk 1972; McCormick 1994), a ratio of the straight-line distance to an actual surface distance acquired by draping a chain over the reef and in all the cracks and crevices. Second, I mapped and counted the number of physical shelters that could be used by lionfish-sized fishes (reef cracks, ledges, caves, and hollow coral bommies) per square meter (Munday & Jones 1998). Third, reef height in meters provided a measure of vertical relief, which is known to enhance fish abundance (Gratwicke & Speight 2005). These three measures were combined into a single composite measure of habitat complexity (range 2-12) by

adding the rugosity measure (range 1-2.5), the shelter measure (range 0-0.05), and the vertical relief (reef height m).

Human activities

I recorded three types of human activity at all study reefs. (1) whether or not the individual lionfish was clipped (0= no, 1=yes, for each individual fish), (2) evidence and/or knowledge of spearfishing for lionfish on the reef (0= no fishing, 1= fishing), and (3) whether or not lionfish densities on the reef had undergone experimental manipulations in previous years (e.g., Ingeman 2016, Kindinger 2016, 2018, Davis 2018, 0= no manipulation, 1= manipulation). Each of these three human activity measures was analyzed separately in the models.

Data analysis

Multi-level mixed effect statistical models were created to analyze both individual-scale traits and reef-scale characteristics. One model was run for each of the dependent variables (frequency, duration, and average distance between sightings). Each of these models included all the predictor variables (individual and average lionfish size, lionfish density, grouper density, prey density, habitat complexity [rugosity, presence of caves, ledges, cracks and hollow bommies], distance to the nearest reef, and level of human activity). Reef and year were random effects. Generalized additive models were created to analyze correlations between lionfish density and habitat complexity, grouper density, and prey density. All variables in the *GAMs* were allowed to be nonlinear. All statistical analysis was done using the *R* packages *lmerTest* (Kuznetsova et al. 2017) and *gam* (Hastie & Tibshirani

1990, Hastie 1991). Best fit models were selected based on AIC scores (Akaike 1998).

3.3 Results

Best fit models for site fidelity (measured as frequency and duration, see methods) included individual and average lionfish size, lionfish density, grouper density, prey density, and habitat complexity as predictors, and reef and year as random effects (Table 1). The best fit model for fidelity measured as distance between sightings included the same variables, with only reef as a random effect (Table 1). None of the human activities (clipping, fishing, or manipulation) or distance to other reefs, were ever significant and were removed from all models. These models were used to evaluate the potential correlations of site fidelity to the predictor variables.

Body size

Individual size of lionfish was not significantly correlated with site fidelity as either frequency, duration of re-sightings, or distance between re-sightings (LMME, $p=0.389$, 0.231 , and 0.903 Table 1). None of the site fidelity measures were significantly correlated with the average size of all lionfish on the reef (LMME, $p=0.481$, 0.680 , and 0.212 , respectively, Table 1).

Lionfish density

Site fidelity as both frequency and duration of re-sightings was significantly positively correlated with lionfish density (LMME, $p<<0.001$ and $p<<0.001$,

respectively, Table 1, Figures 2C, 3). Fidelity as distance between sightings was not correlated to lionfish density (LMME, $p=0.997$, Table 1, Figure 2C).

Grouper density

Site fidelity as frequency and duration of re-sightings as well as distance between sightings was not significantly correlated with native grouper density (LMME, $p=0.48718$, 0.897 , and 0.752 , respectively, Table 1, Figure 2F).

Prey density

Site fidelity as frequency of re-sightings was significantly negatively correlated with prey density, but fidelity as duration between re-sightings was not significantly correlated with prey density (LMME, $p=0.049$ and 0.153 , respectively, Table 1, Figure 2D). Fidelity as distance between sightings was not correlated to prey density (LMME, $p=0.847$, Table 1, Figure 2D).

Habitat complexity

Site fidelity, measured as frequency and duration of re-sightings as well as distance between sightings, was not correlated with habitat complexity (LMME, $p=0.395$, 0.092 , and 0.731 , respectively, Table 1, Figure 2E). On average, lionfish were seen within 8.27m (± 1.23 SEM) of the original spot where they were sighted, and 63% of all fish were re-sighted at least once within 5m of the original location where they were first sighted, although reef diameters ranged from 6 to 26m (mean 15.3 ± 1.61 m, Figures S2 & S3). Of those lionfish sighted within 8m of their original location, 63% were on high complexity reefs, 28% on medium complexity reefs, and

9% on low complexity reefs (Figure S3). There were only two instances in which a lionfish was sighted on more than one reef: one of these was a 34 cm TL fish sighted on two reefs of high structural complexity approximately 100m apart, and the other was a 32 cm TL fish sighted on one reef with low structural complexity and another reef with high structural complexity approximately 150m away.

Additional patterns

Reefs with higher structural complexity had higher average densities of lionfish, grouper and prey (GAM, $p=0.023$, $p\ll 0.001$ and $p\ll 0.001$, respectively, Figures 2A, 2B, and 4). Lionfish density and prey density were not correlated (GAM, $p=0.940$, Figures 2B and 5A). However, lionfish density was positively correlated with grouper density (GAM, $p<0.013$, Figure 5B), and grouper density and prey density were significantly positively correlated (GLM, $p\ll 0.001$, Figures 2B and 5C). The relationship between lionfish and grouper was non-linear when reefs with high, medium, and low lionfish density were compared (Figure 6).

3.4 Discussion

Lionfish site fidelity increased with lionfish density, which suggests potential social influences on lionfish remaining on a particular reef. Previous studies have suggested that lionfish hunt cooperatively with conspecifics (Lönnstedt et al. 2014a). Lionfish could also be drawn to the same reefs where conspecifics are already residing, perhaps using them as an indicator of suitable habitat.

Grouper density had no association with lionfish site fidelity. However, lionfish site fidelity was negatively correlated with prey densities, and this negative interaction suggests that the model detected a long-term effect of lionfish on these sites, whereby high lionfish fidelity is depleting prey. Conversely, grouper density was positively correlated with prey densities, also perhaps because of an aggregative response (*sensu* Murdoch and Oaten 1975, see Hixon and Carr 1997 and Hixon 1998 for reef fish examples). Both grouper and prey densities were positively correlated with high habitat complexity, which is also expected, as both reef fish abundance and species diversity have long been known to increase with habitat complexity (Risk 1972, Luckhurst & Luckhurst 1978, Roberts & Ormond 1987, Caley & John 1996, Beukers & Jones 1997). These positive associations among factors make it challenging to assign causation without additional, preferably experimental, studies.

So why, then, did we not see a positive relationship between lionfish site fidelity and habitat complexity? It is possible that the detectability of lionfish is lower on reefs of higher complexity, so that lionfish fidelity was underestimated on complex reefs. It also is possible that high densities of grouper may interfere in some way with the ability of lionfish to hunt (*sensu* Dill et al. 2003, Pusack 2013), and/or that lionfish and grouper compete for shelter space (Raymond et al. 2015). If high densities of grouper cause lionfish to leave the reef, and the high densities of grouper are not enough to reduce the densities of prey, then the model may have captured only the negative relationship between lionfish fidelity and prey density.

A second reason for the lack of association between lionfish site fidelity and habitat complexity could be that prey densities are depleted on reefs occupied by both grouper and lionfish (Albins 2013, Pusack 2013), and once prey densities are low enough, lionfish leave the reef. Because lionfish had been established in this region for at least five years prior to this study, it is possible that the model captured this long-term effect. A third possibility is that site fidelity of lionfish *is* associated with high habitat complexity and the association is not captured in the full model. Since site fidelity is correlated with high densities of conspecifics, and high lionfish density is correlated to habitat complexity, it seems likely that perhaps the weaker association between site fidelity and complexity is obscured by the strong association with conspecific density (Figure 2).

Overall, it appears that biotic interactions, in particular the density of lionfish, their prey, and native grouper, have a large influence on lionfish site fidelity, more so than human activities and potentially more so than habitat complexity *per se*. Lionfish are more likely to remain on reefs with high densities of conspecifics and have mixed interactions with native species. Understanding the key drivers for lionfish distribution and site fidelity in their invaded range is crucial for targeting effective lionfish removal efforts and informing conservation management options.

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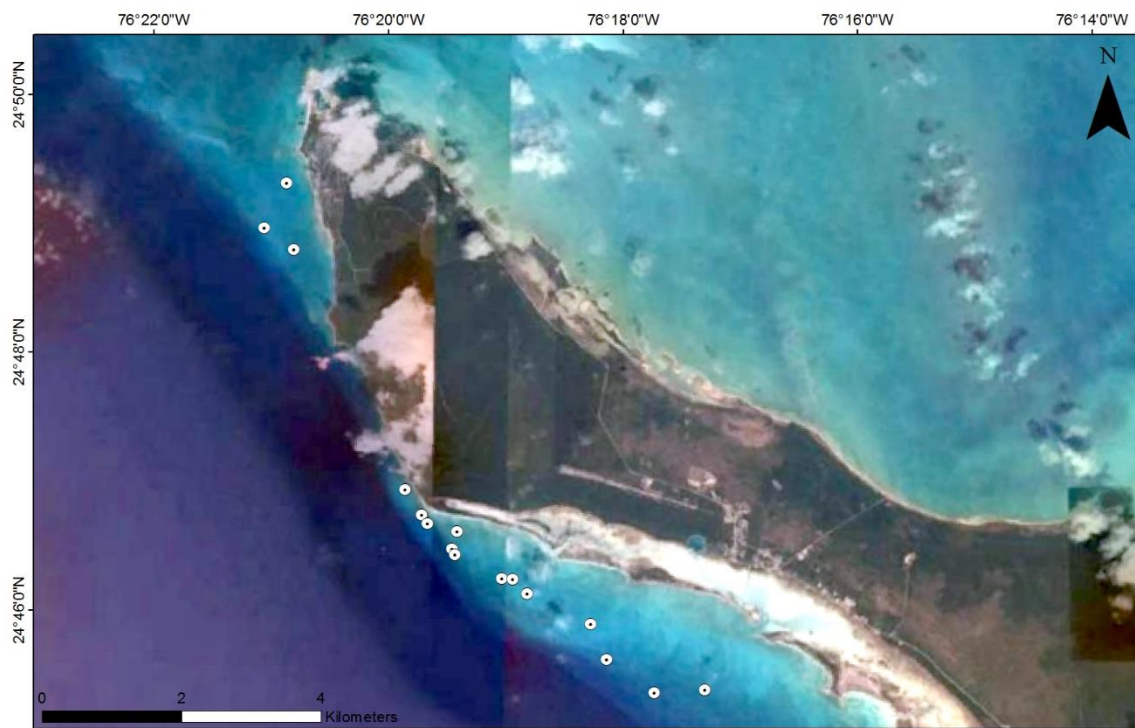


Figure 3.1 Study area off the southwest coast of Eleuthera, Bahamas. White dots show locations of the 16 study reefs. Image courtesy of Google Earth.

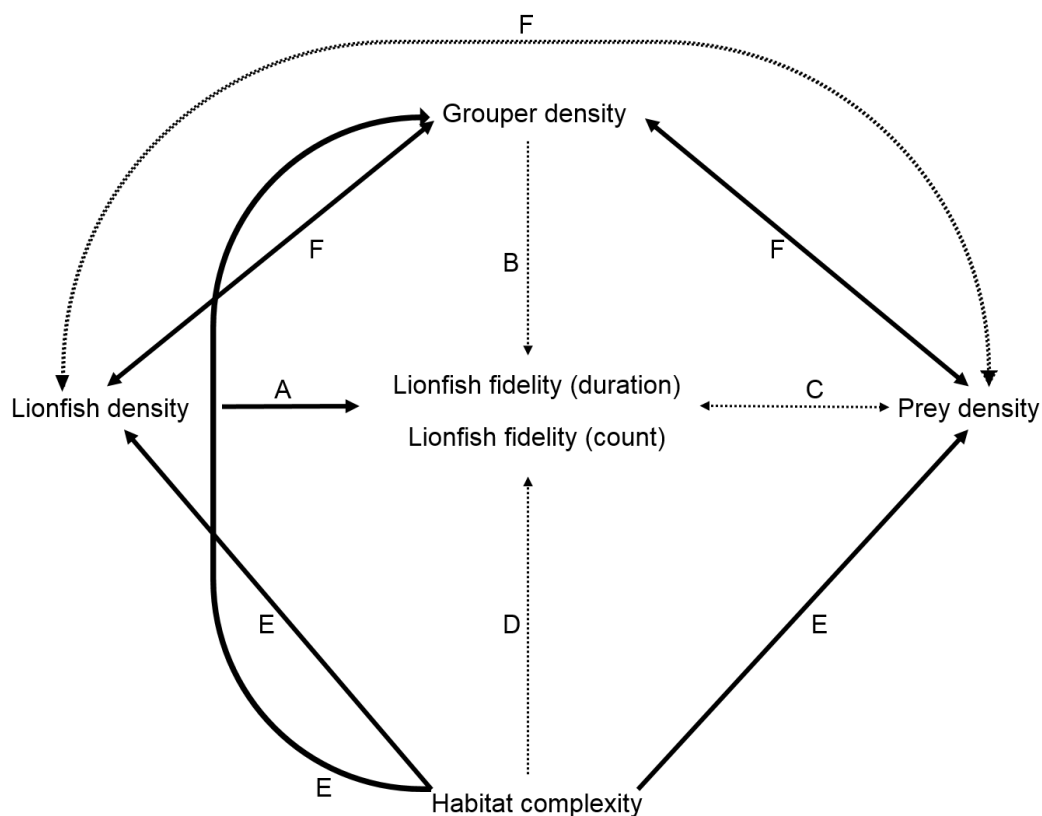


Figure 3.2 Conceptual diagram summarizing relationships of predictor variables with lionfish site fidelity. Solid lines indicate significant positive relationships, dashed lines indicate significant negative relationships, and dotted lines indicate non-significant relationships. Arrowheads indicate predicted directionality of the interaction. A bi-directional arrow implies correlation and causality in both directions, whereas a unidirectional arrow implies that the factor being pointed to is dependent upon the other factor but not vice-versa (e.g. lionfish density and habitat complexity are correlated but lionfish density depends on habitat complexity and not vice-versa).

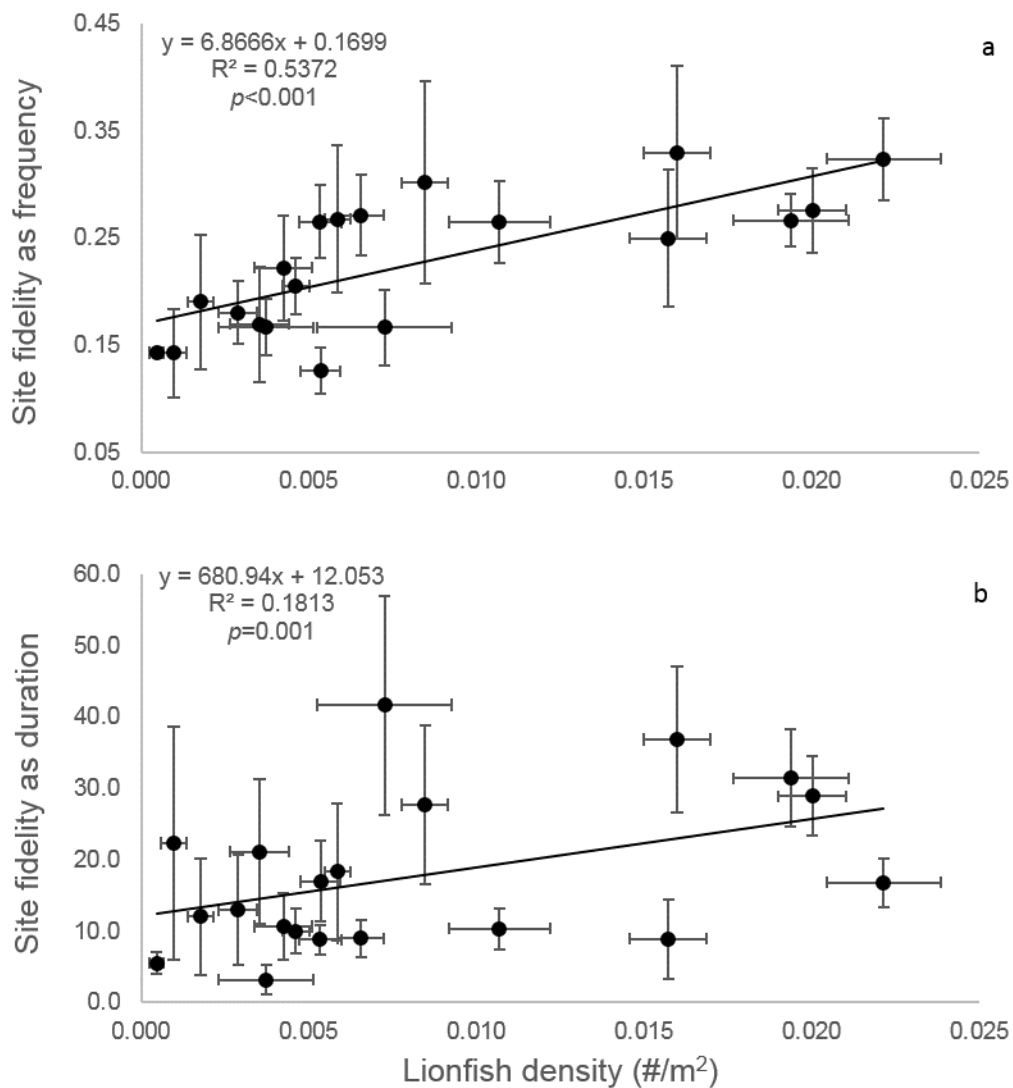


Figure 3.3 Mean (\pm SEM) site fidelity of lionfish measured as a) frequency (total number of sightings / total number of surveys) and b) duration (days between the first and last sighting on the reef) versus mean (\pm SEM) lionfish density (n=20 reef-year combinations).

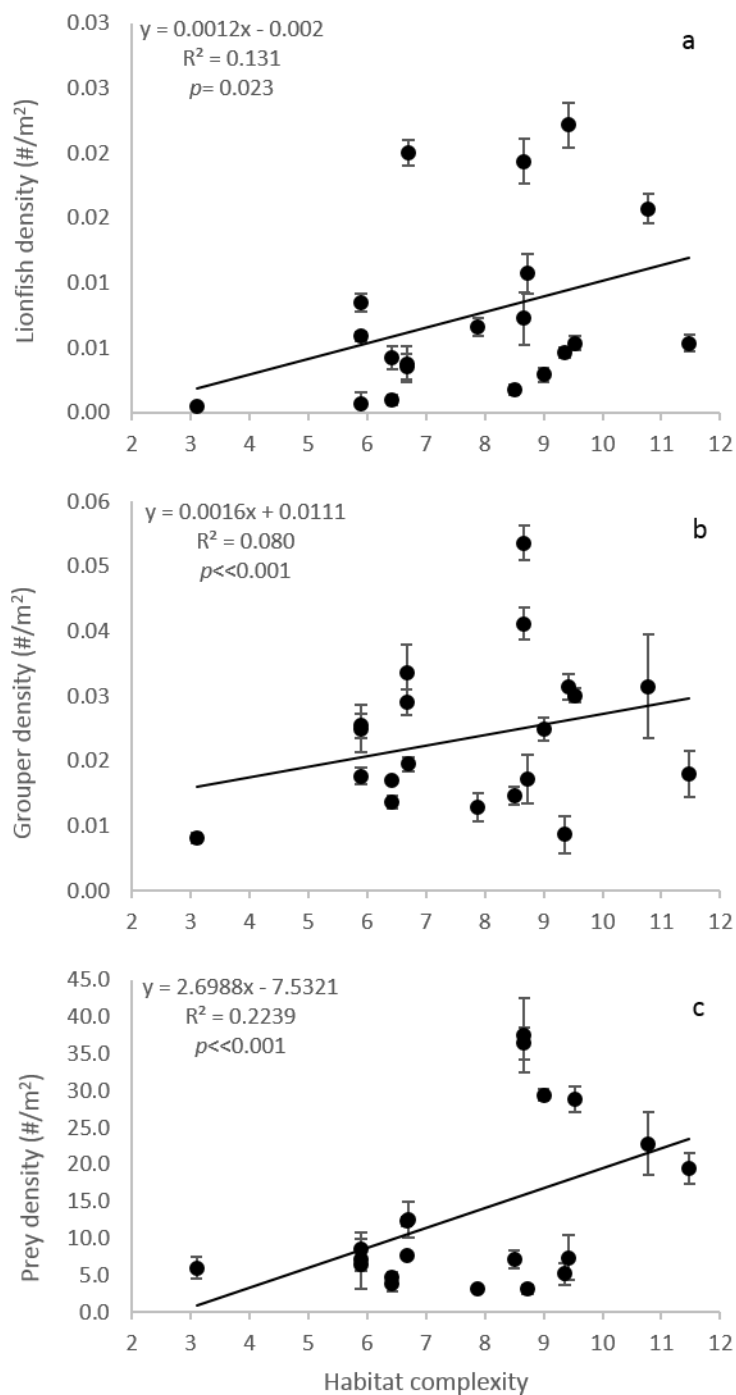


Figure 3.4 Mean (\pm SEM) densities of a) lionfish, b) grouper, and c) prey versus habitat complexity (n=20 reef-year combinations).

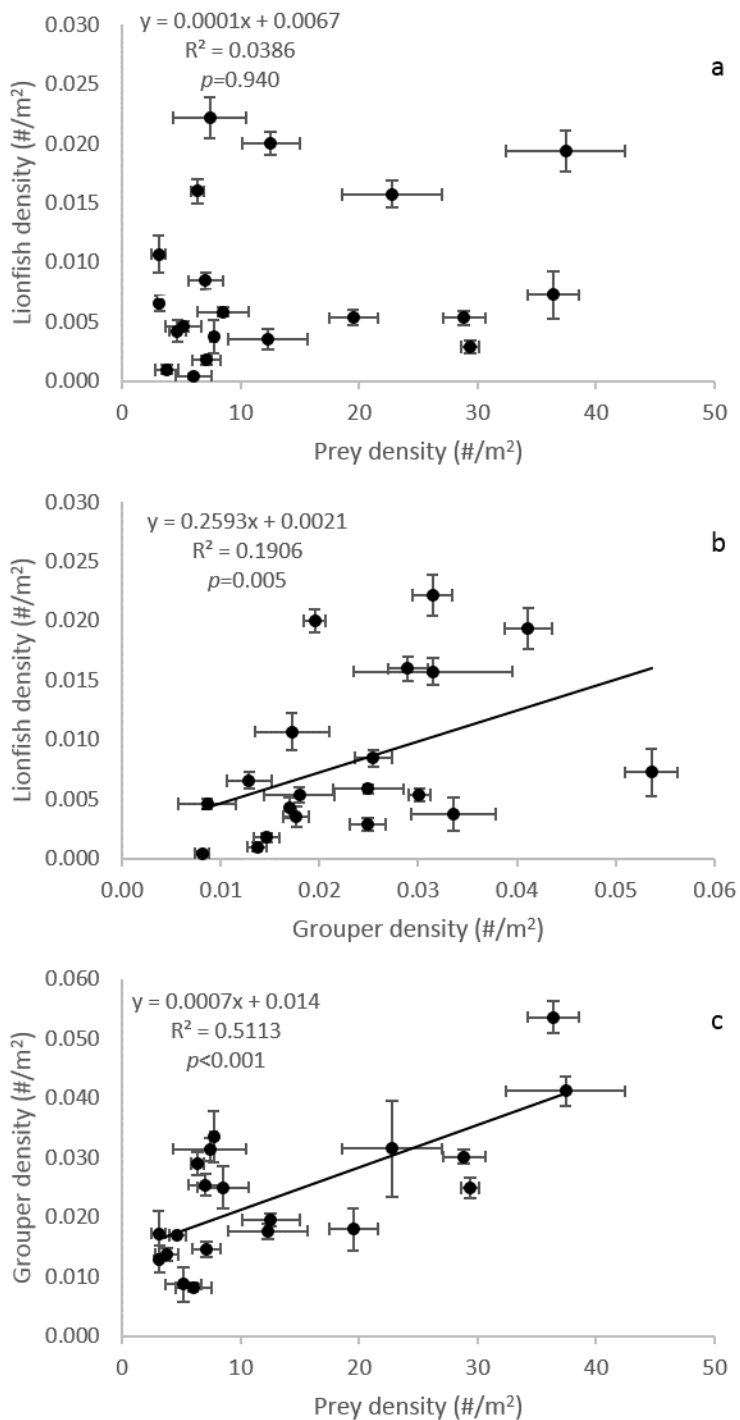


Figure 3.5 Mean (\pm SEM) densities of a) lionfish vs prey, b) grouper vs prey, and c) lionfish vs grouper (n=20 reef-year combinations).

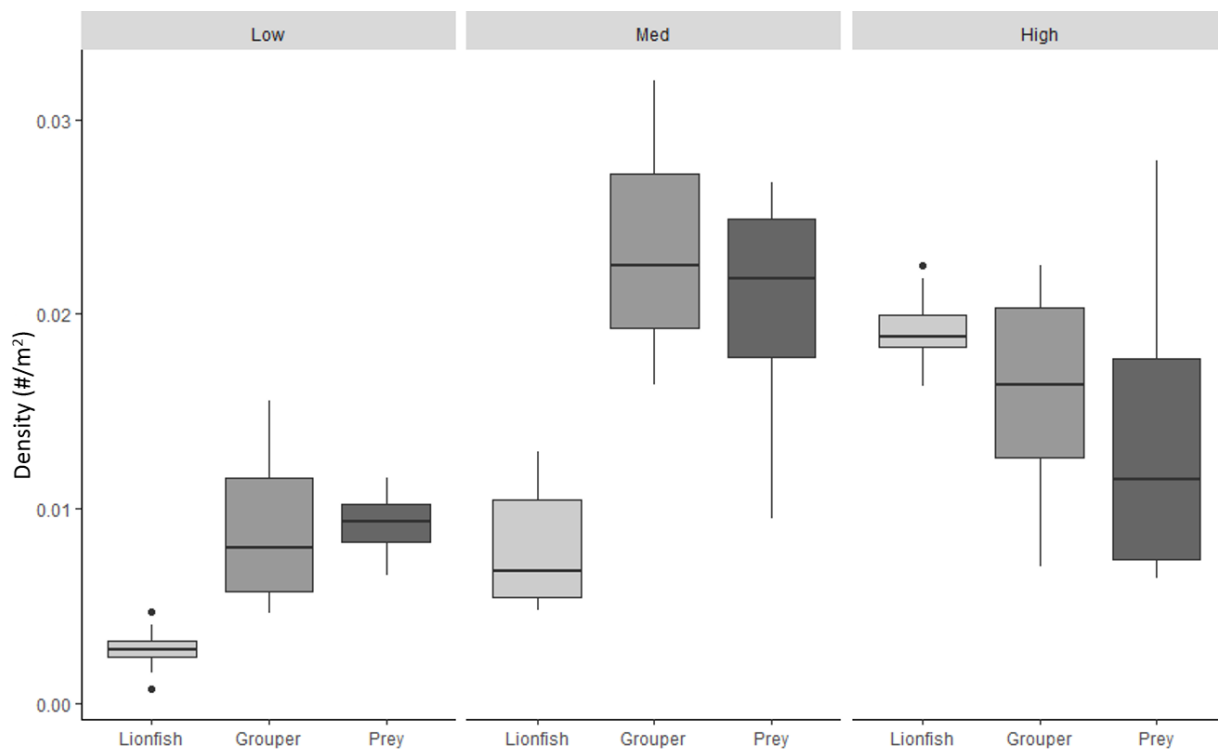


Figure 3.6 Box plot of densities of lionfish, grouper and prey on reefs at high, medium, and low densities of lionfish. Each box shows the median, first and third quartiles, and the minimum and maximum values. Prey density has been scaled (divided by 1000) to fit the same axis as the predators.

Table 3.1 Results of different statistical models exploring environmental factors associated with lionfish site fidelity.

Model	Type	Response	Predictors	P value	Result from Fig. 2
1A	LMME	Fidelity: count	Individual size	0.389	A,B,C,D
			Average size	0.418	
			Lionfish density	<0.001***	
			Grouper density	0.049*	
			Prey density	0.118	
			Habitat complexity	0.395	
			Reef		
			Year		
1B	LMME	Fidelity: duration	Individual size	0.231	A,B,C,D
			Average size	0.680	
			Lionfish density	<<0.001***	
			Grouper density	0.897	
			Prey density	0.153	
			Habitat complexity	0.092	
			Reef		
			Year		
2	LMME	Fidelity: distance moved	Individual size	0.903	NA
			Average size	0.212	
			Lionfish density	0.997	
			Grouper density	0.752	
			Prey density	0.847	
			Habitat complexity	0.731	
			Reef		
3A	GAM	Lionfish density	Habitat complexity	0.023*	E,F
			Grouper density	0.013*	
			Prey density	0.940	
3B	GAM	Grouper	Habitat complexity	<<0.001***	E,F
			Prey density	<<0.001***	
			Lionfish density	0.002**	
3C	GAM	Prey	Habitat complexity	<<0.001***	E,F
			Grouper density	<<0.001***	
			Lionfish density	0.899	

**Chapter 4 – Differential effects of native vs. invasive predators on a common
Caribbean reef fish**

Alexandra C.D. Davis

Abstract Predators may have consumptive (lethal) and non-consumptive (sub-lethal) effects on prey. Non-consumptive effects include altered behavior and reduced growth and fecundity. Native prey may not recognize non-native predators as a threat, and therefore may suffer pronounced effects. Additionally, non-native predators may elicit different behavioral responses from prey compared to native predators. Theory predicts that consumptive effects should be greater for non-native predators (due to prey naiveté), and non-consumptive effects should be greater for native predators (due to predator recognition). To test these hypotheses, I monitored bicolor damselfish (*Stegastes partitus*) in the presence of invasive predatory Pacific lionfish (*Pterois* spp.), a native predator (graysby, *Cephalopholis cruentata*), and an egg predator (bluehead wrasse, *Thalassoma bifasciatum*). Body size and location of lionfish and graysby were monitored on reefs in the Bahamas. Bicolor fecundity was measured as the number and size of egg-masses that individual fish laid. Bicolor fecundity was negatively correlated with lionfish density but not graysby or bluehead density. Neither predator had a detectable effect on bicolor body size, but lionfish density was negatively correlated with the size of mature adult damselfish. I observed behavioral responses of bicolors to the two piscivores, to bluehead wrasse, and to two herbivorous fishes (*Acanthurus coeruleus*, *Scarus* spp.) as non-aggressive controls. Bicolors changed behavior (feeding and aggression) in the presence of all native fishes, but not in the presence of lionfish. Thus, differential effects exist between native and non-native predators, and invasive lionfish pose a non-consumptive threat to bicolor damselfish via reduced growth and fecundity.

4.1 Introduction

Predators may influence populations and communities of their prey both directly by eating them (consumptive effects) and indirectly by their mere presence altering the behavior and other characteristics of prey (non-consumptive effects). While consumptive effects (CEs) are more tangible, non-consumptive effects (NCEs) may be just as or even more important to the overall fitness of prey (Peacor and Werner 2008; Elvidge and Brown 2015). NCEs can affect species even if CEs are small, or almost completely absent (Gosnell & Gaines 2012). NCEs can work in tandem with CEs and amplify their effects, or they can moderate the direct effects of predation if they stimulate behavior that is beneficial to the prey (Peckarsky et al. 2008). Additionally, NCEs do not always affect similar species equally (Gosnell & Gaines 2012, Jermacz & Kobak 2017) because other factors such as habitat quality and food availability can amplify NCEs, such as in the case of reduced egg production (Stephan et al. 2017).

Prey species may evolve traits or behaviors that mitigate the effects of predation (Peacor and Werner 2008). Prey may change morphologically (e.g., develop camouflage, alter body shape, evolve armor), physiologically (e.g., increase stress hormones, delay reproduction), and/or develop anti-predator behavior (e.g., enhanced vigilance, alarms, and defensive attacks). Differences in the attack mode (e.g., stalking vs. ambush), habitat use (e.g., midwater vs. demersal), and body morphology (e.g., camouflage) of multiple predators may force prey species to adopt new anti-predator behaviors. These behavioral changes can be energetically costly because prey must trade one behavior for another (e.g., fleeing for feeding) and/or

shift to using sub-optimal habitat. If prey species fail to recognize a predation threat, then they are unlikely to develop proper anti-predator responses. This could happen for various reasons, such as low encounter rates, cryptic predator morphology or behavior, or if the predator is newly introduced to the system, resulting in prey naivete (Smith et al. 2008b; Sih et al. 2010; Cox and Lima 2006)

The invasion of the greater Caribbean region by Pacific lionfish (*Pterois* spp., Family Scorpaenidae) provides an excellent case study to compare the ecological effects of native and invasive predators. Lionfish are generalist predators (Morris and Akins 2009; Muñoz et al. 2011; Layman and Allgeier 2012; Eddy et al. 2016; Harms-Tuohy et al. 2016) that use a unique roving-stalking foraging technique, corralling prey with their large pectoral fins, and sometime blowing jets of water at prey just prior to consumption (Fishelson 1975; Morris and Akins 2009; Albins and Lyons 2012). Given that invasive lionfish are apparently unfettered by potential native competitors (Albins 2013; Raymond et al. 2014; Bejarano et al. 2015), parasites (Sikkel et al. 2014; Tuttle et al. 2017), and predators (Hackerott et al. 2013), field experiments at multiple spatial and temporal scales have shown that, where lionfish densities are naturally high (e.g., Green and Côté 2009), they can reduce recruitment of over 50 native species of reef fish by up to 90% through predation (Albins and Hixon 2008; Morris and Akins 2009; Albins 2013; Albins 2015; Benkwitt 2015), and may even drive native species locally extinct (Albins 2015; Ingeman 2016). Broad-scale observational studies where lionfish are naturally abundant corroborate these patterns (Green et al. 2012).

Native fish vary in their perception of lionfish as a threat. Native parrotfishes show mixed responses in that their substratum feeding rate and visitation rates to food sources are lower in the presence of lionfish when compared to experimental situations without lionfish (Eaton et al. 2016; Kindinger and Albins 2017), yet parrotfishes did not change school size in the presence of lionfish compared to a native predator (Eaton et al. 2016). Anton et al. (2016) showed that multiple prey fishes, including wrasses, grunts, damselfishes and parrotfishes, allow invasive lionfish to approach up to 42% closer than the native predatory Nassau grouper of similar size, and display limited predator avoidance behavior towards lionfish. Kindinger (2015) showed that adult threespot damselfish (*Stegastes planifrons*), a highly territorial damselfish, did not react to lionfish aggressively when compared to a native predator, a native food competitor, or other common native reef fishes.

Unlike threespot damselfish, which have never been found in lionfish stomach contents (Morris and Akins 2009; Green et al. 2011; Curé et al. 2012; Layman and Allgeier 2012; Valdez-Moreno et al. 2012; Côté et al. 2013a, b), a common prey of invasive lionfish is bicolor damselfish (*Stegastes partitus*, Family Pomacentridae) (Morris and Akins 2009; Barbour et al. 2010; Muñoz et al. 2011). Bicolors are a ubiquitous on reefs throughout the invasive range of lionfish (Emery 1973). They are both planktivores and benthivores and live in semi-social loose aggregations (up to 20 individuals) on distinct coral heads (Myrberg 1973; Hixon et al. 2012). They have small home ranges that allow for accurate density estimates (relevant to measuring consumptive effects) and behavioral observations (relevant to examining non-consumptive effects). Females lay demersal eggs in distinct clutches guarded by

males until hatching (Knapp and Kovach 1991; Knapp 1995), which allows for measuring non-consumptive effects on egg production. They are also common prey of the native graysby grouper (*Cephalopholis cruentata*, Family Serranidae) (Randall 1967). Importantly, previous experimental studies have shown bicolor densities decrease at naturally high lionfish abundances (Albins 2015).

I studied bicolor damselfish in the presence of both invasive lionfish and native graysby grouper to test whether any behavioral changes in this prey species may translate into different consumptive and non-consumptive predatory effects. I hypothesized that consumptive effects (i.e., increased mortality) would be greater in the presence of invasive lionfish compared to native grouper based on prior anecdotal field observations that bicolor damselfish do not exhibit an appropriate anti-predator response to lionfish. Additionally, I expected non-consumptive effects, i.e., less time spent feeding, increased aggression towards predatory species (Lieske & Myers 2002; pers obs), and reduced body size and fecundity, would be greater in the presence of the native graysby grouper and a native egg predator (bluehead wrasse, *Thalassoma bifasciatum*) compared to lionfish and non-threatening native species, based on both preliminary field observations and prior studies (Myrberg 1972b; Knapp and Kovatch 1991; Knapp and Warner 1991).

4.2 Materials and Methods

Study system

This study was conducted during June–September 2015 on the southern end of the island of Eleuthera, the Bahamas (24.829578 N, -76.328444 W). The reef

system consists of two major habitat types: shallow small patch reefs ($\leq 30 \text{ m}^2$) in Rock Sound and larger patch reefs ($100\text{-}1200 \text{ m}^2$) with varying degrees of isolation on the Exuma Sound side of Cape Eleuthera. Rock Sound is generally more protected from wind and swell, and has a 4 m maximum depth. The shelf of the Exuma Sound is more exposed to weather and ranges in depth from 6 to 25 m, where the seafloor then drops-off abruptly to 2000 m depth. All study species were present on most reefs in both systems.

Consumptive effects

An indication of consumptive effects is a negative correlation between predator density and prey density. I therefore sampled nine large isolated patch reefs ($103\text{-}472 \text{ m}^2$ surface area, 6.36-18.18 m depth) in the Exuma Sound that included a natural range of predator densities. To standardize the total area surveyed, I created a 25x25m plot at each reef that included the reef as well as peripheral habitats. Each week for 13 weeks I counted, noted the location, and estimated the total length (TL) of all lionfish, graysby grouper, bluehead wrasse and bicolor damselfish in each study plot.

Non-consumptive effects

To assess egg production (fecundity) of bicolors, I used the approach of Knapp and Warner (1991) as modified by Hixon et al. (2012). My brother created artificial nests made of 6" tubes of 2" PVC pipe and I placed them in conspicuous areas within 1 m of large ($\geq 6\text{cm}$) bicolors on their home coral head. At this size, the bicolors are sexually mature (Schmale 1981) and will readily lay eggs in artificial nests (Hixon et al. 2012). An average of 3 nests (range 2-4) were placed on all 9

large study reefs, the number based on the number of sexually mature bicolors present. Each nest was lined with a sheet of acetate plastic that could be removed to estimate the total egg clutch area by taking tracings of the outline of the clutch (Johnson and Hixon 2011; Hixon et al. 2012). After establishing that each nest was being used by a bicolor damselfish (evident from territorial behavior at the nest and the male moving in and out of the nest), I checked every nest each week for presence of eggs. If eggs were present, then the acetate was removed, the egg clutches were traced without crushing the eggs, and the acetate was returned to the nest. To quantify the size of the egg clutches, I photographed all tracings with a centimeter scale for reference. The images were then analyzed in *Image J* to calculate the area of each clutch. Because eggs are laid in a monolayer, the area of the clutch provides an index of clutch size (Samhuri 2009; Johnson and Hixon 2011; Hixon et al. 2012). I estimated and recorded the body size as total length (TL) of all bicolors visually to the nearest half-centimeter during the weekly visits to the 9 reefs, along with the location of the fish on the reef. I also noted whether the bicolors were sexually mature (6cm TL or greater, Schmale 1981).

Prior to the behavioral study, I placed a GoPro video camera on randomly selected reefs and recorded the activities of bicolors (N=10) for 30-40 minute periods to characterize typical bicolor behavior in the presence of a predator. I used the videotaped bicolors to assign behaviors as belonging to one of three categories (Table C1): feeding, aggression, other (swimming, out of view, hiding). A pair of divers then conducted practice observational trials on bicolors to standardize characterization of behavior between observers before the study began.

To evaluate whether bicolor damselfish have differential responses to native vs. non-native predators, divers conducted experimental trials on bicolors using the model-bottle method developed by Myberg and Thresher (1974) and later used by Kindinger (2015) to study the behavioral effects of invasive lionfish on threespot damselfish (*Stegastes planifrons*). On small, shallow (≤ 3.7 m deep) patch reefs in Rock Sound, an individual bicolor was presented in random sequence (unique to each trial) a lionfish, a graysby grouper, a native egg predator (the bluehead wrasse *Thalassoma bifasciatum*), two native herbivores (the blue tang *Acanthurus coeruleus* and a juvenile parrotfish *Scarus* sp.). Each fish was presented in a clear plastic 1-gallon bottle with a mesh lid to allow for water flow, or an empty-bottle as a control (Figure C1). Intruder fish maximum size was limited by the dimensions of the bottle. Lionfish and grouper ranged from 15 to 19cm (± 0.866 SEM) TL, which falls in the range of predator body size that could eat the bicolors. The herbivores and egg predator ranged from 8 to 12 cm (± 0.320 SEM) TL, which was the size range most aggressive during the pilot study.

Because bicolors eat mostly plankton and occasionally small benthic invertebrates, the two herbivores were treated as non-threatening controls for comparison with potential predators. Each bottle was initially placed 100cm away from the center of the bicolor territory, and the behavior of the bicolor was observed for 5 minutes. The observer then placed the bottle 50cm away and then 0cm away from the territory and recorded observations for 5 minutes at each distance, for a total 15 minute trial per intruder species (or empty bottle). During each trial, the observer

recorded the type of bicolor behavior and either the number of times that behavior was seen (frequency) and the length of time that behavior was exhibited (duration). All observations were made with the observer 1m away from the 100cm bottle location (i.e., 2m away from the bicolor territory) to avoid interference with or disturbance of the focal fish.

Statistical analyses

All statistical analyses were conducted using the R statistical software (R Core Team 2014) with the packages *multcomp* (Hothorn et al. 2008) and *nlme* (Pinheiro et al. 2014). All residuals were examined for gross violations of assumptions of normality and homogeneity of variance. To test for an effect of predator density on bicolor density (consumptive effect), or size and fecundity (non-consumptive effects), I fit separate linear models (LMs) with individual predator species density as the explanatory variables. Examination of the explanatory and response variables over time did not reveal evidence of trends, so all factors were averaged into a single summary per reef (i.e., one lionfish density per reef, one grouper density per reef, etc.). I fit lionfish density against bicolor density, bicolor size, egg clutch size and number in four individual LMs. I then did the same for graysby grouper and fit bluehead wrasse density against egg clutch size and number, for a total of 10 LMs.

For the model-bottle experiment, a two-way ANOVA was run on the sample of 44 bicolor damselfish to examine the non-consumptive effect of species and proximity to the nest on bicolor behavior. One test was run for each behavioral response. I used both time spent in a behavior (treated as a normal response) as well as proportion of total bicolors that displayed aggressive behavior (treated as a

binomial response) as response variables, and species and distance as categorical explanatory variables. Since each bicolor was associated with a total of 18 observations (6 bottle treatments \times 3 distances) an individual identification number for each bicolor was used to add a random effect to account for repeated measures. When a factor was significant, a post hoc multiple comparison of means with Tukey contrasts was run to determine pairwise differences. A full model was run that also included the randomized order of fish presentation but that variable was dropped as it was not significant (i.e., no habituation to bottle presence, LM, $p= 0.585$).

4.3 Results

Consumptive effects

There was no evidence of substantial consumptive effects of either predator on bicolor damselfish in terms of a negative relationship between the densities of damselfish and predators. Bicolor density had a non-significant (albeit slightly negative) relationship with lionfish density (LM, $p= 0.202$). There was also a non-significant (albeit slightly positive) relationship between bicolor density and graysby density (LM, $p=0.318$).

Non-consumptive effects

There was evidence of non-consumptive effects of invasive lionfish on bicolor damselfish. Bicolors used the artificial nests on seven of the nine study reefs, so results on egg production are limited to those 7 reefs. Both egg clutch number and size were significantly negatively correlated with lionfish density (LM, $p=0.034$ and

0.047, respectively) (Figure 4.1). Neither egg clutch number nor size were correlated with graysby or bluehead wrasse densities (GLM, $p=0.982$ and 0.470 , and $p=0.831$ and 0.466 , respectively). Bicolor body size was non-significantly (albeit somewhat negatively) related to lionfish density (LM, $p= 0.068$). Bicolor size had a non-significant (albeit slightly positive) relationship with graysby density (LM, $p= 0.776$).

In the model-bottle experiment, there was a significant interaction between the effects of intruder species and proximity to nest on the time spent in aggressive behavior by bicolors ($F(10, 731)= 7.53, p < 0.0001$), the number of bicolors behaving aggressively ($F(10, 731)= 5.56, p < 0.0001$), and time spent feeding ($F(10, 731)= 7.53, p = 0.0074$). The proportion of bicolors (out of 44) that showed an aggressive response varied among intruder species (Figure 4.2a). The percent of bicolors that responded aggressively was lowest toward the lionfish (average 11%), which along with the empty-bottle treatment (average 21%), was lower than toward all native fishes, which was over 40% averaged across all distances. The higher aggressive responses toward graysby grouper, bluehead wrasse, parrotfish, and blue tang did not vary significantly from each other (multiple comparison of means with Tukey contrast, $p = 0.10-0.97$), except at 100 cm distance where the number of bicolor with an aggressive response towards the graysby was significantly higher than all other treatments (multiple comparison of means with Tukey contrast, $p = 0.009 - 0.0001$) (Figure 4.2a).

The proportion of time spent in aggression toward both lionfish and the empty bottle was near zero (multiple comparison of means: Tukey contrast, all p -values = 1.00), which was lower than aggression toward the native fishes (Figure 4.3b).

Bicolors spent more time (15%) in aggressive behavior in the presence of the herbivorous blue tang than any other treatment, and at 0 cm the amount of time spent in aggressive behavior was significantly higher than all other distance and species combinations (multiple comparison of means with Tukey contrast, all p -values < 0.01) (Figure 4.2b). Time spent in aggression towards graysby grouper, bluehead wrasse, and parrotfish did not differ significantly from each other at any distances (multiple comparison of means with Tukey contrast, $p = 0.08$ - 0.99). However, at 100cm the time in aggression towards graysby was significantly higher than the empty bottle and lionfish treatments (multiple comparison of means with Tukey contrast, $p = 0.03$ and 0.03 , respectively).

On average, bicolor damselfish spent 65% of their time feeding overall, and 76% of their time feeding when lionfish were present. When bluehead wrasse were present, bicolors spent 71% of their time feeding, which was not different from the empty-bottle, lionfish, parrotfish, or blue tang treatments. When blue tang were present, bicolors spent 61% of their time feeding, which was lower than the empty-bottle and lionfish treatments, but only significantly so at 0cm (multiple comparison of means with Tukey contrast, $p = 0.01$ and 0.01 , respectively) (Figure 4.2c). Bicolors spent on average 42% of their time feeding when graysby were present, and this was significantly lower at all distances than all other treatments (multiple comparison of means with Tukey contrast, all p -values < 0.01), except at 0cm, where there was no difference from the time spent feeding in the presence of the blue tang (multiple comparison of means with Tukey contrast, $p = 0.98$) (Figure 4.2c).

The proportion of bicolors that had an aggressive response varied by distance from the nest and with the intruder species. For all species but the graysby grouper and lionfish, the proportion of aggressive fish increased as distance decreased (Figure 4.3a). The number of aggressive bicolors was significantly higher at 0cm compared to 100cm for the empty bottle, bluehead wrasse, parrotfish, and blue tang treatments (multiple comparison of means with Tukey contrast, all *p-values* < 0.01). There was also a significant difference in behavior between 0 and 50cm for the empty-bottle and parrotfish treatments (multiple comparison of means with Tukey contrast, *p* = 0.02 and 0.04, respectively), and between 50 and 100cm for bluehead wrasse and blue tang (multiple comparison of means with Tukey contrast, *p* = 0.02 and 0.05, respectively) (Figure 4.3a).

The proportion of time bicolors spent in aggressive behavior also varied with intruder distance (Figure 4.3b). The proportion was significantly higher when the treatment was 0 cm from the nest compared to 100 cm for the bluehead wrasse, parrotfish, and blue tang (multiple comparison of means with Tukey contrast, all *p-values* < 0.01). There was also a significant difference in time spent aggressively between 0 cm and 50 cm for the parrotfish and blue tang treatments (multiple comparison of means with Tukey contrast, *p* = 0.05 and 0.01, respectively). However, the distance did not influence the time spent in aggressive behavior for graysby grouper (average 9.0%), the empty bottle (average 1.5%), or lionfish (average 0.4%).

The proportion of time bicolors spent feeding also varied with intruder distance (Figure 4.3c). For all native species, time spent feeding generally decreased with distance from the nest. However, there was a significant difference only between

0 cm and 100 cm in the presence of bluehead wrasse and blue tang and between 0 cm and 50 cm for blue tang (multiple comparison of means with Tukey contrast, all p -values < 0.01). In the presence of the empty bottle, lionfish, and graysby grouper, distance from the nest had no effect on feeding behavior (multiple comparison of means with Tukey contrast, $p = 0.96, 0.96$ and 0.27 , respectively). At 0cm, there was a significant reduction in the percentage of time bicolor damselfish spent feeding when grouper, parrotfish, and tang were the intruders, compared to the lionfish treatment (multiple comparison of means with Tukey contrast, $p < 0.01, 0.02$ and 0.01 , respectively), and a reduction when grouper and tang were the intruders compared to the empty bottle treatment (multiple comparison of means with Tukey contrast, both p -values < 0.01).

4.4 Discussion

Lionfish had no detectable effects on the survival and growth rates of transplanted groups of the cleaner goby (*Elacatinus genie*). However, reefs with lionfish had fewer juvenile bluehead wrasse (*Thalassoma bifasciatum*), the most common facultative cleaner on patch reefs, and fewer transient client fishes. The addition of lionfish to patch reefs did not affect the density of all other non-goby cleaners or of resident clients, nor did lionfish alter ordinated community structures of non-goby cleaners and clients.

In previous field studies, lionfish also had no effect on the density of *Elacatinus* spp. cleaning gobies on small patch reefs (Albins and Hixon 2008; Benkwitt 2015), large patch reefs (Albins 2015), and continuous reefs (Green et al.

2012). In a laboratory setting, Tuttle et al. (submitted) identified learning as the likely behavioral mechanism by which lionfish and the cleaner goby weakly interact; while juvenile lionfish initially ate the cleaner goby, they avoided the goby upon subsequent encounters. This learned avoidance was likely due to an unpalatable chemical defense in the goby's skin (Colin 1975) which induced hyperventilation of lionfish that ingested the goby. While I did not witness lionfish striking at cleaner goby during my field experiment, it is possible that lionfish quickly learned, or had already learned prior to their addition to experimental reefs, to avoid eating this species.

While lionfish did not affect the cleaner goby, lionfish did decrease the density of juvenile bluehead wrasse, a facultative cleaner. Declines were most likely caused by predation, as the bluehead wrasse is a very common prey item of lionfish in the region (Albins and Hixon 2008; Morris and Akins 2009; Côté et al. 2013). Few studies have compared the behaviors of obligate cleaners and facultative cleaners on Atlantic coral reefs (Darcy et al. 1974; Johnson and Ruben 1988). Therefore, it is difficult to predict what will be the repercussions of reduced abundance of facultative cleaners on invaded reefs. If lionfish do not affect obligate cleaners, which tend to clean more hosts more often (Johnson and Ruben 1988), but do affect facultative cleaners, there may be little change to the ectoparasite loads and distribution of reef clients. However, if lionfish have strong, negative effects on particular facultative cleaners that strongly interact with particular clients, then changes to the clients' ectoparasite loads and visitation rates to cleaning stations could occur. Future studies should investigate the ecological importance of cleaning by juvenile bluehead wrasse

to better predict how invasive lionfish might indirectly affect cleaning mutualisms via predation of bluehead wrasse.

While there was no clear effect of lionfish on resident clients (those species that spend the majority of their time at one patch reef), lionfish did affect the density of transient clients (those species that move among patch reefs over the course of a day). There was a large increase in the density of transient clients on control reefs without lionfish, but no increase on impact reefs with lionfish. Transient clients most likely came from neighboring patch reefs interspersed among the experimental patch reefs, all of which were spread across an area of approximately 11 x 4 km. There was no indication that the relative spatial distribution of control vs. impact reefs should have influenced the presence vs. absence of transient clients on experimental reefs. During visits of transient species to patch reefs used in this study, these fishes are often cleaned by obligate and facultative cleaners (*unpublished data*). Over the course of the experiment, there were increases in the densities of non-goby cleaners and prey-sized fishes on all reefs due to the accumulation of new settlers during the summer recruitment season (most species in this region except cleaning gobies experience recruitment peaks in July to August). These increases were significantly greater on control vs. impact reefs. As a result, the increase in transient species on control reefs only is likely attributable to an aggregative response of transient species to cleaners and/or prey, as has been described on coral patch reefs in the region (Hixon and Carr 1997; Hixon 1998). Lionfish may have suppressed the number of cleaners and prey below a threshold that would otherwise induce aggregative responses by transient species to patch reefs. This is the first documentation of

lionfish affecting the density of transient reef species, indicating that the effects of lionfish may extend beyond those already documented for resident reef species.

While I did not observe any effects of invasive lionfish on the native cleaner goby over the experimental period (the goby was in the presence of lionfish for one month), this outcome does not preclude longer-term effects on the goby via relatively prolonged, reduced densities of potential clients on patch reefs. Overall, however, there is little evidence to suggest that lionfish affect the cleaner goby. Lionfish may have similarly weak interactions with other *Elacatinus* spp. cleaning gobies throughout the invaded western Atlantic and Caribbean region, where there are 27 species in the *Elacatinus* genus, 7 of which are obligate cleaners (Taylor and Hellberg 2005). If this is true, then cleaning gobies are among the remarkably few fishes on invaded reefs to escape the effects of lionfish. The continued presence of cleaning gobies on invaded reefs should limit cascading effects that are mediated by these cleaners. However, by consuming other cleaners, invasive lionfish may alter the structure and function of native reef communities.

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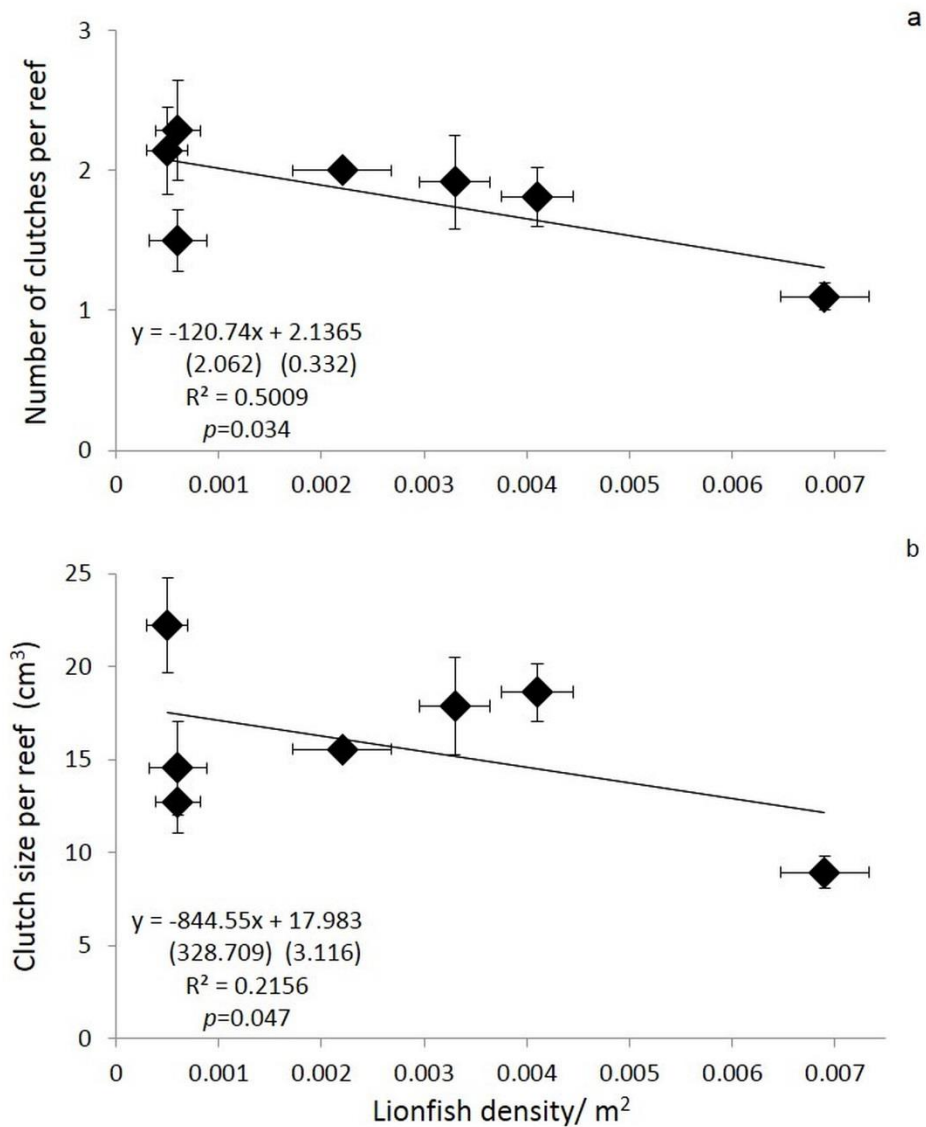


Fig. 4.1 Mean (\pm SEM) (a) number and (b) size of individual egg clutches per artificial nest averaged over entire reefs as a function of lionfish density ($N = 7$ reefs). Numbers in parentheses are the standard errors of the regression parameter estimates.

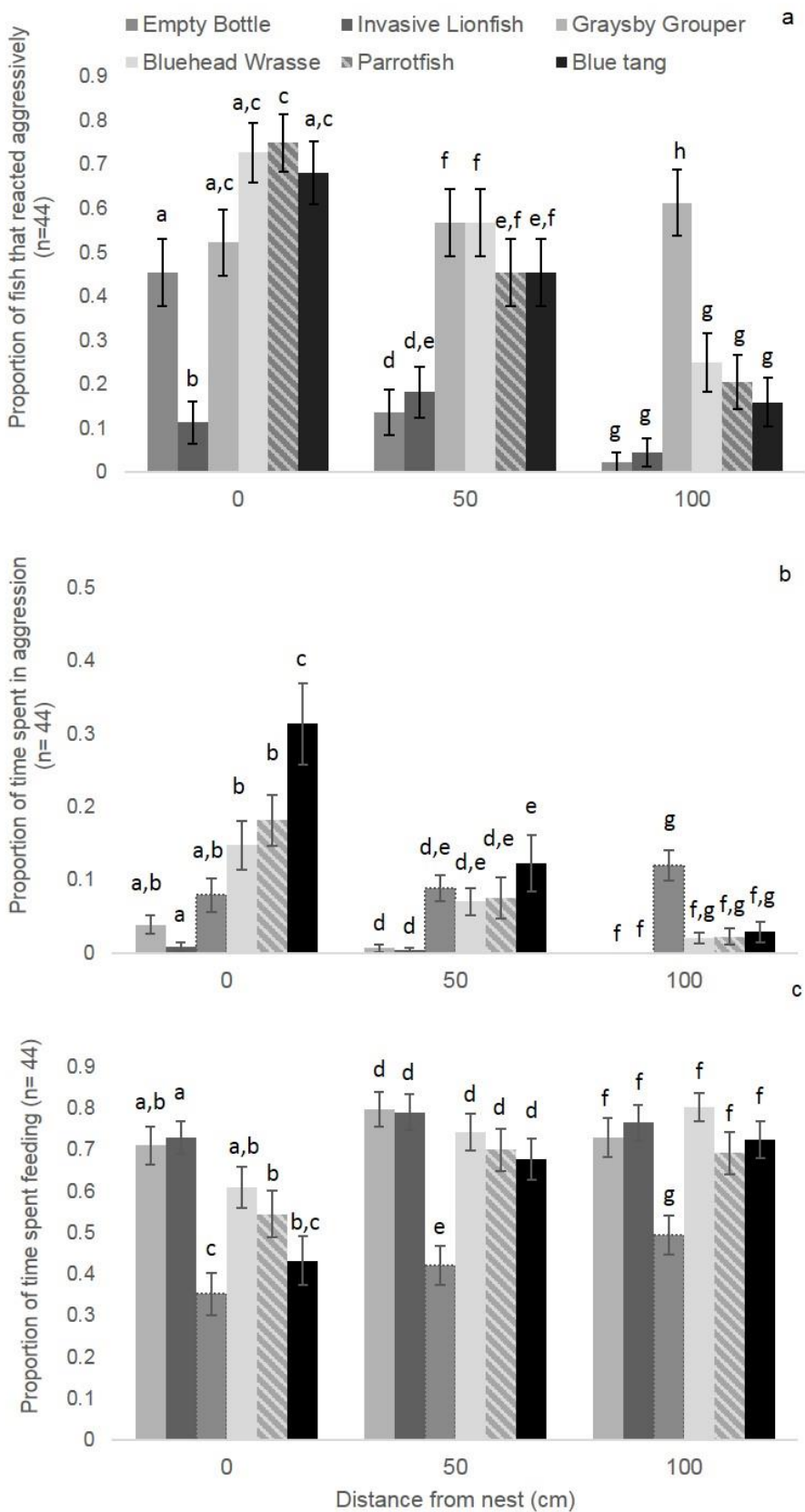


Fig. 4.2 The mean (\pm SEM) of 44 bicolor damselfish (a) proportion acting aggressively, (b) time acting aggressively and (c) time feeding during 15-minute model-bottle trials for each of 3 distances from the nest comparing 6 intruder treatments. Within each distance, intruder bars labelled with the same letters are not significantly different.

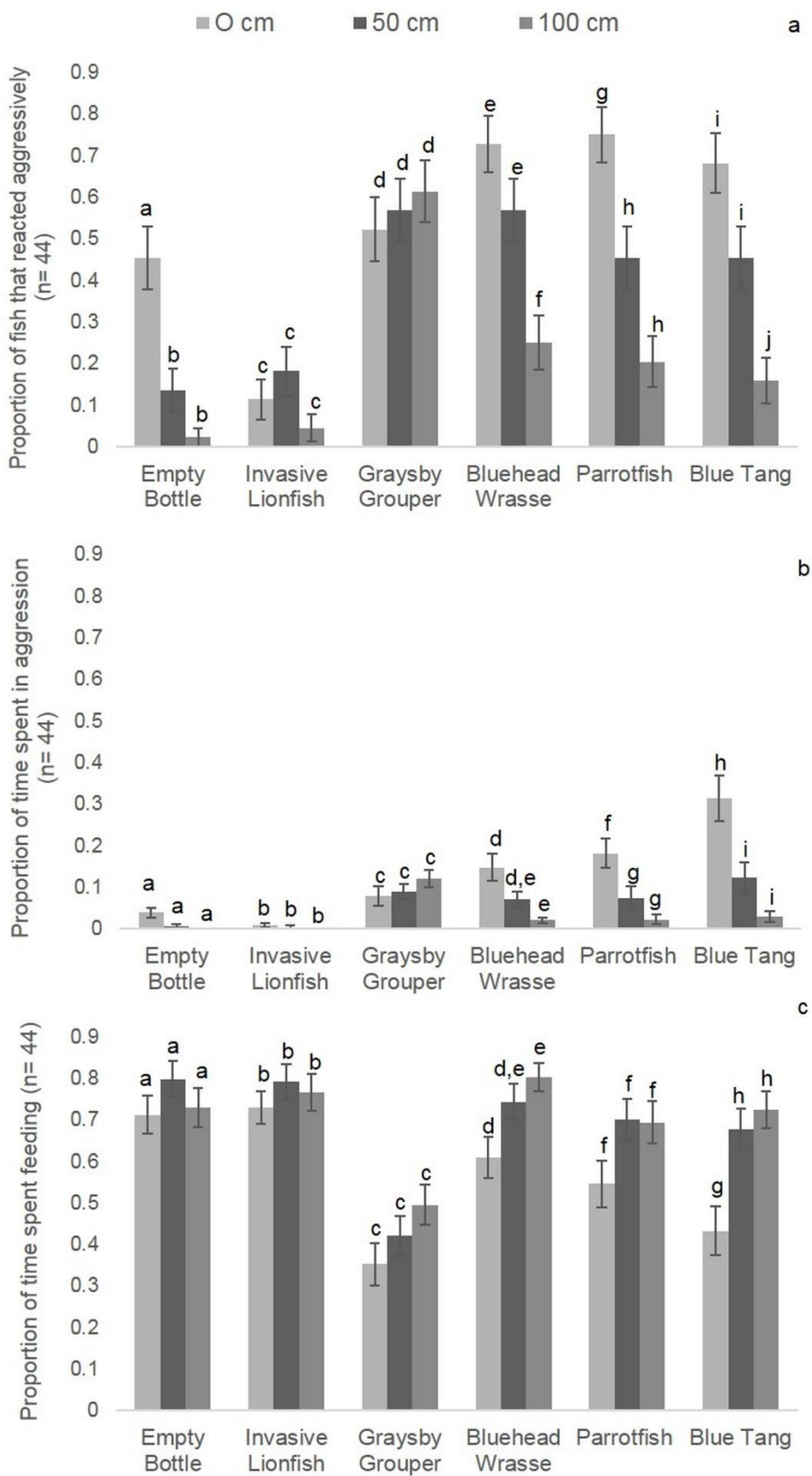


Fig. 4.3 The mean (\pm SEM) of 44 bicolor damselfish (a) proportion acting aggressively, (b) time acting aggressively and (c) time feeding during 15-minute model-bottle trials for each of 6 intruder treatment comparing 3 distances from the nest. Within each treatment, distance bars labelled with the same letters are not significantly different.

Chapter 5 – General Conclusions

This dissertation examined the species and habitat interactions of the lionfish invasion at multiple scales in the Bahamas, where the range of invasive lionfish has been expanding since the early 2000s and now extends through the entire archipelago. The research was based on a combination of traditional ecology techniques such as behavioral observation, abundance surveys, and habitat classification, as well as using remotely sensed satellite data, which is becoming more commonly applied in marine ecology studies. At the broadest scale, the research tested predictions about the relative importance of various factors that influence the distribution and abundance of lionfish in their invaded range in the Bahamas. A finer-scale observational study examined the effects of biotic and abiotic factors on lionfish site fidelity. At the finest scale, an experimental study tested how the presence of lionfish affects the behavior and fecundity of common prey species on coral reefs.

In chapter 2, I asked if remotely sensed data could be used to accurately predict lionfish distribution and abundance in their invaded range. Additionally, I wanted to determine if diver collected microhabitat and biotic data added to the accuracy of the predictive model. To address this question, broad scale, remotely sensed, spectral data of habitat were used to create a map of lionfish locations, and this map was able to accurately predict lionfish locations in 71% of cases. The inclusion of field-surveyed observations of habitat features such as rugosity and fine scale micro-habitat increased map accuracy to 89%. However, the inclusion of biotic data, specifically the density of large bodied Nassau grouper reduced accuracy to

68% in the model for presence/absence, and increased accuracy to 74% in the density model. Further studies should test to see if the model is applicable in other locations in the invaded range. This will be especially valuable in places with continuous reef where lionfish have the ability to move more freely between suitable habitats. Finding areas in multiple systems where there is likely to be high densities of lionfish will be valuable for removal and management.

In Chapter 3 I sought to determine what biotic and abiotic reef characteristics influence lionfish site fidelity on reefs in the invaded range. To address this question, models were fitted to predict observed lionfish site fidelity based on repeated observations over a two-year period of individual lionfish and the biotic and abiotic features of a set of 16 small coral reefs separated by areas of sand and seagrass near the island of Eleuthera, the Bahamas. In contrast to Chapter 2, which demonstrated the importance of physical habitat complexity in predicting lionfish presence/absence as well as density, the results of this study indicated that physical habitat did not affect the fidelity of individual lionfish. Instead, factors such as high densities of conspecifics and prey availability were more closely related than physical habitat to two measures of site fidelity: the number of times an individual fish was seen and the length of time an individual fish was observed on a single reef. Nevertheless, the density of lionfish, grouper, and prey was positively related to the complexity of physical habitat. Moreover, average site fidelity of lionfish on each study reef was positively correlated to the density of lionfish on each study reef. Therefore it is possible that site fidelity of individual lionfish is affected by physical habitat complexity. Tagging with radio telemetry tags could give more insight into how the

lionfish are moving between reefs. Additionally, in order to extend these findings to other areas characterized by continuous reef, it would be important for future research to determine how lionfish site fidelity is related to within-reef variability, such as micro-habitat features.

In Chapter 4 I asked, if invasive lionfish have consumptive (lethal) and non-consumptive (sub-lethal) effects on a common reef fish. The study involved adapting the model bottle method (Myrberg and Thresher 1974), to observe the behavior of bicolor damselfish (*Stegastes partitus*) while lionfish and other native fish were present, but contained in large clear bottles with flow through lids. Moreover, fecundity was measured as the size and number of egg clutches deposited in artificial nests. Results of the experiment indicated that the prey species, the bicolor damselfish, does not react to lionfish as a predation threat, confirming other studies that demonstrate that native fish species on coral reefs are vulnerable to mortality through predation by invasive lionfish. In addition, the result of the fecundity observations indicated that fecundity was reduced on reefs with high lionfish densities. The average size of adult bicolor damselfish was negatively related to the density of lionfish on the study reefs, implying that lionfish predation on damselfish may be changing the demographics of the populations, therefore indirectly reducing average fecundity. To investigate these hypotheses, further studies should include tagging male and female individuals of damselfish to determine growth rates, effects of predation by lionfish on the size of individuals of the prey species, and the relationship of lionfish densities on average sizes of males or females of prey species. In addition, observations of bicolor and lionfish interactions while the lionfish is not

confined in a bottle could show directly whether or not lionfish are interrupting the courting behavior of bicolor damselfish.

Overall this dissertation contributes to our understanding of species interactions and effects of habitat at multiple scales. Results confirm that lionfish distribution and fidelity is influenced by both biotic and abiotic factors. The findings contribute to knowledge of how invasive lionfish are affecting native species in the invaded range by providing evidence that lionfish indirectly affect some native species by reducing the size of adult fish and their fecundity. The findings in this dissertation highlight the importance of examining ecological systems at multiple scales to fully understand and manage systems, and can ultimately be used to help implement and maintain a marine reserve system.

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APPENDICES

Appendix A Chapter 3 Supplementary Material



Figure A1. Example of an individually marked lionfish with the 3rd and 4th dorsal spines removed.

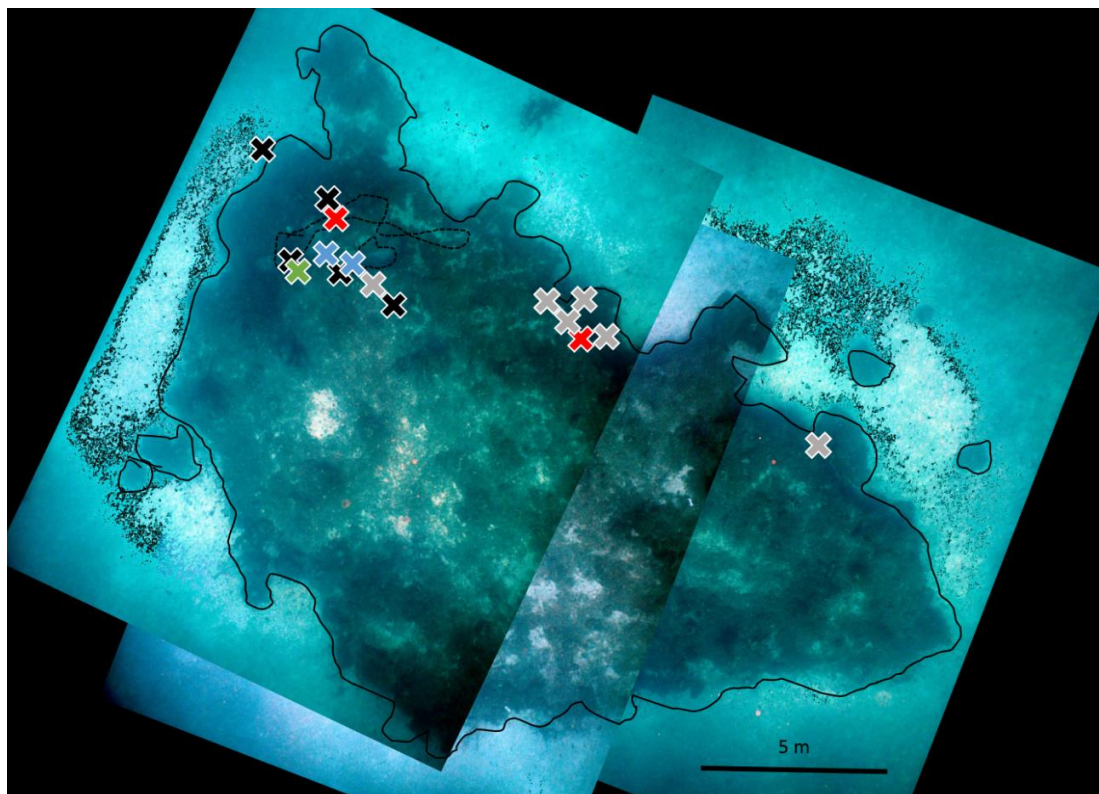


Figure A2. Spatial clustering of lionfish sightings on a sample study reef. Xs indicate position of lionfish during the study. The lionfish were almost exclusively found near ledges and undercuts on this reef. Black Xs represent fish that were seen only once. Fish that were seen multiple times have a unique color; for example, the fish represented by the grey Xs was seen 6 times in 3 locations.

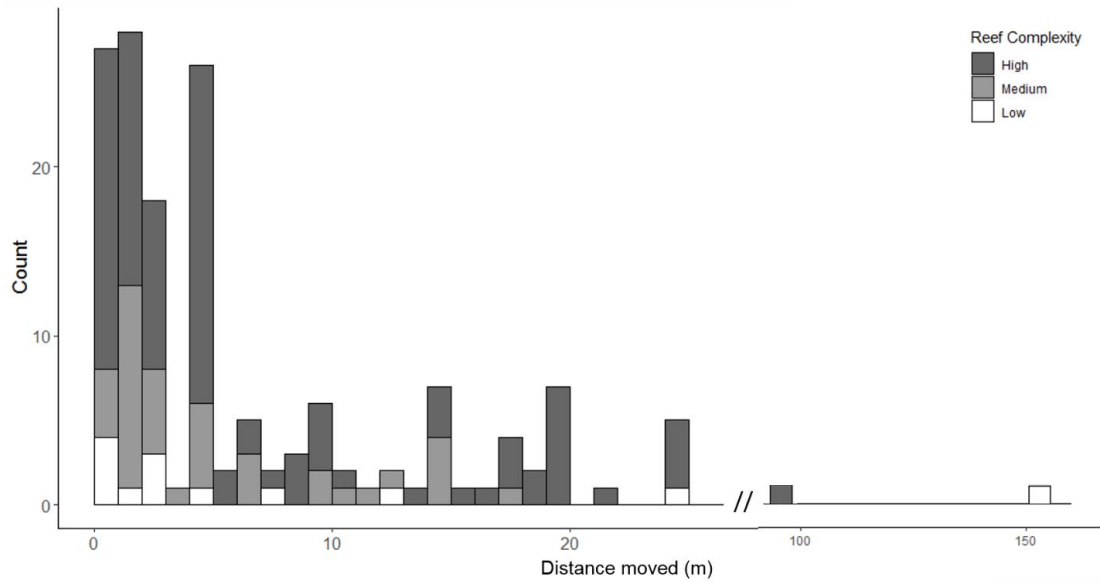


Figure A3. Histogram of maximum distances moved (m) by individual lionfish between successive observation periods. Bars are coded by reef complexity.

Table A1. Physical characteristics of reefs used in study.

	Reef Name	Year(s) surveyed	Previous lionfish treatment	Depth at base (m)	Vertical relief (m)	Surface Area (m ²)
1	Minas Tirith	2014	Removal	13.03	4.5	190.85
2	The Two Towers	2014	Addition	13.03	4.3	562.43
3	Helm's Deep	2014	NA	8.48	3.9	1155.08
4	Mines of Moria	2014	NA	14.54	3.8	511.81
5	The Reef of Requirement	2014	NA	10.00	4.0	751.57
6	The Lonely Mountain	2014	NA	13.63	8.2	1241.51
7	Dirty Diana	2014	NA	6.67	4.3	620.04
8	The Shire	2014	NA	7.58	2.4	828.15
9	Dudley Dursley	2014, 2015	NA	6.06	1.5	320.59
10	Vernon Dursley	2014, 2015	NA	7.57	2.2	471.75
11	Petunia Dursley	2014, 2015	Addition	7.58	2.3	268.19
12	P.Y.T.	2014, 2015	Addition	16.66	3.0	137.70
13	Ministry of Magic	2015	Removal	17.27	2.6	343.77
14	Rohan	2015	NA	7.27	1.4	303.44
15	Bag End	2015	NA	5.58	1.0	625.00
16	Twin Peaks	2015	Removal	13.03	4.0	400.85

Appendix B Chapter 4 Supplementary Material

Figure B1 Model-bottle study design, adapted from Kindinger (2015). The shaded grey oval represents the bicolour damselfish territory, with the focal fish above. For each intruder treatment, the bottle in each trial was placed sequentially at 100, 50, and 0 cm away from the center of the territory (invasive lionfish pictured here). Behavior was monitored for 5 minutes at each distance (total 15 minutes per trial)

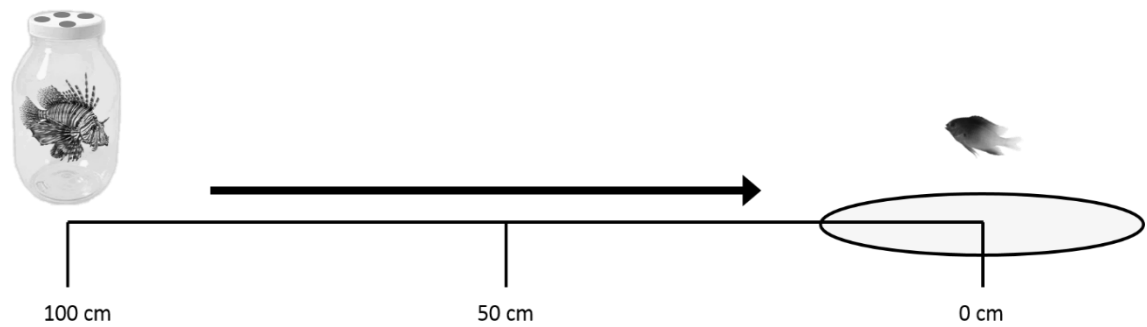


Table B1 Description of bicolor behaviors observed during model bottle experiment

Behavior	Description	Type of metric
Feeding	Positioned in water above the coral head, picking plankton out of the water column OR nipping at the substrate surrounding the nest area	Time
Aggression		
at bottle	Orienting head toward the bottle, approaching the bottle (investigative)	Time and/or #
Nip	Hitting the bottle with the snout or mouth	#
Charge	Swimming aggressively at the bottle, can end in a nip	#
Butt	Hitting the bottle with the caudal fin	#
Shimmy	Orienting the caudal fin at the bottle from >20cm away and shaking the fin	#
Other		
Patrol	Swimming around the perimeter of territory	Time
Retreat	Entering a hole or shelter of territory	Time and #
Chase	Chasing other fish aggressively away from the territory	# and species
Max Distance	Maximum distance focal bicolor traveled away from the center of their territory during the trial	Distance in cm

