# Assessing the ecological and socioeconomic impacts of the lionfish invasion in the Wider Caribbean Region

by

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# Ethics Statement

The author, whose name appears on the title page of this work, has obtained, for the research described in this work, either:

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# Abstract

Environmental changes of different scales and magnitudes are occurring at an alarming pace throughout the globe. As natural and human systems resist, cope, and/or adapt to global changes, new equilibrium states might be reached. To understand these changes we need to obtain information relevant to both biological and human systems and the interactions within and between them. My thesis combines approaches from ecology and socioeconomic to investigate the impacts of a specific stressor - invasive Indo-Pacific lionfish - on coral reef ecosystems. First, I explore how this invasion has changed trophic interactions and food web dynamics of coral reef fish communities. Second, I investigate how the impacts of an invasive predator can scale up to affect and change socioeconomic systems associated with natural systems. I found that the trophic niche of lionfish has changed over time, concomitant with large changes in native fish prey abundance. I also found that lionfish predation is having impacts on energy flow through coral reef fish communities even in the absence of marked changes in fish community structure. Combined, these changes could affect ecosystem function. I also present some of the first evidence of economic impacts of this invasion in regions that depend on reef-related tourism. I show that reductions in lionfish abundance through management actions should be beneficial to the reef tourism industry, and that tourist user fees are an acceptable means of financing such actions. As new management strategies are explored, the popularity of lionfish tournaments (derbies) has increased, premised on the idea that involving the public could help to tackle this invasion. However, my results show that such events are most likely to be successful only when lionfish densities are high and where there is a large pool of participants. This dissertation sheds light on the need to study and manage the impacts of biotic invasions from a multidisciplinary and integrated perspective since impacts will rarely be limited to the natural system affected by invaders.

**Keywords:** Coral reef conservation; Coral reef ecology; Global environmental change; Invasive species management; Latent-class analysis; Lionfish invasion; Marine invasions; Marine-tourism management; Stable isotope ecology; Stated preference choice experiments; Trophic ecology.

# Resumen

Cambios en el medio ambiente están ocurriendo de manera alarmante en todo el mundo. A medida que los sistemas naturales y humanos resisten, y/o se adaptan a estos cambios, dichos sistemas pueden alcanzar nuevos estados de equilibrio. Para entender estos cambios se necesita información del componente biológico y social así como las interacciones entre estos. Mi tésis combina aproximaciones del área ecológica y socioeconómica para estudiar los impactos de un estresor específico - el pez león - sobre ecosistemas arrecifales. En primera instancia estudié los cambios que esta invasión ha tenido en las interacciones tróficas y la dinámica de la cadena alimentaria de las comunidades de peces arrecifales. Posteriormente estudié como los impactos de un depredador invasivo pueden escalarse hasta afectar los sistemas socioeconómicos asociados a los sistemas naturales. La información obtenida indica que el nicho trófico del pez león ha cambiado con el tiempo, y dicho cambio se encuentra asociado a grandes cambios en la abundancia de peces presa. También encontré que la depredación del pez león está ocasionando grandes impactos en el flujo de energía a través de las comunidades de peces arrecifales incluso en la ausencia de cambios marcados en la estructura de las comunidades de peces arrecifales. La combinación de estos impactos puede afectar la función ecosistémica. En este trabajo también presento una de las primeras evidencias del impacto económico de esta invasión en zonas que dependen del turismo en arrecifes. Los resultados que presento muestran que reducciones en la abundancia de pez león a través de acciones de manejo pueden beneficiar a la industria del turismo en arrecifes, y que cuotas implementadas a los turistas puede ser aceptado y ayudar a financiar dichas acciones. En la medida que diferentes estrategias de manejo de esta invasión son exploradas, la popularidad de torneos de captura de pez león se ha incrementado. Estos eventos se basan en involucrar al público para ayudar a hacerle frente a esta invasión. Sin embargo, mis resultados indican que dichos eventos tienen mayor probabilidad de éxito solo cuando la densidad de pez león en la zona es alta y cuando hay un número grande de participantes potenciales. Esta disertación indica la necesidad de estudiar y manejar los impactos de invasiones biológicas desde una perspectiva multidisciplinaria e integral ya que los impactos de dichas invasiones en pocas ocasiones se limitarán únicamente a los sistemas naturales.

# Dedication

Cinco años son una vida en cierto sentido, y de la misma manera, los valores, objetivos e inspiraciones que obtenemos de un camino así van cambiando a lo largo del mismo. Este camino empezó hace muchos años, gracias a una semilla de inspiración que mis papás plantaron en mi, dicha semilla fue el disfrute y respeto por el mundo natural y todos los organismos que habitan en él, gracias a ellos decidí inicialmente emprender este camino profesional y es a ellos a quienes inicialmente dedico este trabajo y este logro académico.

Mi caminar no habría estado completo si no hubiera conocido a mi compañera de aventuras, hemos pasado momentos felices y otros difíciles, pero a pesar del paso del tiempo y los obstáculos encontrados mi amor y admiración por ti solo aumentan, gracias por ser quien eres y por haberme aceptado en tu vida, a ti dedico la determinación y empeño que este trabajo representa.

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# Chapter 1

# General Introduction

Environmental changes of different scales and magnitudes are occurring at an alarming pace throughout the globe (Hughes et al., 2003; Wright, 2005; Halpern et al., 2008). There is no doubt that natural systems are responding to most of these changes, and due to the interconnectedness of our world, impacts will also be felt sooner or later in human systems (Corvalan et al., 2005; Lade et al., 2013). As natural and human systems resist, cope, and/or adapt to global changes, new equilibrium states might be reached (Folke et al., 2004; Scheffer et al., 2009; Lade et al., 2013). To understand changes and transitions between states, it is important to obtain relevant information from the different components and interactions within and between biological and human systems.

Biotic invasions are among the major global change stressors, along with climate change, pollution, overharvesting and habitat destruction (Ormerod et al., 2010; Gutiérrez et al., 2014; Chapman, 2016). The spread of non-native species is enhanced by an array of anthropogenic actions and, once established outside of their native range, non-native species are capable of disrupting ecosystem processes and altering the ecological equilibrium of invaded areas (Carlton, 1999; 2000). When ecosystem processes are affected, the seemingly local impacts of invasive species can scale up and disrupt ecosystem services, upon which human socioeconomic systems depend (Simberloff et al., 2013; Gutiérrez et al., 2014).

The invasion of the northwestern Atlantic (including the Gulf of Mexico and Caribbean) by lionfish (*Pterois volitans/miles* complex; Hamner et al., 2007; Freshwater et al., 2009) presents an unprecedented, large-scale, successful invasion by a marine predator (Whitfield et al., 2002; Green and Côté, 2009; Schofield, 2009; Hixon et al., 2016). Early studies focused on ecology and documented the direct predatory impacts of lionfish, which include decreased abundance, richness, and recruitment of native reef fish (Lesser and Slattery, 2011; Albins, 2012; Green et al., 2012; Ballew et al., 2016). We also now understand the dietary preferences of lionfish (Morris and Akins, 2009; Muñoz et al., 2011; Côté et al., 2013; Dahl and Patterson, 2014) and the features that make prey fish vulnerable to the unique hunting mode of this invader (Green and Côté, 2014). Taken together, these studies have shed much light on the ecological strategies that have allowed lionfish to thrive in their newly invaded environment. However, such large direct impacts are almost certainly accompanied by a suite of indirect ramifications, which we are only beginning to unravel. In some areas, lionfish predation on herbivorous fishes appears to have kickstarted cascading effects onto benthic primary producers (Lesser and Slattery, 2011). However, many more indirect effects are expected (Albins and Hixon, 2011; Arias-Gonzalez et al., 2011; Eaton et al., 2016). From an ecological perspective, the predation pressure exerted by lionfish will almost certainly change food web dynamics and ultimately the structure and function of invaded coral reef ecosystems, but such effects remain undocumented.

Concerns also exist regarding the potential impact of the lionfish invasion on economic activities (Albins and Hixon, 2011; Johnston et al., 2015; Hixon et al., 2016). Most of these concerns involve the direct predatory impact on juveniles of commercially important species such as groupers or snappers, or potential competition for prey or space between adults of these species and lionfish. Few studies have yet documented impacts of lionfish on fisheries (see Johnston et al., 2015; Johnston et al., 2017). Moreover, it is highly likely that the lionfish invasion could also affect other economic activities that depend on coral reef ecosystems, such as tourism, but no study has so far addressed this potential concern (but see Johnston et al., 2015).

To deal with what has been deemed one of the most pressing conservation issues in the region (Sutherland et al. 2010), an integrated approach is needed that combines several sources and types of information. Furthermore, any information on ecological or socioeconomic impacts should be used to better inform and produce sound management strategies. While there have been great planning efforts at the regional, national and international levels, there is currently no coordinated strategy to tackle the lionfish invasion (Johnston and Purkis, 2015). A case in point is the rise of culling as the preferred tool to remove lionfish and potentially reduce their impacts (Akins, 2012). Promoted by non-government organizations (NGOs), academia, and concerned individuals, culling is being implemented haphazardly through the region, often as locally organized lionfish derbies, without much understanding of the goals, advantages or limitations of the method.

In this thesis I address some of these gaps in knowledge regarding the lionfish invasion, which I use as a model for invasive species that have profound and varied impacts, and I point out the need for an integrated approach when dealing with such a complex stressor. The two main components of this thesis focus on the ecological and socioeconomic impacts of the lionfish invasion. The ecological component comprises Chapters 2 and 3, where I go beyond the known direct predatory impacts of lionfish and assess the indirect trophic effects of lionfish predation. To do this, in Chapter 2 I revisit the trophic niche concept (Elton, 1927; Hutchinson, 1957 ; Bearhop et al., 2004), and use stable isotope analysis to assess changes in lionfish trophic niches over two years, as an integrated reflection of the rapid changes in prey availability driven by lionfish. My results show that the trophic niche of the lionfish population I studied has changed over time, concomitant with large changes in native fish prey abundance and community structure. Then in Chapter 3 I examine, again with stable isotopes, the reverberating impacts of lionfish predation on whole food webs. By adopting a trophic niche perspective, this study reveals that lionfish can have an effect on energy flow through coral reef fish communities even in the absence of marked changes in fish community structure at this location.

I address the socioeconomic component in Chapters 4 and 5. I first assess the potential socioeconomic impacts of the lionfish invasion on the diving tourist industry of invaded areas in the Caribbean and explore the potential support of tourists for management actions in Chapter 4. I find that tourist attitudes towards lionfish and its impacts vary according to their diving or snorkeling experience, but all tourists prefer good condition of reef features that can be affected detrimentally by lionfish to a greater extent than they like lionfish. These results suggest that managing the lionfish invasion should be beneficial to the local reef tourism industry. Lastly in Chapter 5, I examine the characteristics of lionfish derbies, one of the commonest forms of lionfish control in the wider Caribbean region, and ask what are the drivers of public involvement and success at lionfish removal during derbies in the Western Atlantic. I find that the number of lionfish caught increases with effort and with time since lionfish were established in an area, while participation is best predicted by national wealth (GDP per capita) and number of local dive shops. In the final chapter I combine the findings from the two parts of this dissertation and show how an integration of ecological and social information can be used to better understand the broad impacts of the lionfish invasion and improve management.

# Chapter 2

# Temporal changes in the trophic signature of an invasive marine predator

## 2.1 Abstract

Invasive predators can have large impacts on prey populations and change substantially the structure and function of recipient ecosystems. Many successful invasive species have generalist diets, but the extent to which they can track changing or depleting resources has seldom been documented. Using stable isotope analysis, I measured the extent of dietary shift over time by Indo-Pacific lionfish (*Pterois volitans*), invasive predators that are well established throughout the western North-Atlantic and Caribbean where they have caused significant decreases in native reef fish populations. I found that the trophic niche of lionfish, as inferred from trophic niche metrics derived from stable isotopes, changed significantly between 2008 and 2010, concomitant with large changes in native fish prey abundance and community structure. The niche of large (>263 mm total length) lionfish has expanded, increasing in trophic diversity at the population level and showing lower individual trophic similarity, while that of small lionfish has remained similar in size but has shifted towards more $^{15}$N-enriched and $^{13}$C-depleted prey sources. These size-dependent differences in isotopic niche trajectories have been most likely driven by intra-specific competition and declining resources. The ability of lionfish to modify their dietary preferences over time may facilitate their expansion and persistence at high densities across the invaded range despite local prey depletion.

## 2.2 Introduction

Eurytopy − the ability to thrive under a broad range of conditions − is a trait that is common among successful invaders across different taxa and environments (Ricciardi and Rasmussen, 1998; McKinney and Lockwood, 1999). Two key aspects of a successful eurytopic species are having a broad diet (i.e., feeding on many different food resources) and showing dietary plasticity (i.e., shifting dietary resources after behavioral or cognitive adaptations, or as a result of tracking resource availability; Ribeiro et al., 2007; Falk-Petersen et al., 2011; Ruffino et al., 2011; Pagani-Núñez et al., 2016). A generalist habit might facilitate prey switching to track resource availability, which is expected on theoretical grounds (Charnov, 1976). For example, invasive rats (*Rattus rattus*) and cats (*Felix catus*) on tropical islands have been shown to shift seasonally from targeting seabirds, their main food source, to alternative prey such as sea turtles (*Chelonia mydas*), insects and rodents, when seabirds are not nesting (Caut et al., 2008; Peck et al., 2008). Similarly, the diets of invasive South American cichlids in Mediterranean-type rivers, and of invasive roach (*Rutilus rutilus*) in Irish lakes varied seasonally and between localities, reflecting a high level of dietary plasticity (Ribeiro et al., 2007; Hayden et al., 2014). Therefore, shifts in diets of invasive predators in the face of changing or depleting resources may be a general phenomenon.

Documenting dietary shifts in any species, but particularly for predators, is challenging. Direct observations of predators foraging are impossible in many environments, and diet shifts are hard to capture through the snapshot nature of gut contents analysis (Arrington et al., 2002). As an alternative, stable isotope analysis (SIA) is increasingly used as a proxy to assess feeding behavior and dietary preferences (Tieszen et al., 1983; Hobson and Clark, 1992; Boecklen et al., 2011), especially when diet composition cannot be directly described. Ratios of heavy to light carbon ($^{13}C/^{12}C$, expressed as $\delta^{13}C$), and nitrogen ($^{15}N/^{14}N$, expressed as $\delta^{15}N$) isotopes provide an integrated assessment of various food web processes in the ecosystem (DeNiro and Epstein, 1978; 1981; Minagawa and Wada, 1984). Specifically, $\delta^{15}N$ values represent trophic level of consumers and $\delta^{13}C$ values represent sources of basal primary productivity (DeNiro and Epstein, 1978; 1981; Minagawa and Wada, 1984).

Isotopic signatures, and the metrics derived from them, can be powerful to detect changes in diet. For example, nitrogen isotope enrichment is often observed with increasing body size within and across fish species, both in temperate and tropical marine ecosystems, which reflects the fact that as fish grow, they consume larger prey that occupy higher trophic levels (Davenport and Bax, 2002; Jennings et al., 2002; Cocheret de la Morinière et al., 2003a). In contrast, carbon isotope values generally do not vary as substantially with fish size, but when they do, it often reflects ontogenetic habitat shifts and associated changes in diet. For instance, adult fishes that live and forage on coral reefs are more depleted in $^{13}C$ than juveniles of the same species sampled from nursery habitats (i.e., mangroves and seagrass beds; Cocheret de la Morinière et al., 2003b). The carbon and nitrogen isotope axes can also be combined in a two-dimensional isotopic space where the area occupied by one or more species approximates the 'trophic niche' of that species or community (Bearhop et al., 2004; Layman et al., 2007). Several metrics have been proposed that describe aspects of trophic niche (see Layman et al., 2007; Jackson et al., 2011). For instance, the total isotopic area occupied reflects the overall breadth of dietary resources of a species or a group of consumers (Elton, 1927; Hutchinson, 1957 ; Bearhop et al., 2004), while the range in nitrogen and carbon isotope values reveal vertical or horizontal trophic diversity (i.e. the trophic interactions between species and food web levels in a community; Hurtubia, 1973; Jørgensen and Svirezhev, 2004; Duffy et al., 2007; Villéger et al., 2008). Changes in these metrics over time can reveal dietary shifts (Schmidt et al., 2007; Layman et al., 2012), including in invasive species. For example, trophic position shifts, inferred by changes in $\delta^{15}$N values caused by changes in diet due to prey depletion, have been reported in invaders of terrestrial [e.g., invasive argentine ants (*Linepithema humile*) in California; (Tillberg et al., 2007)], and freshwater ecosystems [e.g., Louisiana swamp crayfish (*Procambarus clarkii*) in Kenya; (Jackson et al., 2012)], but to my knowledge, not from marine environments.

My aim was to examine whether the diet of a high-profile marine invader, the red lionfish (*Pterois volitans*), has shifted over time, as inferred from changes in trophic niche metrics. Lionfish are predators that have become established in the Western North Atlantic, Caribbean and Gulf of Mexico (Schofield, 2009). Lionfish have reached high densities in some parts of the invaded range (Whitfield et al., 2007; Green and Côté, 2009; Darling et al., 2011), and at these locations, they have decreased native reef fish recruitment, biomass and diversity (Albins and Hixon, 2008; Albins, 2012; Green et al., 2012). Their diet appears to be broad, including many fish and invertebrate species (Morris and Akins, 2009; Muñoz et al., 2011; Layman and Allgeier, 2012; Côté et al., 2013; Dahl and Patterson, 2014), which might give them scope to target alternative prey as populations of preferred prey fish become depleted. I evaluated changes in trophic niche of lionfish on coral reefs of The Bahamas, as inferred through stable isotope analysis, over a period during which lionfish predation drove prey fish biomass down by 65%, on average (Green et al., 2012). To better understand the factors underpinning any changes in lionfish trophic niche, I also investigated changes in prey fish community structure on the same reefs over the same time period. I predicted that trophic niche area of lionfish would either expand (if a broader number of prey are consumed; Tilley et al., 2013) or contract (if consumers preferentially exploit specific prey; Fanelli et al., 2015). I also expected that if prey biomass depletion increases intraspecific competition (Jackson et al., 2016), niche partitioning between groups – as reflected by lower overlap of trophic niches (Evangelista et al., 2014) – could be observed. Moreover, any shifts in prey assemblages towards species that use different basal resources (e.g. pelagic vs. benthic) or feed at different trophic levels would be reflected in shifts in the core of the lionfish trophic niche along the carbon and nitrogen isotope axes, respectively. This is the first study to assess changes through time in the trophic niche of lionfish in their invaded range.

## 2.3 Methods

### 2.3.1 Study sites and sample collection

I surveyed lionfish prey communities and collected lionfish specimens at nine sites along a continuous coral reef wall bordering the Tongue of the Ocean trench, off southwest New Providence, The Bahamas in 2008 and 2010. Sites were 10-20 m deep, marked by a mooring buoy, each separated by at least 1 km. I collected lionfish in 2008, four years after initial reports of lionfish in New Providence, and again in 2010. In 2008, lionfish density was already very high (>390 fish $\mathrm{ha}^{-1}$; Ribeiro et al., 2007; Green and Côté, 2009). While some removals of lionfish by recreational divers occurred, there was no systematic culling at these sites in the following two years, and lionfish densities in 2010 were comparable to those in 2008 (Green et al., 2012).

I collected lionfish for stable isotope analysis using one of two methods. Some were collected with hand nets and euthanized at the surface in a clove oil and seawater solution. Others were speared with a prong paralyzer underwater, placed in a water-filled dry bag, and then brought to the surface. All specimens were kept on ice until brought into the laboratory. The collection and handling of all lionfish specimens for this study was approved by the Simon Fraser University Animal Care Committee and met Canadian Council on Animal Care animal usage guidelines and policies (permit 947B-09).

### 2.3.2 Prey fish abundance

To estimate prey fish abundance on each reef, I conducted underwater surveys during the summers of 2008 and 2010. I surveyed $6 - 12$ 30 m x 2 m transects laid parallel to the crest reef at each site, carefully searching crevices and overhangs. I recorded the number and estimated total length (TL, to the nearest 1 cm) of each potential lionfish prey encountered. I considered as potential fish prey all fish $< 15$ cm total length (TL), i.e., the maximum prey size for gape-limited lionfish at these sites (Green and Côté, 2014).

### 2.3.3 Stable isotope processing

I removed a portion of dorsal muscle from 106 individual lionfish in 2008 and 78 fish in 2010. Each sample was cleaned, labeled and stored frozen, in individual containers. Samples were then dried at 60ř C for 24 − 48 h and 0.5 − 1.0 mg of finely ground tissue was placed in pre-cleaned tin capsules. I did not extract lipids from muscle tissue because the C:N ratios indicated a low lipid content (mean ± SD: 3.22 ± 0.12; see Post et al., 2007). Samples were sent to the UC Davis Stable Isotope Facility where C and N stable isotope ratios were analyzed using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20−20 isotope ratio mass spectrometer. The long-term standard deviations of the laboratory's internal standard (sucrose and ammonium sulfate) were ± 0.20‰ for $^{13}$C and ± 0.30‰ for $^{15}$N, respectively.

I elected to sample fish muscle instead of other tissues because muscle has a relatively slow carbon and nitrogen isotopic turnover rate, with a reported half-life of 49 − 173 days for other fish species (summer flounder *Paralichthys dentatus*, (Buchheister and Latour, 2010); bluegill *Lepomis macrochirus*, largemouth bass *Micropterus salmoides*, and yellow perch *Perca flavescens*, (Weidel et al., 2011)). A slow turnover rate tissue should dilute any short-term variability in baseline producers (e.g., brief pulses due to seasonal oceanographic processes and micro-scale individual movements; (O'Reilly et al., 2002; Montoya, 2007).

### 2.3.4 Statistical analyses

#### Change in prey biomass and community structure

I converted prey fish lengths (cm) to biomass (g) using species-specific allometric scaling constants obtained from FishBase (Froese and Pauly, 2015) and verified in the primary literature. If species-specific constants were not available, I used allometric constants for closely related species with a similar body shape. The average decline in combined biomass of all prey fish for my study sites and time period (2008−2010) was reported by (Green et al., 2012), based on a linear mixed-effects model that compared the biomass of fish between years (fixed effect), with transects nested within sites (random effects). Here, I disaggregated the same data to show biomass change at individual sites and used species-level information to investigate shifts in fish community assemblages.

To assess changes in prey fish community structure between 2008 and 2010 I calculated a Bray-Curtis similarity index on mean prey fish species abundance per site standardized by transect area. I estimated similarity matrices, and ran an analysis of similarities (ANOSIM) in fish communities between years. ANOSIM generates an R statistic, which varies between 0 (samples are as similar across groups as they are within group) and 1 (all samples within groups are more similar to each other than to any sample across groups) and is tested for difference from zero with a permutation test (in this study, N = 999 permutations). I graphically represent the differences in prey fish assemblages through time using a non-metric multi-dimensional scaling (nMDS) plot in which sites that are more similar in community composition appear closer together than more dissimilar sites. Stress values of $<0.1$ suggest that distances among sites in an MDS plot accurately reflect the extent of community differences (Clarke and Warwick, 2001). I applied the similarity percentage (SIMPER) routine to estimate the contribution of individual fish species to dissimilarity between years. I deemed species to be important to differences between years if their individual dissimilarity contribution was 1.8% or more, which is twice the expected value if dissimilarity were evenly partitioned among all species in the analysis (i.e., 100% divided by 109 prey fish species, multiplied by two). I used the “vegan” package in R (Oksanen et al., 2016) to run all community structure analyses.

### Lionfish body size and stable isotope ratios

Because I observed some evidence of $^{15}$N and $^{13}$C enrichment with lionfish body size [Fig. A.1, see also (Dahl and Patterson, 2014; O’Farrell et al., 2014; Curtis et al., 2017)], I followed the size-based analytical approach of (O’Farrell et al., 2014). I only used data from lionfish spanning similar size ranges ($>150$ mm) across the two years. I divided this normally distributed sample into two size classes (i.e., ‘small’ and ‘large’), separated around the median length of the pooled sample (263 mm). Small and large classes comprised 93 and 86 individuals, respectively. These two classes were used in comparisons of trophic niche metrics between years.

### Estimating trophic niche changes

I calculated various isotope niche metrics proposed by (Layman et al., 2007) to assess temporal changes in trophic niche of lionfish in R (R Core Team, 2016). For each year, I first estimated (1) total niche area (TA), i.e. the total amount of niche space occupied by lionfish along the $\delta^{13}$C and $\delta^{15}$N axes, as estimated by the maximum convex hull, (2) the carbon range (CR; maximum − minimum $\delta^{13}$C values), and (3) the nitrogen range (NR; maximum − minimum $\delta^{15}$N values), using the R package ‘SIAR’ (Parnell and Jackson, 2013). I then used a Bayesian procedure using SIBER (Stable Isotope Bayesian Ellipses in R; (Jackson et al., 2011), also within the R package ‘SIAR’ (Parnell and Jackson, 2013), to estimate changes in two metrics between the two years: (1) standard ellipse area corrected for small samples (SEAC), i.e. the core isotopic niche space occupied, and (2) Bayesian estimates of standard ellipse area (SEAB). I also implemented the nested linear models and residual permutation procedure (RPP) by Turner et al. (2010) in R (R Core Team, 2016) to compare: (1) the difference in centroid location (CL), which is the mean position of all the points in the convex hull; (2) the mean distance to centroid (CD), which provides a measure of the average degree of trophic diversity at the population level, (3) the mean nearest-neighbour distance (NND), which describes the degree of trophic similarity among individuals, and (4) eccentricity (E), which describes departure from isotopic scatter in the $\delta^{13}$C and $\delta^{15}$N dimensions for each year. In addition to RPP, I used Hotellings' T2 test to examine differences in CL between years. The approach by Turner et al. (2010) tests two sets of null hypotheses: (1) the Euclidean distance between each pair of centroids over time does not differ from zero, and (2) the absolute value of the difference in estimates of CD, NND, and E between years does not differ from zero.

## 2.4 Results

### 2.4.1 Change in prey biomass and community structure

Between 2008 and 2010, the combined biomass of prey species declined by 65%, on average, across the study reefs (Fig. 2.1a; linear mixed-effects model (LMM): $t = 4.5$, $df = 105$, $p < 0.001$; see Green et al., 2012). Prey fish community structure differed significantly between the two years (ANOSIM, $R = 0.20$, $p = 0.002$), and there was little overlap in fish assemblages between 2008 and 2010 (Fig. 1b; stress = 0.137). A three-dimensional nMDS plot yielded a lower stress value (stress = 0.091) but the same clear pattern (Fig. A.2). Seven species (Table A.1) contributed disproportionately to community dissimilarity between years (SIMPER analysis, Table A.1). Of these, six (86%) were reported in the stomach contents of lionfish from these same sites and time period (Green et al., 2012), and all possessed morphological and behavioral characteristics that make them vulnerable to lionfish predation (Green and Côté, 2014). By comparison, 41% of prey species that were not disproportionately important to between-year differences in fish community structure were confirmed prey of lionfish.

### 2.4.2 Trophic niche changes

The diet of lionfish, as inferred by isotopic trophic niche metrics, changed over time, but these temporal differences varied between lionfish size classes. Between 2008 and 2010, the range in carbon isotope values (CR) increased for both size classes of lionfish; however, the range for nitrogen values (NR) increased for large lionfish while it decreased for small lionfish (Table 2.1). Standard ellipse area analysis indicates a core niche overlap (SEAC) between years of only 20% for small lionfish but 95% for large lionfish (Fig. 2.2). For both

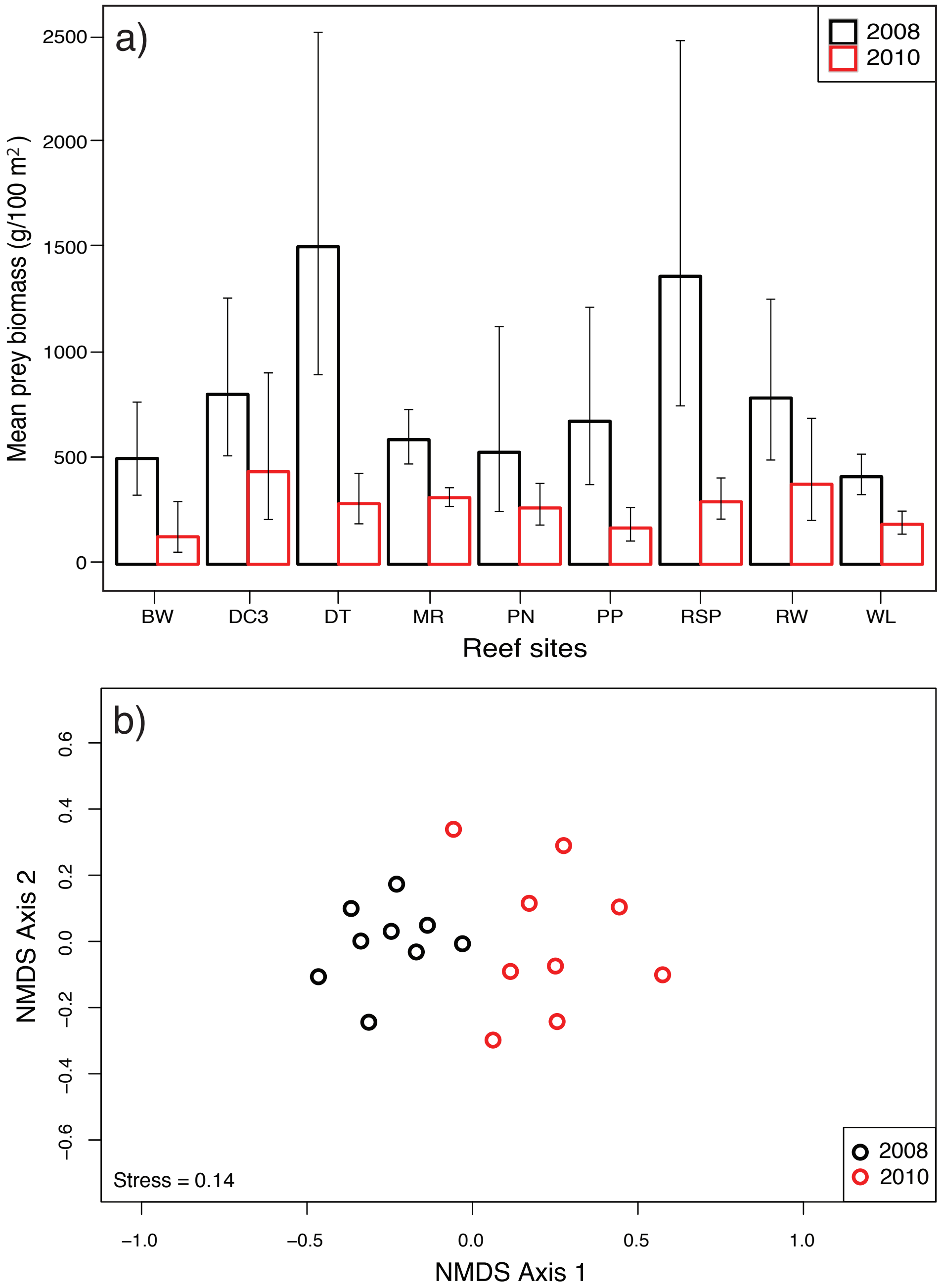

Figure 2.1: Changes in biomass and community structure of lionfish prey ($<$ 15 cm TL) surveyed at nine reef sites off New Providence, The Bahamas, in 2008 and 2010 after the lionfish invasion, which began in 2004. (a) Mean prey fish biomass (g 100 m$^{-2}$) at each reef, error bars represent 95% CI; (b) Non-metric multidimensional scaling (nMDS) plot of prey fish community structure, based on mean prey fish density and species identity in 2008 and 2010. Each point is a coral reef site.

Table 2.1: Mean carbon and nitrogen isotope ratios and trophic niche metrics of small and large lionfish captured off New Providence, the Bahamas in 2008 and 2010. The trophic niche metrics include: carbon range (CR), nitrogen range (NR), mean distance to centroid (CD), mean nearest neighbour distance (NND), eccentricity (E), and centroid location change (CL). Significance (p values) of between-year differences in CD, NND, E, and CL was estimated based on Turner's et al. (2011) nested linear models and residual permutation procedure (RPP). Directional Hotelling's tests were also used to estimate the significance of between-year differences in CL. Statistical significance values *$p < 0.05$, **$p < 0.001$.

| | | **Year** | | | | | |
|---|---|---|---|---|---|---|---|
| Size class | Metric | 2008 | 2010 | Difference between years | *RPP* *p* value | Hotelling's $T^2$ | Hotelling's *p* value |
| Small | $\delta^{13}$C | -13.82 | -14.11 | 0.29 | | | |
| | $\delta^{15}$N | 8.31 | 8.79 | 0.48 | | | |
| | CR | 4.09 | 4.84 | 0.75 | | | |
| | NR | 2.67 | 1.93 | 0.74 | | | |
| | CD | 0.75 | 0.95 | 0.21 | 0.10 | | |
| | NND | 0.15 | 0.24 | 0.08 | 0.15 | | |
| | E | 0.69 | 0.87 | 0.18 | 0.26 | | |
| | CL | | | 0.55 | <0.01* | 29.60 | <0.001** |
| Large | $\delta^{13}$C | -13.58 | -13.46 | 0.12 | | | |
| | $\delta^{15}$N | 8.73 | 8.92 | 0.19 | | | |
| | CR | 4.19 | 5.78 | 1.59 | | | |
| | NR | 1.68 | 2.97 | 1.29 | | | |
| | CD | 0.79 | 1.19 | 0.41 | 0.02* | | |
| | NND | 0.19 | 0.29 | 0.09 | 0.03* | | |
| | E | 0.91 | 0.87 | 0.04 | 0.53 | | |
| | CL | | | 0.23 | 0.09 | 4.97 | 0.42 |

small and large lionfish, the Bayesian trophic niche width (SEAB) was larger in ~99% of Bayesian posterior draws in 2010 than in 2008 (Fig. 2.2).

There was a significant shift between years in centroid location (CL) of the isotope niche of small lionfish but not of large lionfish (Table 2.1; Fig. 2.2). Population-level trophic diversity of lionfish, as estimated by distance to centroid (CD), was significantly larger for large lionfish in 2010 than in 2008 (Table 2.1). Nearest-neighbour distance (NND) was also larger for larger fish in the second year. Neither parameter was temporally variable for small lionfish (Table 1). Eccentricity (E) did not vary significantly between years or size classes (Table 2.1).

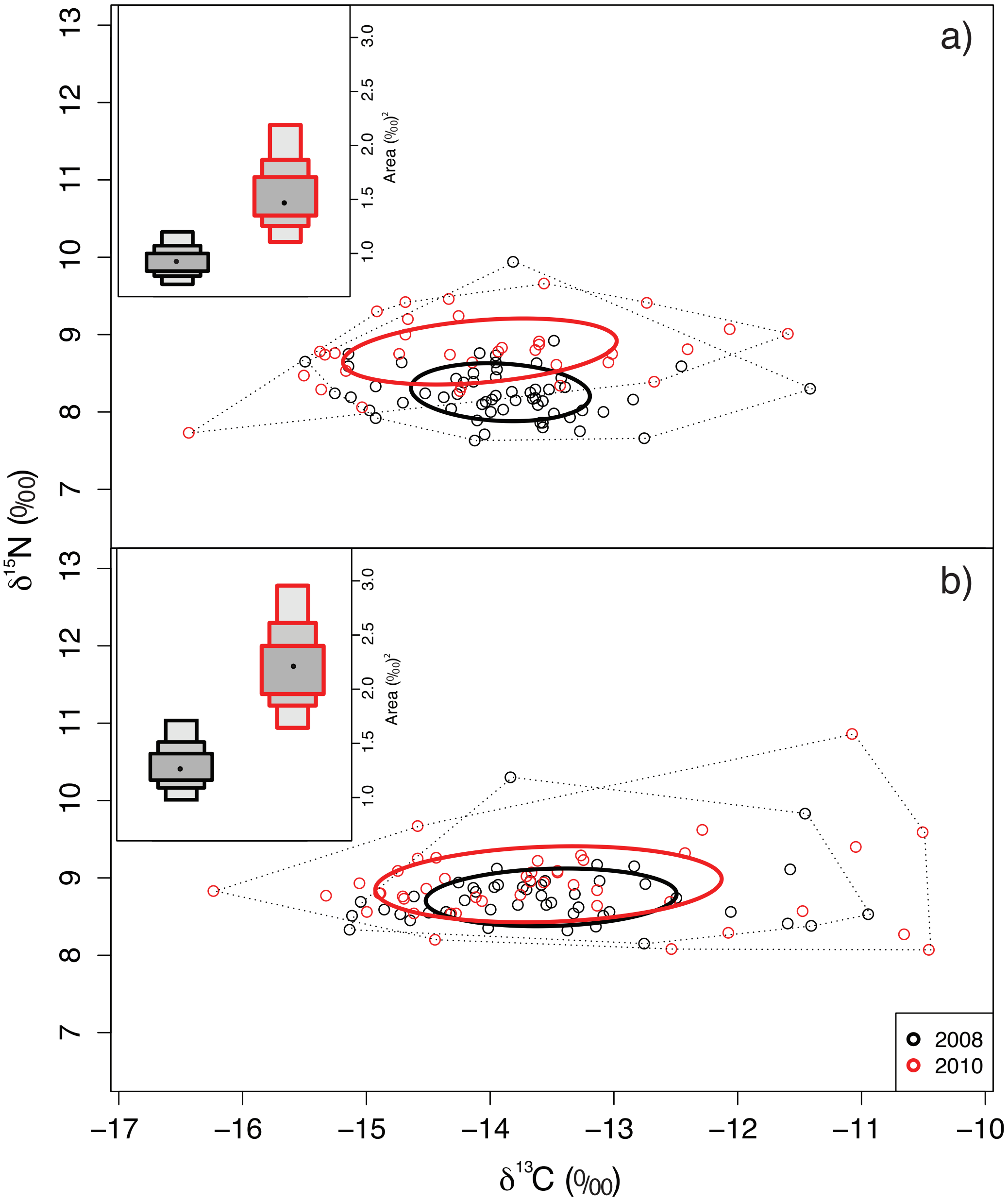

Figure 2.2: Isotopic trophic niche width of (a) small and (b) large lionfish sampled off New Providence, The Bahamas, in 2008 (open black dots) and 2010 (open red dots). The solid lines delimit the standard ellipse areas corrected for small samples (SEAC) and the black dotted lines, the total area (TA) of the isotopic niches of lionfish, as determined by convex hull. The insets show density plots of posterior draws from Bayesian standard ellipse area (SEAB), where the black points correspond to the mean standard ellipse areas while the grey boxed areas reflect 95, 75 and 50% confidence intervals.

## 2.5 Discussion

I found some evidence of changes in the trophic niche of lionfish over a two-year period during which the invasive predators reduced prey biomass (Green et al., 2012), and altered prey community structure significantly on coral reefs. The trophic shifts differed between small ($<$ 263 mm TL) and large lionfish ($>$ 263 cm TL). The isotopic niche of small lionfish became larger over time, mainly because of a broadening of the carbon isotope range, and the location of its centroid shifted to become more enriched in nitrogen and less enriched in carbon (Table 2.1, Fig. 2a). The isotopic niche of large lionfish also increased, due to widening of both carbon and nitrogen ranges, but its centroid location did not shift. Instead, the broader dispersion of individual isotopic signatures suggests an increase in trophic diversity (i.e., larger mean distance to centroid, CD) at the population level, and a decrease in trophic similarity between individual lionfish (i.e., larger mean nearest-neighbour distances, NND) (Table 2.1, Fig. 2.2b). My results suggest that individuals in the lionfish population studied show a high degree of dietary plasticity, allowing them to shift diet in the face of changing or depleting resources – a trait that might have contributed to their invasion success in the wider Caribbean region.

### 2.5.1 Change in prey biomass and community structure

Lionfish have had a major impact on native Caribbean reef fish communities. Studies of lionfish predation on artificial and natural reefs show that they can significantly decrease native reef fish recruitment, biomass and diversity (Albins and Hixon, 2008; Albins, 2012; Green et al., 2012). Here, I revisited the overall prey biomass changes reported by Green et al. (2012), to show that all nine study reefs posted severe declines in prey biomass. Furthermore, I documented for the first time significantly altered prey community structure on these reefs over time and that prey species targeted by lionfish have largely driven these changes (Fig. 2.1b, Table A.1). Green et al. (2012) ruled out any differences between year in disease, predation by native predators and in oceanographic conditions affecting recruitment, concluding that lionfish predation was the main driver of change in native fish communities on these reefs over this time period.

### 2.5.2 Trophic niche changes

Concomitant with large changes in native fish prey abundance and community structure, the trophic niche of lionfish changed between 2008 and 2010. Across all lionfish classes, the isotopic niche area broadened, which is a common response to resource depletion in trophically flexible consumers (Chapman et al., 1989; Peck et al., 2008). However, the isotopic niches of small and large lionfish changed differently. Taken together, the various isotope niche metrics suggest that the niche of large lionfish has simply expanded, increasing trophic diversity at the population level and reducing trophic similarity among individuals, while that of small lionfish has shifted towards more $^{15}$N-enriched and $^{13}$C-depleted prey sources.

Size-dependent differences in isotopic niche trajectories might have been driven by intraspecific competition. Between 2008 and 2010, lionfish densities were high on the reefs studied (Green and Côté, 2009; Green et al., 2012), creating scope for competition. There is little evidence for direct interference competition in lionfish (personal observations); however, intraspecific exploitation competition is the most likely mechanism behind the density-dependent growth rates of lionfish on artificial reefs (Benkwitt, 2013; 2016). Furthermore, size-based dominance in competitive interactions is a common phenomenon in marine fishes (Brown and Maurer, 1986). This process has been invoked in the partitioning of isotopic niche space between large and small lionfish in a snapshot study on Bahamian forereefs (O'Farrell et al., 2014), as well as the lower site fidelity of small than large lionfish (Tamburello and Côté, 2015). Low prey availability coupled with dominance by larger individuals may force smaller lionfish to exploit a different pool of prey over time, resulting in the isotopic niche shifts observed in my study.

Changes observed in trophic niche metrics might also be attributed to factors other than changes in lionfish trophic interactions. Seasonal oceanographic processes and terrestrial inputs can shift carbon and nitrogen baselines in coastal marine systems (Montoya, 2007; El-Sabaawi et al., 2012; McMahon et al., 2013). In addition, $\delta^{13}$C and $\delta^{15}$N gradients related to isotopic baseline differences exist within and between ecosystems (Radabaugh et al., 2013). Hence, isotopic baseline changes between years could alter isotopic signatures of low trophic level consumers, with repercussions at higher trophic levels (Goering et al., 1990; Vizzini and Mazzola, 2003). However, if the trophic niche changes observed were the result of a system-wide process that altered isotopic baselines, I would have expected both size classes of lionfish to be affected similarly, which was not the case. Alternatively, recent larval settlement (Herzka and Holt, 2000), or ontogenetic movements between mangroves, shallow and deep reefs (Cocheret de la Morinière et al., 2003b) could be responsible for isotopic differences between years. However, the size range I studied ($150 - 399$ mm TL) was well above lionfish settlement size, and most individuals would have been mature (size at maturity: $100 - 200$ mm TL; Morris, 2009; Gardner et al., 2015). The size range was also similar across years. Furthermore, there is little evidence of ontogenetic habitat shifts in lionfish (Barbour et al., 2010; Claydon et al., 2012; Pimiento et al., 2015).

Lionfish have been previously classified as a generalist predator (Muñoz et al., 2011; Layman and Allgeier, 2012; Côté et al., 2013). However, apparent diet generality at the population level can belie individual specialization (Bolnick et al., 2003; Araujo et al., 2011). My results support this notion (Layman and Allgeier, 2012). The wide isotopic niche and increase in trophic diversity of large lionfish observed over time are indicative of a generalist predator at the population level. However, the decrease in trophic similarity among large individuals, likely as a result of prey depletion and competition between conspecifics, suggests some level of individual specialization. It is notable that despite large changes in prey abundance and community structure, no prey species have been reported as extirpated from this area (Green et al., 2012). Therefore, in spite of the evidence of individual specialization in lionfish, the large overlap in isotopic niches between years may also suggests that large lionfish have potentially continued to consume previously exploited prey groups, despite their rarity (Fig. 2.2). However, stable isotope data from prey species are needed to substantiate this hypothesis.

### 2.5.3 Ecological implications of findings

The evidence I provide of trophic niche changes of lionfish, as inferred by stable isotopes, is notable, particularly given that lionfish were already well established in The Bahamas at the onset of my study (Schofield, 2009). It seems likely that much more extensive changes to native fish assemblages and to the lionfish trophic signature would be documented if baselines from earlier stages of the lionfish invasion were available. In the absence information on stomach contents, I unfortunately cannot assess whether the trophic niche shifts observed are the result of targeting different fish prey, incorporating additional invertebrate prey and/or foraging more extensively in non-coral habitats. While it is now well established that lionfish consume a wide variety of prey (see Morris and Akins, 2009; Muñoz et al., 2011; Layman and Allgeier, 2012; Côté et al., 2013; Dahl and Patterson, 2014), ours is the first report that documents potential prey changes over time. Stomach contents analyses should be conducted to confirm the evidence I present based solely on stable isotope analysis. If these uphold my results, it would add weight to the idea that the dietary plasticity of lionfish helps them to cope with changes in prey abundance and intraspecific competition, and is likely to be a factor that facilitates their continued expansion and persistence at high densities despite local prey depletion.

## Chapter 3

# Shadows of predation by invasive lionfish on trophic niches of Caribbean reef fish communities

### 3.1 Abstract

Through direct consumption and various indirect effects, predators have profound impacts that regulate and stabilize communities. Invasive predators often have stronger consumptive effects than native predators on novel communities. Predation and competition exerted by non-native predators can change the trophic niche of native populations and communities, but the direction of these impacts and the mechanisms involved are not fully understood. Through intense predation, invasive lionfish (*Pterois volitans/miles*) is causing significant impacts on coral reef communities in the wider Caribbean region. As this invasion continues, it disrupts local trophic interactions, and these impacts can be larger on reefs with intrinsically vulnerable characteristics, such as low habitat complexity. I used trophic niche metrics (Carbon Range, Nitrogen Range and Total Niche Area; as inferred from stable isotope analysis of carbon and nitrogen) of reef fish communities from reef patches with varying lionfish density, habitat complexity and either subjected to lionfish removals or no removals. I predicted a reduction in trophic niche metrics at sites with higher lionfish density, and longer and more complex food webs at sites with higher habitat complexity. I found that the three trophic niche metrics increased with habitat complexity, and decreased with lionfish density, but only at sites where no lionfish were removed. Unexpected interactions between habitat complexity, lionfish density, and lionfish removal resulted in positive or negative relationships with the three trophic niche metrics depending on removal regime. Results suggest tantalizing patterns that point to complex consumption- and behaviour-mediated

effects of predation on trophic niche metrics on invaded reefs, which should be considered when assessing the larger-scale impacts of this invasion.

## 3.2 Introduction

The movement of energy and nutrients arising from trophic interactions in an ecosystem is inextricably linked to species diversity. Trophic interactions underpin ecosystem functioning by driving productivity, transferring energy, and creating a complex web of dependencies among species, populations, and communities (Streit, 1995; Garvey and Whiles, 2016; Guerrero-Ramírez and Eisenhauer, 2017). These interactions between species and food web levels constitute the trophic diversity of a community and reflect species abundance and diversity (Hurtubia, 1973; Jørgensen and Svirezhev, 2004; Duffy et al., 2007; Villéger et al., 2008). Environmental characteristics, such as habitat complexity and heterogeneity, which can determine species abundance, diversity and richness (Tews et al., 2004; Graham and Nash, 2013; Richardson et al., 2017), can also affect the structure and function of food webs in an ecosystem (Warfe and Barmuta, 2006; Layman et al., 2007b; LeCraw et al., 2014). Furthermore, the structure and function of a food web can be altered by stressors that lead to changes in assemblages of species and how they interact (Coll et al., 2011; Lurgi et al., 2012; O'Gorman et al., 2012). For example, in the current context of global change, changes in community composition result from the loss of biodiversity, shifts in species distribution, and the introduction of new species. Given the interconnectivity that exists in a food web, any alteration to community structure can have trophic repercussions throughout the community and the ecosystem (Dobson et al., 2006; Rodríguez-Lozano et al., 2015).

Through direct (consumption) and various indirect effects, predators have profound impacts that regulate and stabilize communities. These top-down processes can, for example, limit the abundance of species at lower trophic levels, and consequently regulate the biomass of primary producers (e.g., 'green world' hypothesis; Hairston et al., 1960; Terborgh et al., 2001; Terborgh et al., 2006). Non-native predators that find themselves in novel communities as a result of human agency often have stronger consumptive effects than native predators (Snyder and Evans, 2006; Strayer et al., 2006; Gallardo et al., 2016). These predator additions can result in declines in native prey species abundance, changes to community structure, and in extreme cases extirpation or extinction of native species, as has been documented in several terrestrial (Ringler et al., 2015), aquatic (Kadye and Booth, 2012; Jackson et al., 2014) and marine (Edelist et al., 2013; Hixon et al., 2016) ecosystems. These stronger predatory impacts can also result in invasive predators outcompeting native predators and reducing their abundances (Sharpe and Chapman, 2014; Rodríguez-Lozano et al., 2015). The combined effects of predation and competition exerted by non-native predators therefore have the potential to produce large changes to the trophic niche, i.e. the range of dietary resources (Elton, 1927; Hutchinson, 1957 ; Bearhop et al., 2004), of native populations and communities (Ripple and Beschta, 2012; Edelist et al., 2013; Simberloff et al., 2013). However, while impacts on the trophic niche of native communities as a consequence of invasive non-native predators are expected, there is not yet a clear understanding of the direction of these impacts and the mechanisms involved.

Indo-Pacific lionfish (*Pterois volitans* and *P. miles*) are invasive predatory fishes that have had significant impacts on coral reef communities in the northwestern Atlantic, Gulf of Mexico and Caribbean (Hixon et al., 2016). Through direct predation, they have caused severe reductions in richness, diversity, biomass and recruitment of native coral reef species (Albins and Hixon, 2008; Lesser and Slattery, 2011; Green et al., 2012). Lionfish predation has also been proposed as a cause of benthic shifts to algal-dominated communities (Lesser and Slattery, 2011). As lionfish continue to invade new coral reef locations, they create and disrupt local trophic web interactions, which can have concomitant impacts on ecosystem function. The trophic impacts of lionfish might be expected to be larger on reefs with intrinsic characteristics, such as low habitat complexity, that can lead to reduced trophic diversity (e.g., through low abundance and/or diversity; Tews et al., 2004; Hempson et al., 2017; Richardson et al., 2017).

Trophic relationships between and among groups of consumers in a community can be elucidated with stable isotope analysis (SIA). By determining the isotopic ratios of carbon and nitrogen in animal tissues (expressed as $\delta^{13}$C and $\delta^{15}$N, respectively; DeNiro and Epstein, 1978; 1981; Minagawa and Wada, 1984), one can evaluate both the trophic level (via nitrogen) and the base of the food web (via carbon) upon which an individual has been foraging over temporal scales lasting from days to years, depending on the tissue analyzed (Vander Zanden et al., 2015). Taken together across individuals, these two isotopic signatures can be used as a proxy to determine the trophic niche width of populations, species, and communities (Bearhop et al., 2004; Layman et al., 2007a). Layman et al. (2007a), proposed specific quantitative metrics to measure community-wide aspects of trophic structure that are comparable across communities. These metrics are sensitive enough to reveal changes in trophic niche of species and communities under environmental stress (Reddin et al., 2016), or experiencing environmental disturbances such as overexploitation (Hamilton et al., 2014), habitat change (Moss et al., 2016; Reuter et al., 2016), climate change (Bond and Lavers, 2014; Young and Ferguson, 2014), ocean acidification (Vizzini et al., 2017), and species introduction (Fanelli et al., 2015).

My main aim was to examine the effects of the lionfish invasion on the trophic interactions of coral reef fish communities, as understood by trophic niche metrics. I assessed these effects by estimating trophic niche metrics of reef fish assemblages, inferred from stable isotope analysis of carbon and nitrogen, from 16 reef patches with varying lionfish density as well as habitat complexity. On eight of these reef sites ongoing experimental culling aimed to maintain lionfish densities at low levels. While the direct effects of lionfish predation on reef fish communities (Albins and Hixon, 2008; Lesser and Slattery, 2011; Green et al., 2012), as well as their dietary preferences across the invaded range (e.g. Morris and Akins, 2009; Green et al., 2011; Muñoz et al., 2011; Côté et al., 2013; Chappell and Smith, 2016), have been previously assessed, the indirect effects of this invader and potential impacts on trophic webs have not received much attention (but see Layman and Allgeier, 2012; Dahl and Patterson, 2014; O'Farrell et al., 2014; Curtis et al., 2017). I predicted that sites with more lionfish, and hence higher predation mortality, should present trophic niche shifts, likely to shorter and narrower niches as a result of changes in community structure compared to sites with fewer lionfish (Vander Zanden et al., 1999a; Vander Zanden et al., 1999b; Gorokhova et al., 2005; Nilsson et al., 2012). On the other hand, longer and more complex food webs are expected at sites with higher habitat complexity, which usually harbor higher abundance and species richness (Almany, 2004; Karnauskas et al., 2012). Lionfish abundance and habitat complexity could also interact: at sites with higher habitat complexity, which might provide more shelter, the effect of lionfish predation could be reduced, while the converse might be observed at sites with lower habitat complexity.

## 3.3 Methods

### 3.3.1 Study sites, surveys, and sample collection

The study took place on 16 reef patches in Rock Sound, a large, shallow bay at the southern end of Eleuthera Island, The Bahamas (Fig. 3.1). All study reefs were ~3 m deep and ranged in area from 15 to 200 m$^2$. The patches were separated by at least 100 m and varied in habitat complexity. Live coral cover was generally low (10-20%) but similar to the average cover for The Bahamas (Wilkinson, 2008). The 16 reef patches were part of a long-term lionfish removal experiment. At the time of this study, eight of the reefs had been subjected to lionfish culling every three to six months for 2 years, while lionfish were not controlled on the remaining reefs. Culling efficiency was relatively high (90-100%) but recolonization between removal events (Smith et al., 2017) meant that no reef remained lionfish-free for the entire inter-culling periods.

I estimated the abundance of all fish species on each reef patch every three months from June 2012 to June 2013. To do so, I surveyed three or four 8 x 2 m transects laid parallel to the long axis of each reef, carefully searching crevices and overhangs within each transect. I also conducted predator-focused surveys to estimate lionfish and native predator (snappers

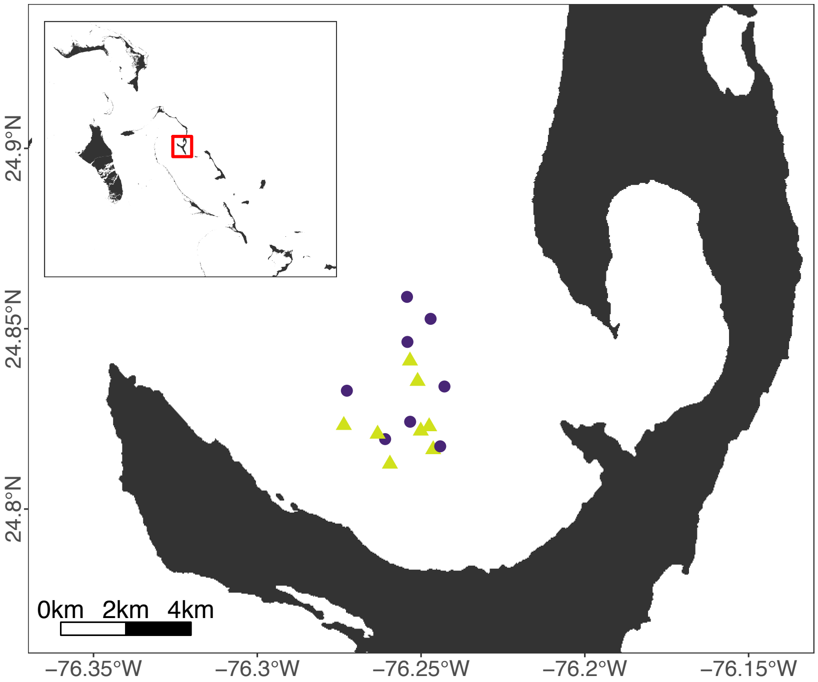

Figure 3.1: Map of Rock Sound with the location of reef patches where lionfish were removed (triangles) or not removed (circles). Inset map shows The Bahamas archipelago and the area of study off Eleuthera Island (square).

and groupers) abundance on each reef. Two or three divers searched around and over the reef in an S-shaped pattern, carefully searching crevices and overhangs. Immediately after the survey, divers compared notes on the size and location of predators observed to minimize double counting and missing individuals. I recorded the number and estimated total length (TL, to the nearest 1 cm) of each fish encountered.

I assessed habitat complexity of each patch reef in June 2013 using the habitat assessment score (HAS) methodology of (Gratwicke and Speight, 2005). I placed a 1 $m^2$ quadrat at 10 random locations along each of three transects laid parallel to the longest axis at each site. I estimated six features on a five-point scale (1 = least, 5 = most): 1) number of holes, 2) volume of holes, 3) percentage of total area covered by live benthic cover, 4) percentage of total area covered by hard substrate (live or dead), 5) substrate height above the sand, and 6) rugosity. Using the scores for each feature, I obtained an average HAS estimate for each quadrat. I then used these values to produce a mean HAS score that estimates habitat complexity for each reef.

I collected tissue samples from reef fish, primary producers, and zooplankton at each reef patch in June and July 2013. From each reef site, I collected samples from as many fish species as possible, trying to obtain representatives from three major food web groups (i.e., herbivores, invertivores, and mesopredators). To minimize impacts to the ongoing lionfish removal study, I used an array of non-lethal collection methods, such as hook and line, fishnets, gillnets, bottom nets, and hand-nets. Clove oil diluted with ethanol (1:10) was used to anesthetize fish and facilitate their extraction from shelters. After capture, fish were placed in a water-filled dry bag, brought to the surface, and kept in the bag or transferred to a live-bait tank on a boat. All fish were measured (total length, TL) to the nearest mm and fin clipped (anal fin, $\sim 2$ mm$^2$) with ethanol-sterilized scissors. Fish were then released back to the point of capture. No more than 30 min elapsed between capture and release. The collection and handling procedures were approved by the Simon Fraser University Animal Care Committee (permit 1084B-13) and met Canadian Council on Animal Care animal usage guidelines and policies.

I collected samples from primary producers from every study reef. I used ethanol-sterilized scissors to cut $\sim 2$ cm$^2$ from *Lobophora variegata*, the dominant macroalgal species on my reef patches (personal observations), and seagrass (*Thalassia testudinum* and *Syringodium filiforme*). I scraped off small portions ($\sim 2$ cm2) of the epilithic algal communities (EAC) from hard substrates using ethanol-sterilized pincers and a scalpel, and the samples were placed in a mesh-bag after collection and brought to the surface. I also collected zooplankton from the water above each reef site as a proxy of oceanic isotopic contribution. To collect zooplankton I towed a 150 $\mu$m plankton net at a depth of $\sim 1$ m from an outboard motorboat for 15 minutes at a speed of $\sim 2$ knots moving in circles around each reef site. At the end of the tow, the net was rinsed with seawater to concentrate the sample into the cod end, the seawater was drained, and I recovered all zooplankton material with ethanol-sterilized pincers. I cleaned all samples with distilled water, labeled and stored them at -4°C in individual containers (2 mL microcentrifuge tubes) to await processing.

### 3.3.2 Stable isotope sample processing

I analyzed a total of 383 individual fin clips, 64 samples of primary producers, and 16 samples of zooplankton. Thawed samples were dried at 60°C for 24-48 h and 0.5 -1.0 mg of finely ground tissue was placed in pre-cleaned tin capsules. Samples were sent to the UC Davis Stable Isotope Facility where $^{13}$C and $^{15}$N isotope ratios were analyzed using a PDZ Europe ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer. The standard deviations of the laboratory's internal standard (sucrose and ammonium sulfate) were $\pm$ 0.20‰ for $^{13}$C and $\pm$ 0.30‰ for $^{15}$N, respectively. I mathematically corrected stable isotope ratios from fin samples with C:N ratios $> 3.5$ indicative of high lipid content ($\delta^{13}$C untreated $-$ 3.32 + 0.99 $\times$ C:N; after Post et al., 2007).

### 3.3.3 Statistical analysis

#### Structure, abundance and variability of reef fish community

I assessed variation in prey fish community structure from the transect survey data. To do so, I ran permutation-based, non-parametric multivariate analyses of similarity (ANOSIM; Clarke, 1993) using PRIMER (v. 6.0; Clarke and Gorley, 2006). I compiled abundance matrices (species by site), where abundance was calculated as average number of individuals per 16 $m^2$ (i.e., the area of one transect, averaged across the three transects at a site). Abundance data were square-root-transformed to reduce the influence of very abundant species. Bray-Curtis similarity coefficients were computed between all pairs of patch reefs (Clarke and Warwick, 2001). The similarity matrix thus generated was used to run four analyses of similarity (ANOSIM) in fish communities: (1) between years (2012 and 2013), (2) between reefs with lower and higher lionfish density (following a natural break at 2 lionfish per 100 $m^2$), (3) between removal and control reefs, and (4) between reefs with low and high habitat complexity (following a natural break at HAS score = 2.2). ANOSIM generates an R statistic, which varies between 0 (communities are as similar across groups as they are within group) and 1 (all communities within groups are more similar to each other than to any community across groups) and is tested for difference from zero with a permutation test (in this study, N = 999 permutations in each case).

I assessed variation in density of lionfish, native predators (groupers and snappers) and obligate reef species (i.e., those species that spend the majority of their juvenile and adult stages associated to coral reef structures (Choat and Bellwood, 2013; Sale, 2013)) surveyed on reefs by creating linear mixed-effects models (LMMs). I used removal treatment and year (i.e., June 2012 vs June 2013) as fixed effects and reef sites as random effects. I also explored differences in the variability of average lionfish and native competitor abundance (derived from predator-focused surveys) across sites and time between removal treatments through an F-test of equality of variances. I visually checked model residual plots to ensure homoscedasticity and normality. I used R version 3.3.2 (R Core Team, 2016) to assess differences in variances and the lme4 (Bates et al., 2015), and sjPlot (Lüdecke, 2017 ) packages to build and visualize the LMMs.

#### Estimating trophic niche width metrics

I classified fish species into trophic groups based on reported dietary preferences from FishBase (Froese and Pauly, 2017) and verified in the primary literature. Thus, parrotfish and damselfishes were grouped as herbivores, wrasses and grunts as invertivores, and grouper species as mesopredators. I subdivided wrasses and grunts into separate invertivore groups (resident and migratory, respectively) based on literature indicating that grunts migrate to forage in seagrass beds adjacent to reefs at night (Robblee and Zieman, 1984; Nagelkerken et al., 2000), and hence should be expected to differ in their carbon stable isotope composition. This a priori classification was supported by stable isotope differences among species (see Results).

I estimated trophic niche metrics (Layman et al. 2007) at each site using these four trophic groups as proxies for the whole reef fish community using a Bayesian framework (Jackson et al. 2011) in R [package "SIAR", (Parnell et al., 2008; Parnell and Jackson, 2013)]. Specifically, I estimated: (1) $\delta^{13}$C range (CR), i.e. the distance between maximum and minimum $\delta^{13}$C values; (2) $\delta^{15}$N range (NR), i.e. the distance between maximum and minimum $\delta^{15}$N values, and (3) total area (TA), i.e. the total amount of niche space within the convex hull encompassing the mean values of each trophic group in an isotope bi-plot. Other trophic niche metrics have been proposed, such as the mean nearest-neighbor distance (i.e., the degree of trophic similitude among species in a community), the standard deviation of nearest-neighbor distance (i.e., a measure of the evenness of trophic niches), and distance to centroid (i.e., the average degree of trophic diversity within a food web; Layman et al., 2007a). I opted not to investigate these metrics because their interpretation might be biased because I am using trophic groups rather than species or populations, and because some of these metrics add little information to the three metrics I present. All analyses were performed in R version 3.3.2 (R Core Team, 2016).

### Bayesian modeling

I modeled the effects of habitat complexity, lionfish density, and removal treatment (removal vs. no-removal) on the three trophic niche metrics calculated (CR, NR, and TA) using Bayesian approach to propagate uncertainty around trophic niche metrics estimated from each reef site (Fig. B.1). I included lionfish density and removal treatment as separate predictors because the two were not confounded: lionfish density on some culled reefs was actually higher than on non-removal sites. Moreover, culling alters the colonization dynamics of lionfish on patch reefs (Smith et al. 2017; see also Results section), with potential trophic consequences for the native fish community. The general form of the linear hierarchical model was as follows:

$$
\begin{gathered}
y_i \sim \text{Normal}\left(y_i^{\text{true}}, \tau_i^2\right), \\
y_i^{\text{true}} = \beta_0 + \beta_1 H_i + \beta_2 L_i + \beta_3 R_i + +\beta_4 R_i L_i + \epsilon_i, \\
\epsilon_i \sim \text{Normal}(0, \sigma^2),
\end{gathered}
$$

where $y_i$ and $\tau_i$ represent the mean and standard deviation of the log-transformed posterior of one of my response variables for site $i$, $y_i^{true}$ represents the 'true' unobserved value of that response variable, the $\beta$ parameters represent estimated coefficients, and $H_i$, $L_i$, and $R_i$ represent habitat complexity, lionfish density, and removal treatment (as a binary variable), respectively, for each site $i$. The variable $\epsilon_i$ represents independent, normally distributed, residual error with mean 0 and standard deviation $\sigma$.

To make the magnitude of coefficients approximately comparable across predictors, I scaled each continuous predictor by subtracting its mean and dividing by twice its standard deviation (Gelman, 2008). I scaled by *twice* the standard deviation to make the coefficients of the continuous predictors approximately comparable to the removal treatment binary predictor (Gelman, 2008).

I fitted these models in a Bayesian framework using Stan 2.14.1 (Carpenter et al., 2017; Stan Development Team, 2017a) and R 3.3.2 (R Core Team, 2016; Stan Development Team, 2016) to incorporate the measurement uncertainty, $\tau$. I assigned weakly informative priors on all parameters: Normal $(0,2^2)$ priors on the slope parameters $\beta_1$ through $\beta_5$, a Normal $(0, (10)^2)$ prior on the intercept $\beta_0$, and a half-$t$ (3,0,2) prior (i.e., degrees of freedom of 3 and scale of 2) on $\sigma$. I ran four chains and 3,000 iterations, discarding the first 1,500 iterations of each chain as warm up. I checked for chain convergence visually with trace plots, ensured that $\hat{\text{R}}<1.05$ (the potential scale reduction factor), and that the effective sample size was greater than 200 for all parameters (Gelman et al., 2014). I increased the target acceptance rate in Stan to 0.99 and used a 'non-centered' parameterization of my hierarchical model letting $\epsilon_i = \sigma Z$, where $Z$ Normal (0,1), implying $\epsilon_i \sim$ Normal $(0,\sigma^2)$, to increase sampling efficiency and ensure unbiased estimates (Monnahan et al., 2016; Stan Development Team, 2017b).

## 3.4 Results

I analyzed a total of 383 fish fin clips from 9 different species (Table 3.1). The fish species used in my analysis were among the four most abundant fish families present on each reef at the time of sampling (i.e., Haemulidae, Labridae, Pomacentridae and Scaridae; Fig. B.2). Habitat complexity varied from 1.7 to 2.6 on the 5-point HAS scale.

### 3.4.1 Reef fish community structure and abundance

Fish community structure did not vary between levels of any of the factors assessed (i.e. years, lionfish density levels, removal treatment, or habitat complexity levels; all two-way

Table 3.1: Species name, family, size range in total length (TL), and number of individuals sampled.

| Common name | Scientific name | Family | Size range (cm TL) | n |
|---|---|---|---|---|
| Striped parrotfish | *Scarus iserti* | Scaridae | 7.50 - 8 | 53 |
| Dusky damselfish | *Stegastes adustus* | Pomacentridae | 7.75 - 9 | 43 |
| Beaugregory | *Stegastes leucostictus* | Pomacentridae | 5.50 - 6.50 | 49 |
| Yellowhead wrasse | *Halichoeres garnoti* | Labridae | 9 - 10.50 | 42 |
| White margate | *Haemulon album* | Haemulidae | 25 - 30.25 | 71 |
| Graysby | *Cephalopholis cruentata* | Serranidae | 18.35 - 23.50 | 32 |
| Black grouper | *Mycteroperca bonaci* | Serranidae | 27.75 - 43.50 | 15 |
| Nassau grouper | *Epinephelus striatus* | Serranidae | 27 - 35.50 | 49 |
| Lionfish | *Pterois volitans/miles* | Scorpaenidae | 15.50 - 23.50 | 29 |

ANOSIMs, $R < 0.2$, $p > 0.1$). However, the removal of lionfish was associated with a significant increase (+36%) in overall density of obligate reef fish and an even greater increase (+63%) in density of small prey fish (<15 cm) compared to no-removal reefs (Fig. B.3). There was no difference in density of obligate reef fishes (overall and small fish) between years (Fig. B.3). In contrast, there were differences in density of lionfish and native predators on reef sites between years, with significantly fewer mesopredators in 2013 than in 2012 (-82% and -57%, for lionfish and native predators, respectively), but no effect of removal treatment (Fig. B.3). The density of lionfish and native predators was more variable over time on reefs subject to lionfish removals ($F - tests$; lionfish: $p < 0.001$, $F = 0.23$, $df = 29/31$; native predators: $p < 0.001$, $F = 0.12$, $df = 29/30$; Fig. 3.2).

### 3.4.2 Reef community isotope space

As expected, seagrass species (turtlegrass *Thalassia testudinum* and manatee grass *Syringodium filiforme*) were more $^{13}$C-depleted than the macroalga *Lobophora variegata* (Fig. 3.3). All three species showed more limited carbon isotopic variability than EAC, which was highly variable among reef sites (Fig. 3.3). This is expected given the array of primary producer species that make up the EAC community (Borowitzka et al., 1978; Hatcher and Larkum, 1983; Scott and Russ, 1987). Zooplankton was more $^{15}$N-enriched than the primary producers and varied little both in carbon and nitrogen ranges (Fig. 3.3).

Reef fish isotopic values presented in *delta*-space show the expected pattern of separation of trophic guilds (Fig. 3.3). Native mesopredators (i.e., Nassau grouper *Epinephelus striatus*, black grouper *Mycteroperca bonaci*, and graysby *Cephalopholis cruentata*) occupied the highest trophic positions (highest $\delta^{15}$N values) in the community, followed closely by invasive lionfish. Both invertivore groups have similar nitrogen isotopic composition but differ greatly in their carbon isotopic composition, with migratory invertivores (white grunt

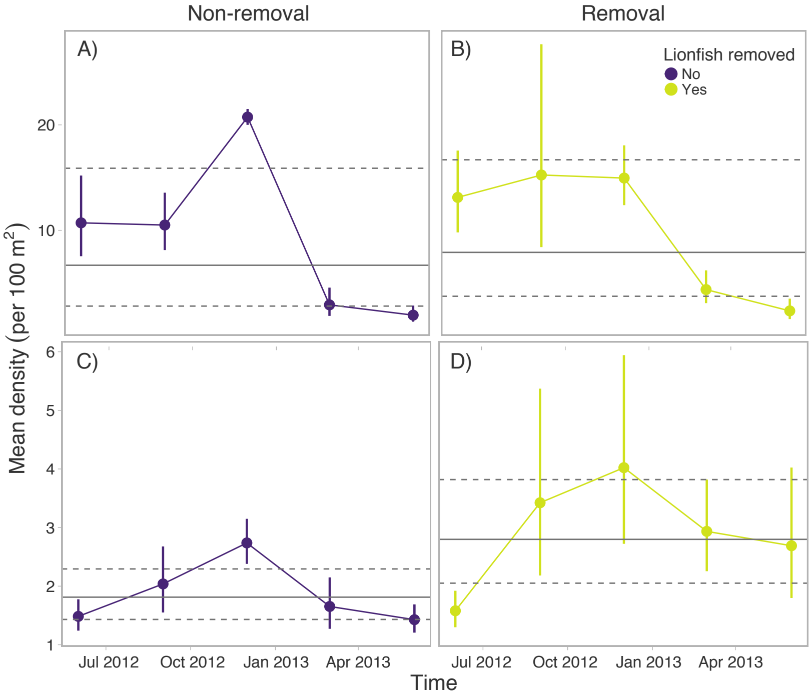

Figure 3.2: Mean density of lionfish (A and B) and native predators (groupers and snappers; C and D) sampled at 16 reef patches in Rock Sound, Eleuthera Island, The Bahamas, from June 2012 to June 2013. Error bars are standard errors. Horizontal solid line indicates mean density over time. Horizontal dashed lines indicate upper and lower 95% confidence intervals around the overall mean. Note the different scales on the Y-axes of the top and bottom panels.

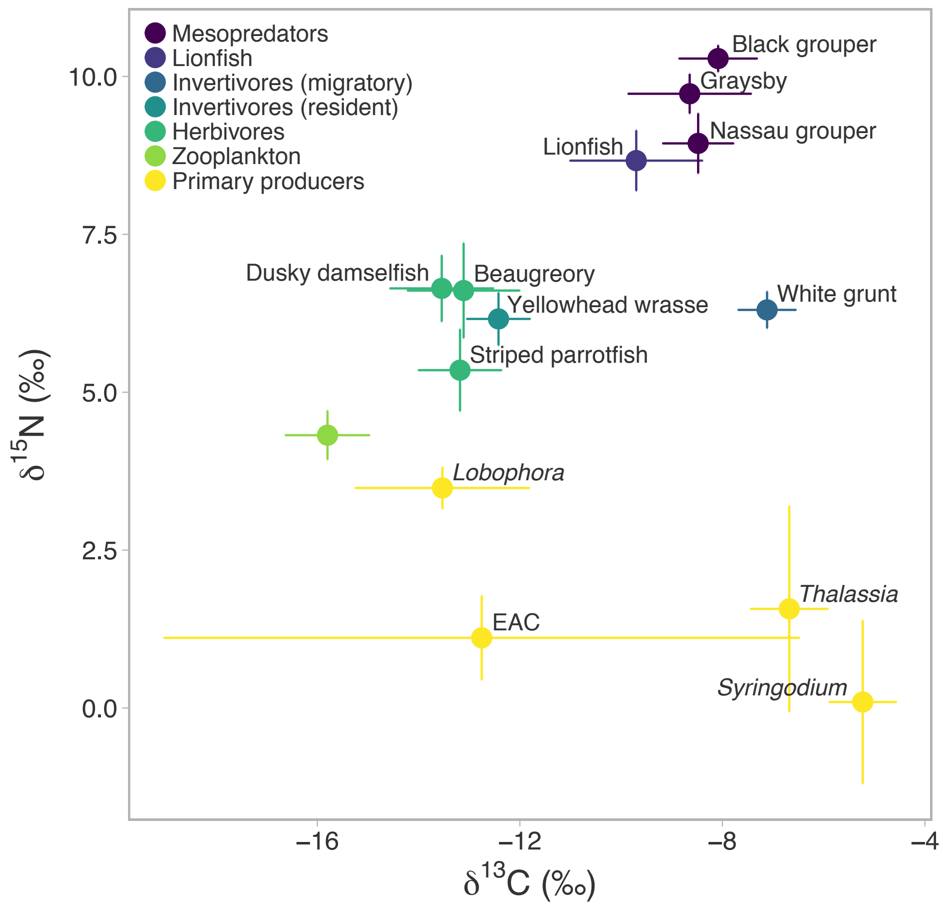

Figure 3.3: Mean stable isotope composition (±1SD) of different reef fish species, zooplankton and primary producers sampled from 16 reef patches off Eleuthera Island, The Bahamas. Sample sizes vary from 16 to 71.

*Haemulon plumierii*) being more $^{13}$C-enriched (∼5‰) than resident invertivores (yellowhead wrasse *Halichoeres garnoti*). Herbivorous fishes overlapped greatly in $\delta^{13}$C values, but dusky damselfish (*Stegastes adustus*) and beaugregory damselfish (*S. leucostictus*) were slightly enriched in $^{15}$N (∼2‰) compared to stripped parrotfish (*Scarus iserti*). Herbivores and resident invertivores overlapped in both $\delta^{13}$C and $\delta^{15}$N values (Fig 3.3).

### 3.4.3 Trophic niche metrics

I found a high probability (0.79-0.90) that the three trophic niche metrics increased with habitat complexity (at sites where lionfish had not been removed; Fig. 3.4). Carbon range increased by a median of 22%, nitrogen range by 23%, and total area by 41% for every unit increase of habitat complexity score. (Note that coefficient effects are median values from posteriors here and throughout the following results section.) All three metrics also decreased with increasing lionfish density (at sites where lionfish had not been removed), with high probability (0.73-0.96) (Fig. 3.4). Carbon range decreased by 3%, nitrogen range by 5%, and total area by 9% for every additional lionfish per 100 $\mathrm{m}^2$. In the invaded range, the highest mean lionfish density reported is ∼4 individuals per 100 $\mathrm{m}^2$, while in my study system I found a mean density of ∼2 lionfish per 100 $\mathrm{m}^2$, with a minimum of ∼1 individual per 100 $\mathrm{m}^2$ and a maximum of ∼6 individuals per 100 $\mathrm{m}^2$. Finally, the value of the three trophic niche metrics decreased slightly − a median of 9% for carbon range, 6% for nitrogen range, and 14% for total area - at sites where lionfish were removed, compared to non-removal sites (for sites with average lionfish density and habitat complexity; Fig. 3.4; probability of decrease = 0.84−0.93). Changes in total area mirrored the changes in carbon range and nitrogen range associated with each predictive variable and showed the strongest probabilities of varying with habitat complexity, lionfish density, and lionfish removal (Fig 3.4; probability = 0.89-0.96).

There was a high probability of a positive interaction between lionfish density and removal on total area (probability = 0.95) and a moderately high probability (0.79 and 0.75) of a positive interaction between these variables on carbon and nitrogen ranges (Figs 3.4, 3.5 top row). The relationship between the three trophic metrics (i.e., carbon range, nitrogen range and total area) and lionfish density was negative when no lionfish were removed (probability = 0.73, 0.83, and 0.96, respectively) but positive when they were removed (probability = 0.70, 0.55, and 0.80, respectively), showing a median increase of 4% for carbon range, 1% for nitrogen range, and 7% for total area.

There were also interactions between lionfish removal and habitat complexity (Fig. 3.4), which had a high probability (0.92) of being negative for carbon range, and total area (probability = 0.90). We can visualize these interactions in Fig. 3.5 (bottom row). The relationship between carbon range and habitat complexity was positive ( median increase of 23%) when no lionfish were removed but negative (median decrease of −26%) when lionfish were culled (Fig. 3.5b). The interaction was similar for total area with a median decrease of 22% when lionfish were culled (Fig. 3.5f). However, there was a weaker interaction for nitrogen range: the relationship between nitrogen range and habitat complexity was positive (probability = 0.80), but only marginally steeper for sites where lionfish were removed with a large median increase of 44% in nitrogen range (probability = 0.68; Fig. 3.5d).

## 3.5 Discussion

The direct predatory impacts of invasive lionfish are now well documented, but the indirect repercussions of this invasion are only beginning to be understood. As in previous studies, I observed higher native reef fish densities, particular of small, prey-sized fish (<15 cm

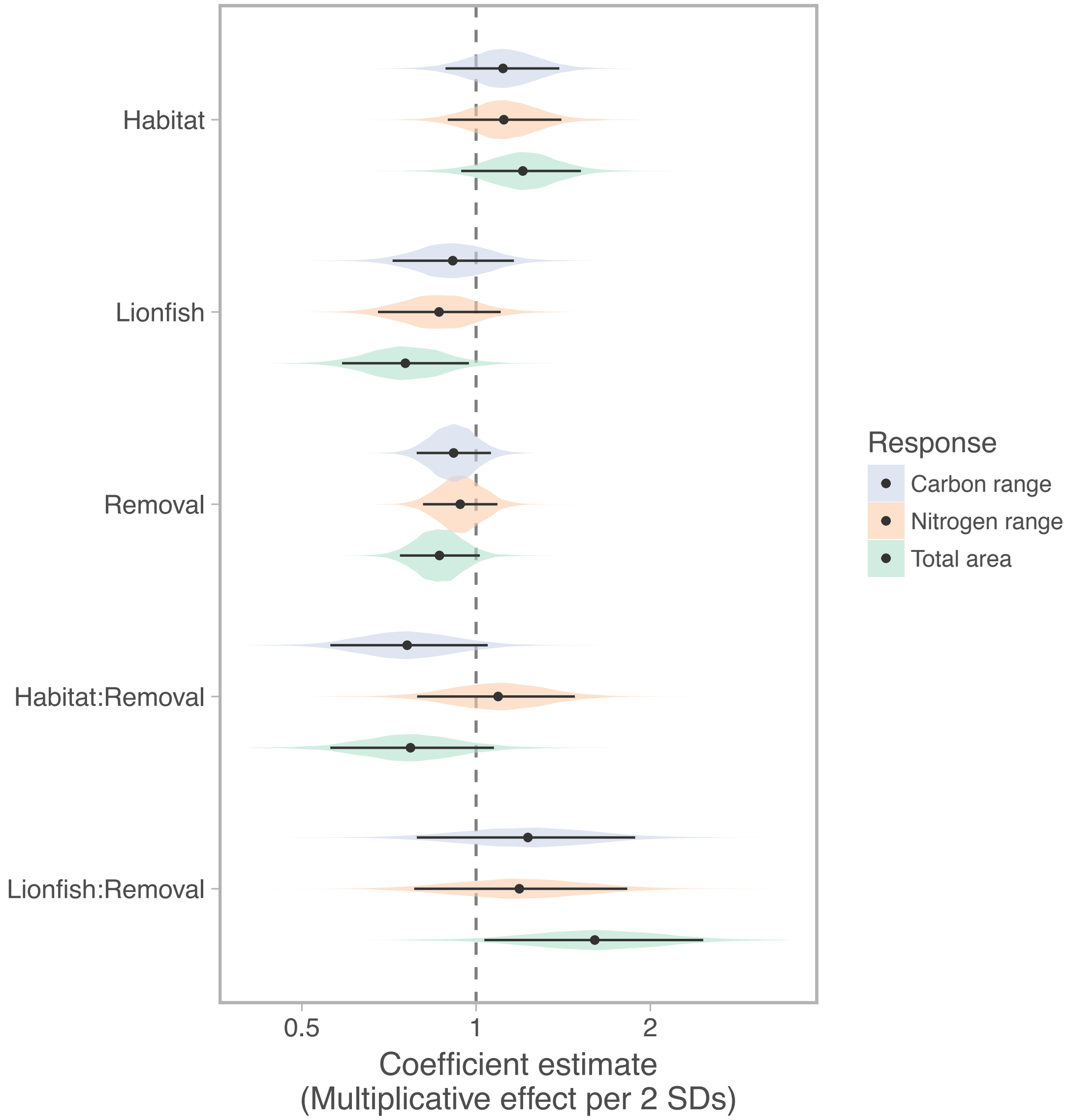

Figure 3.4: Effect of ecological variables (habitat complexity, lionfish density (per 100 $m^2$), and lionfish removal treatment) on trophic niche metrics (nitrogen range, carbon range, and total area) of reef fish communities sampled from 16 reef patches off Eleuthera Island, The Bahamas. Dots represent scaled (divided by 2 SD for continuous variables) parameter estimates. Horizontal bars indicate 90% credible intervals. Violin plots represent posterior density distribution of coefficient estimates. Coefficient estimates represent the exponentiated (multiplicative) effects indicating the respective change a response variable will take if the predictor variable increases by 2 SD for the continuous variables (i.e. habitat complexity and lionfish density), or if lionfish are removed for the lionfish removal variable. Percentage values at the right column represent the probability that a given coefficient is positive or negative (i.e., the multiplicative effect is above or below 1).

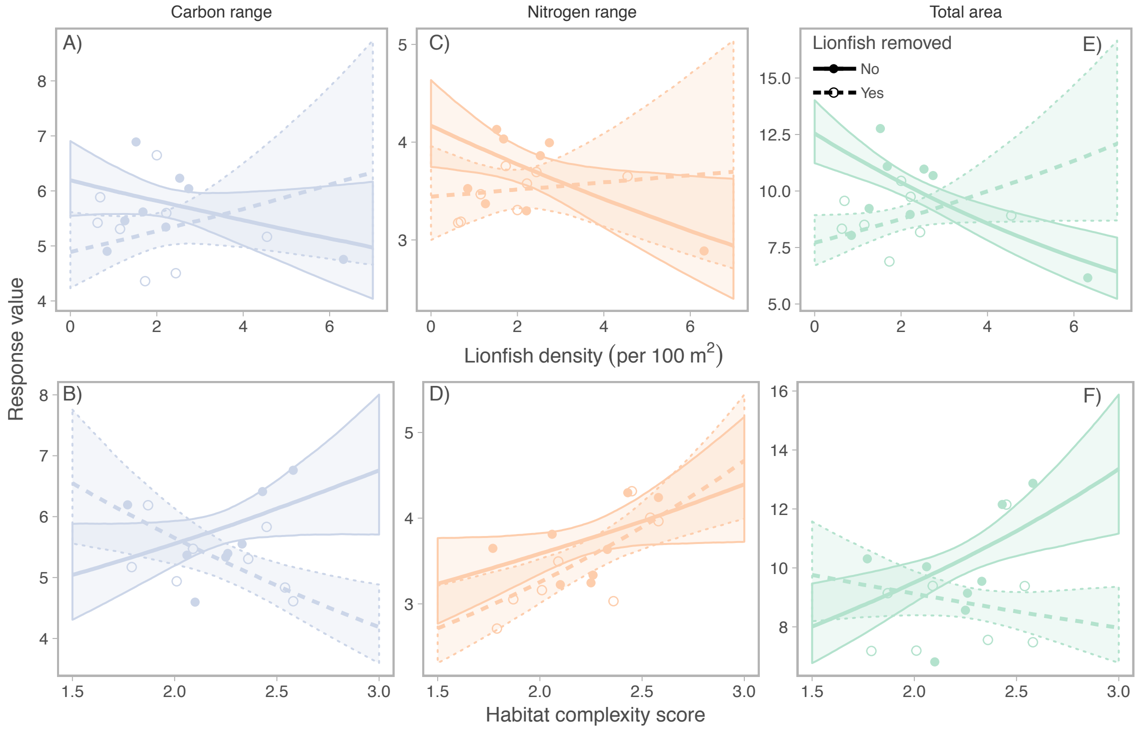

Figure 3.5: Relationships between the continuous predictors lionfish density (top panels) and habitat complexity (bottom panels) with three trophic niche metrics as response variables (i.e. Carbon range (A and B); Nitrogen range (C and D); and Total area (E and F). Relationships are shown for reefs with and without lionfish removal efforts at average habitat complexity (top panels) and lionfish density (bottom panels). Note that the response value of total area (Y-axis, E and F) is in squared values. Points represent observed data, while continuous lines represent fits to each model's predicted values. Shadowed areas indicate 80% credible intervals of model fits.

TL), on patches where lionfish were removed. Although these changes in prey fish densities did not result in detectable changes in reef fish community structure, either between removal treatments or over time, I found evidence of considerable variation in fish community trophic niche metrics. As predicted, carbon range, nitrogen range and total isotopic niche area increased with habitat complexity, and decreased with lionfish density, but only at sites where no lionfish were removed. The observed differences in the trophic niche metrics are consistent with a possible broadening of diet among small reef fishes with habitat complexity and a constricting of diet in response to high levels of lionfish density. Unexpected interactions between habitat complexity, lionfish density, and lionfish removal resulted in positive or negative relationships with the three trophic niche metrics depending on the presence or absence of removals. These interactions suggest lionfish removals are mediating the effect of habitat complexity and lionfish density, probably as a result of changes in lionfish movement and population size structure, and the associated predation and competition interactions with the reef fish community. The overall magnitude of change in carbon and nitrogen ranges was small while changes for total trophic niche area were larger. Some of my estimates have high uncertainty, which warrants cautious interpretation, particularly if extrapolated to other systems. Understanding both the direct and indirect effects of lionfish can help to better assess the true impacts of this invasion at the ecosystem scale.

### 3.5.1 Fish community interactions and trophic processes

Despite the gains in native fish prey density at sites where lionfish were removed, I cannot attribute the observed changes in fish community trophic metrics to shifts in community structure. Changes in community structure (e.g., loss of a group or species or differences in proportions of species within a community) can lead to the loss or addition of trophic interactions between basal resources and primary consumers (Finke and Denno, 2004; O'Connor and Crowe, 2005; Beschta and Ripple, 2009) or between prey and predators (Sharpe and Chapman, 2014; Rodríguez-Lozano et al., 2015). Although there is evidence that changes in community structure can occur as a result of lionfish predation (Lesser and Slattery, 2011; Chapter 2), and that lionfish predation can lead to local species extirpation (Ingeman, 2016), I did not observe such changes in my system and over the time window analyzed. I only found differences in fish density between removal regimes, which alone are not expected to alter trophic interactions. Therefore, other mechanisms should be considered to explain the observed changes to the trophic niche metrics.

Interactions among species in a community are more than just direct consumption interactions (Grabowski et al., 2008; Kéfi et al., 2012). For example, behaviourally mediated indirect interactions can change significantly the way in which species interact (Dill et al., 2003). 'Fear effects', i.e. perceived risk of predation, drive a wide range of predator avoidance behaviours. The mere presence of predators can alter diet selection, the rates at which herbivores forage, and where they forage (Fortin et al., 2005; Catano et al., 2016). In addition, predation risk enhances competition between herbivores sharing similar resources, which affects grazing patterns and associated trophic interactions (Hall and Kingsford, 2016; Davis et al., 2017). Such changes in behaviour can lead to behavioural cascades, akin to trophic cascades, that change the trophic structure and function of food webs (Dill et al., 2003; Fortin et al., 2005; Schmitz et al., 2008; Valeix et al., 2009). Furthermore, these behavioural shifts can occur in response to varying levels of predation (Wirsing et al., 2007; Wirsing et al., 2008; Valeix et al., 2009; Hall and Kingsford, 2016) and habitat complexity (White et al., 2010; Nunes et al., 2015; Catano et al., 2016), the variables that I explored in this study. Therefore, I surmise that the observed trophic niche changes might reflect how the different fish groups are feeding, coping with competition or avoiding predation, associated with lionfish predation pressure and habitat complexity gradients.

### 3.5.2 Lionfish removals and demographic processes

At first glance, it seems puzzling that lionfish density and lionfish removal treatment had interactive effects on fish community trophic niche metrics. I included both factors in my analysis because they were not highly correlated. How could lionfish removals not be closely linked to lionfish density? The answer may lie in the frequency of removals. Culling lionfish is effective to lower lionfish numbers in the short term (Green et al., 2014; Smith et al., 2017). However, sites where lionfish are removed infrequently (such as ours, where removals occurred quarterly) have high lionfish recolonization rates (Smith et al., 2017,) because lionfish tend to relocate from high-density to lower-density (i.e., culled) sites (Tamburello and Côté, 2015). Thus, removal sites become lionfish 'sinks', with quarterly pre-culling densities that are equivalent to those of non-removal sites.

The predation dynamics are likely different on patches where lionfish are and are not removed. At the no-removal sites, lionfish densities are relatively stable and lionfish predation pressure is constant over time, whereas at removal sites, pulses of low predation pressure when lionfish are culled are followed by increasing predation pressure as patches are recolonized. Moreover, lionfish of small and intermediate sizes are most likely to migrate between reef patches due to density-dependent processes (Tamburello and Côté, 2015), and these smaller lionfish appear to have different dietary preferences than larger individuals (Chapter 2). Therefore, temporal variation in lionfish numbers as well as potential differences in lionfish size class prevalence between removal and non-removal sites might result in different competitive processes between native predators and lionfish as well as different predator-prey interactions. These processes, in combination, could account for the different effects observed between removal and no removal sites on the trophic metrics studied.

Below, I consider more specifically the mechanisms that could lead to the interactions of removals with lionfish density and habitat complexity.

### 3.5.3 Lionfish density effect on community trophic niche

I observed reductions in community-wide carbon range with increasing lionfish density, at sites where lionfish were not removed. The native fish community at these sites therefore appears to be exploiting a narrower range of primary producer sources when lionfish density is high. Under high risk of predation, consumers sometimes forage more indiscriminately - and hence have a broader carbon range - if they have to reduce their foraging time to reduce their exposure to risk [e.g.,(Catano et al., 2014)]. Alternatively, consumers can shift to safer foraging areas or times of day and be able to specialize on the most profitable prey or plant available, which narrows the carbon range used (e.g., Zandonà et al., 2011). My results suggest that relatively more species in the fish communities I studied might be doing the latter rather than the former on reefs where lionfish are abundant. Interestingly, early studies concluded that native Atlantic prey fish did not appear to recognize invasive lionfish as a potential predator (Marsh-Hunkin et al., 2013; Kindinger, 2015). However, herbivore fishes and particularly Caribbean parrotfish now do respond to lionfish presence by lowering their grazing rates, lowering their algae consumption and, presumably, altering their selectivity (Eaton et al., 2016; Kindinger and Albins, 2017).

I also observed community-level declines in nitrogen range, suggesting relatively shorter food chains with increasing lionfish densities at sites where lionfish were not removed. Yet, this change occurred in the absence of detectable changes in prey community structure. A different behavioural mechanism is likely to underpin this pattern: competition among predators. Competition between predator species can have variable outcomes: it can lead to trophic niche partitioning (Hayden et al., 2013; Matich et al., 2017) or to trophic niche expansion (Bolnick et al., 2007; Svanbäck et al., 2008; Cachera et al., 2017), and it is currently unclear what determines the direction of change. A novel predator added to a community of diverse native predators can also increase competition, resulting in variable changes in trophic niches of native predators (Sharpe and Chapman, 2014; Rodríguez-Lozano et al., 2015). In the case of lionfish, there is evidence of competition (O'Farrell et al., 2014; Curtis et al., 2017), and niche partitioning (Layman and Allgeier, 2012) between the invader and native predators. Niche partitioning also seems to occur between lionfish of different sizes (Chapter 2). A possible mechanism that could explain the nitrogen and total trophic niche area patterns observed is that larger lionfish occur at sites where lionfish were not removed (see subsection below; Smith et al., 2017). These larger individuals feed preferentially on fish (Morris and Akins, 2009), which depletes fish resources and lead native predators to exploit alternative prey at lower trophic levels (e.g., more invertebrates), resulting in a reduced community-wide nitrogen range which in turn drives a shrinking trophic niche area. A similar mechanism has been invoked to explain reductions in trophic niche area at the community level as a result of interspecific competition with invasive species in freshwater decapods and Mediterranean fishes (Fanelli et al., 2015; Jackson et al., 2016).

Surprisingly, lionfish removals seem to be mediating lionfish density effects. I believe that changes in lionfish size structure towards smaller fish as a result of removals (Smith et al., 2017), and associated changes in predation and competition effects, could reverse (in the case of carbon range and total area) or slightly dampen (in the case of nitrogen range) the relationships between niche metrics and lionfish density. Removing invasive species can produce such drastic effects. For example, Nigro et al. (2017) found that removing invasive rats on tropical islands produced a dramatic widening of the trophic niche of native crabs. While their study did not account for variability in invasive rat density it shows the changes in trophic interactions that can result from eliminating the impacts of strong predation and/or competition on native species.

Ultimately, it remains possible that there were, in fact, changes in prey community structure as a result of lionfish predation that I did not detect. Such predatory impacts could explain the negative relationships observed between trophic niche metrics and lionfish densities (Albins and Hixon, 2008; Green et al., 2012). If lionfish removals reverse changes to prey community structure (Green et al., 2014; Smith et al., 2017; but see Dahl et al., 2016), this would also explain why the negative effect is dampened (for nitrogen range) or reversed (for carbon range and total area) when removals are implemented. Additional studies are needed to confirm whether lionfish predation is having an effect on both fish community structure as well as on the structure of food webs of invaded coral reefs.

### 3.5.4 Habitat complexity effect on trophic niches

As expected, the ranges of carbon and nitrogen, as well as total trophic niche area, increased with habitat complexity on reefs where lionfish were not removed. Higher complexity is thought to increase basal resource availability (i.e. carbon range), for example by providing more substrate for primary producers (Diehl, 1992; Persson et al., 1992; Kondoh and Ninomiya, 2009; Darling et al., 2017), which in turn allows organisms at more, different trophic levels to co-occur (i.e., wider nitrogen range; Wang et al., 2016). It is also possible that increasing habitat complexity changes predator-prey dynamics by providing prey more opportunities to hide from predators (Beukers and Jones, 1998; Forrester and Steele, 2004; Nunes et al., 2015), and/or predators more opportunities to stalk and capture prey (Catano et al., 2016). Such behavioural changes can increase or decrease trophic interactions between prey and predators, leading to trophic niche shifts in generalist fish (Vejříková et al., 2017), and changes in the structure and function of food webs (Grabowski, 2004; Finke and Denno, 2006; Stephen Gosnell et al., 2012; Bellmore et al., 2015).

My results suggest that lionfish removal is also mediating habitat complexity effects. The relationship between habitat complexity and both carbon range and total trophic niche area was reversed on reefs where lionfish were removed compared to reefs where no removals occurred. On removal sites the abundance of smaller lionfish (Smith et al., 2017) could result in lower predation pressure on fish as a result of the preference of smaller lionfish for invertebrates (Morris and Akins, 2009). I argued earlier that in this system, lower predation risk appears to be associated with greater foraging selectivity and a reduced community-wide carbon range. In contrast to its effect on carbon range, removing lionfish did not change the relationship between nitrogen range and habitat complexity, which suggests that this relationship is not sensitive to the changes in lionfish population dynamics caused by lionfish removals.

### 3.5.5 Ecological implications

My study points to the importance of assessing not only the direct consumption effects of invasive species, but also their broader impacts on fish community structure and ecosystem processes. In the context of global change, it is necessary to understand how different disturbances will affect species interactions at the community level. While a growing body of literature exists on impacts of disturbances on trophic niche metrics, no general patterns have yet emerged, and it is clear that different mechanisms could lead to increases or declines of these metrics under different natural and anthropogenic processes. Furthermore, more studies are needed to understand how changes in trophic niche metrics translate (or not) into changes in ecosystem function. In the context of the impacts of the lionfish invasion, while some of my results have high uncertainty, they suggest tantalizing patterns that point to complex consumption- and behaviour-mediated effects of predation on trophic niche metrics on invaded reefs. My study shows that the lionfish invasion has effects that go far beyond reductions in abundance, which should be considered when assessing the larger-scale impacts of this invasion.

# Chapter 4

# Heterogeneous attitudes of tourists towards lionfish in the Mexican Caribbean: Implications for invasive species management [1]

## 4.1 Abstract

Indo-Pacific lionfish (*Pterois volitans* and *P. miles*) are invasive predators established throughout the Wider Caribbean. They have already caused significant ecological impacts and have the potential to affect local economies that depend on coral reefs. Snorkeling and scuba diving are important activities that rely on aesthetically pleasant reefs. I asked whether lionfish-invaded reefs have lower aesthetic value and whether fees to help control the invasion might be acceptable to recreational divers and snorkelers in the Mexican Caribbean. To do so, I conducted a choice experiment in which tourists were asked to indicate their preferences for coral reef images with varying attributes that can be affected by lionfish. I specified a priori two classes of respondents, i.e. snorkelers and divers, but two latent classes of recreational divers (casual vs. committed) emerged on the basis of their preferences. Tourist age, commitment to snorkeling /diving, and lionfish awareness explained class membership. Casual divers and snorkelers preferred reefs with lionfish and accepted their impacts on the reefs. In contrast, committed divers disliked lionfish and associated impacts, and would elect to dive elsewhere if such impacts were high. Casual divers and

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[1] A version of this chapter appears as, Malpica-Cruz, L., Haider, W., Smith, N.S., Fernández-Lozada, S., Côté, I.M. 2017. Heterogeneous attitudes of tourists towards lionfish in the Mexican Caribbean: Implications for invasive species management. Frontiers in Marine Science. 4:138.

snorkelers preferred options with low lionfish control fees, while committed divers were willing to pay high fees. My results indicate potential economic impacts of the lionfish invasion in regions that depend on reef-related tourism, and that lionfish control fees might be acceptable to some but not all recreational users. However, because all tourists favored to a greater extent reef features that can be affected detrimentally by lionfish than they favored lionfish themselves, I predict that managing the lionfish invasion should be beneficial to the local reef tourism industry.

## 4.2 Introduction

Understanding how human activities impact coral reefs and devising management strategies that effectively maintain the goods and services provided by these ecosystems are two key challenges to coral reef conservation (Naeem et al., 1999; Loreau et al., 2001; Hughes et al., 2005). Coral reefs are ecologically complex and species-rich ecosystems that provide many ecosystem services, including food provisioning (Russ 1991), flood protection (Guannel et al., 2016), medicines (Faulkner and Fenical 1977), and opportunities for sustainable job creation via ecotourism, particularly in 'developing countries' (i.e., the 'global south'; Moberg and Folke, 1999). Multiple natural and anthropogenic stressors - that is, acute or chronic disturbances that affect ecosystem function (Hughes and Connell, 1999) - are currently affecting coral reefs. Climate change, habitat destruction, coastal and watershed development, overfishing, and invasive species all threaten the productivity, diversity and, in extreme cases, the survival of these ecosystems (Moberg and Folke, 1999; Jackson et al., 2001; Hughes et al., 2003; Hoegh-Guldberg, 2011).

Whatever the cause of stress, degraded coral reefs (i.e., reefs with reduced biological diversity, coral cover and structural complexity) have lower aesthetic value (Dinsdale, 2009; Gill et al., 2015; Haas et al., 2015). This change can adversely impact non-extractive ecotourism activities, such as recreational snorkeling and diving, which depend on the 'beauty' of coral reefs (Cesar et al., 2003; Charles and Dukes, 2007; Pejchar and Mooney, 2009), particularly in small-island states where tourism can generate up to 50% of gross domestic product (European Commission, 2002; Cesar et al., 2003). Environmental valuation methods have been used to assess the aesthetic value of coral reefs and the socioeconomic impact of stressors on these systems (White et al., 2000; Brander et al., 2007; Rodrigues et al., 2015). Calculating tourist willingness-to-pay (WTP) for conservation management interventions on reefs is a common technique with which tourists are directly asked how much they would be willing to pay for a good (e.g., seeing a sea turtle on a dive) (Depondt and Green, 2006; Casey et al., 2010; Emang et al., 2016). Common environmental valuation methods used to estimate tourist WTP include contingent valuation and Discrete Choice Experiments (DCE), which have been used to assess the economic value to marine tourists of certain coral reef attributes (Schuhmann et al., 2013; Gill et al., 2015; Shideler and Pierce, 2016). In DCEs, survey respondents are typically asked to choose between different bundles of environmental characteristics (i.e., the 'attributes'), which are described in terms of different levels (Inglis, 1999; Leon et al., 2015). This approach combines characteristics of 'theory of value' and 'random utility theory' from economics (Lancaster, 1966; Manski, 1977; Louviere et al., 2002), to estimate the overall 'utility' (i.e., sense of satisfaction) associated with a good. When applied to the non-extractive value of coral reefs for recreation, the focus is usually on the diving/snorkeling experience (i.e., the 'good') of respondents. In general, valuation methods reveal that divers are attracted to areas with 'intact' and species-rich environments (Rudd and Tupper, 2002; Uyarra et al., 2005; Schuhmann et al., 2013). Divers also generally prefer dive site attributes such as clear water and warm temperatures (Uyarra et al., 2005), the presence and abundance of species (Rudd and Tupper, 2002; Uyarra et al., 2005; Schuhmann et al., 2013), small diving group size and restricted site access to manage impacts on dive sites (Inglis, 1999; Leon et al., 2015), all of which contribute to a positive experience.

Some reef stressors can, however, skew diver and snorkeler perception of coral reef health, which usually matches remarkably well ecological measures of integrity (Uyarra et al., 2005; Dinsdale, 2009; Gill et al., 2015; Haas et al., 2015; Rodrigues et al., 2015). This is the case of invasive species, which can change local species composition, alter ecosystem processes, and negatively affect ecosystem services (Andersen et al., 2004; Blackburn et al., 2011). The addition of one or more invasive species to an ecosystem artificially enhances local richness (Thomas and Palmer, 2015), a key feature in diver and snorkeler satisfaction (Rudd and Tupper, 2002; Uyarra et al., 2005), and the impacts of invaders might not be noticeable, at least to first-time visitors.

In this study, I focus on the Indo-Pacific lionfish (*Pterois volitans* and *P. miles*). These species have colonized most of the western Atlantic, Gulf of Mexico and Caribbean (Schofield, 2009) where, through predation, they have substantially reduced recruitment, abundance and diversity of native reef fish on coral reefs (Albins and Hixon, 2008; Albins, 2012; Green et al., 2012). By preying on herbivorous fish, lionfish can trigger trophic cascades that culminate in benthic community shifts from coral- to algal-dominated reefs (Lesser and Slattery, 2011). Lionfish can also potentially compete directly for prey with native predators (Albins and Hixon, 2011). The detrimental ecological impacts of lionfish on coral reef features known to be important to dive tourism, such as the abundance and diversity of fishes (Albins and Hixon, 2008; Green et al., 2012) and the abundance of corals (Lesser and Slattery, 2011), could lead to adverse socioeconomic impacts on the industry. However, the addition of a relatively large (up to 45 cm in length), arguably attractive (Moore, 2012), and easily observable species to Caribbean reefs might instead be deemed an asset by tourists.

My study had three objectives. First, I evaluated the appeal of coral reefs to marine tourists presented with different lionfish invasion scenarios in the Cozumel Reefs National Park, Mexico. Second, I evaluated whether control fees implemented to reduce lionfish numbers might be acceptable to tourists engaging in snorkeling and diving. Lastly, I explored the attitudes of tourists engaged in different underwater activities (i.e., snorkeling vs scuba diving) towards various hypothetical invasion and management scenarios. Diving and snorkeling tourists are expected to seek areas with the highest aesthetic value (Rudd and Tupper, 2002; Uyarra et al., 2005). I therefore predicted that, as the ecological impacts of lionfish invasion became evident, tourists would be deterred from visiting highly impacted areas. Furthermore, I expected that the reef preferences and support for lionfish control fees of tourists might increase with their experience level and pro-environmental attitudes (Luo and Deng, 2007; Nisbet et al., 2009). I tested these predictions with a discrete choice experiment and latent-class analysis to assess diver and snorkeler preferences, and intended behavior. Then, I developed a decision support tool using the latent class model results, which I used to simulate tourist behavior under possible future scenarios of lionfish invasion. This study provides a novel contribution to our understanding of the potential socioeconomic impacts of the lionfish invasion beyond the widely reported ecological impacts.

## 4.3 Methods

I conducted my experiment in Cozumel, Mexico. Cozumel has a reputation as a world-class diving destination and tourism associated with diving and snorkeling is an important source of revenue for the region. Lionfish were first reported in Cozumel in 2009 (Schofield, 2009; 2010) and their densities are now high ($\sim$250 fish ha$^{-1}$; Sosa-Cordero et al., 2013). Lionfish numbers in Cozumel are controlled non-systematically, through haphazard removals by dive guides, yearly lionfish tournaments (derbies) (Abelardo Brito, pers. comm.), and artisanal fishing whereby some fishers target lionfish as an alternative during lobster season closures in areas adjacent to the Cozumel Reefs National Park (Eduardo Pérez Catzim, pers. comm.). I interviewed tourists visiting the Cozumel Reefs National Park during the peak tourist seasons (July, August and December) in Cozumel in 2014. I targeted two groups: 1) tourists that engaged in recreational snorkeling, and 2) tourists that engaged in recreational SCUBA diving. I refer to these groups as ‘snorkelers’ and ‘divers’, respectively.

### 4.3.1 Discrete Choice Experiment design

I assessed the intended behavior of snorkelers and divers using a Discrete Choice Experiment (DCE), which is a multivariate method that aims to identify the drivers of an individual’s

Table 4.1: Attributes and corresponding levels used in the Discrete Choice Experiment (DCE). A description of the attributes and estimation of levels is included, as well as data sources. DCE denotes levels used for Discrete Choice Experiment design and choice sets preparation; LC indicates the values of levels once linearized or combined for latent-class model analysis (see 'DCE data analysis' subsection in the 'Methods' for further details on the linearization procedure).

| **Attribute** | **DCE levels** | **LC levels** | **Description and Justification** | **Data source** |
|---|---|---|---|---|
| Lionfish density | 0 | 0 | Densities based on current (2014) local estimates and population increases based on published data | Green et al. (2014); Hackerott et al. (2013); Sosa-Cordero et al. (2013) |
| | 1 | 1 | | |
| | 10 | 10 | | |
| | 25 | 25 | | |
| Control fee (USD) | \$0 | \$0 | Levels based on reports from areas where fees to dive in Marine Protected Areas have been implemented | Green and Donnelly, (2003) |
| | \$5 | \$5 | | |
| | \$10 | \$10 | | |
| | \$15 | \$15 | | |
| Grouper density | 0 | -1.31 | Estimated local densities and potential lionfish impacts based on existing data | Hackerott et al. (2013), Smith et al. (2017) |
| | 1 | -0.56 | | |
| | 2 | 0.19 | | |
| | 4 | 1.69 | | |
| Reef shark | Absent | Absent | 1 shark visible in Present scenario, based on personal experience (LMC) | - |
| | Present | Present | | |
| Coral cover | < 5% | 5-15% | Status quo based on local and regional surveys; levels chosen arbitrarily | García-Salgado et al. (2008) |
| | 10-20% | 35-75% | | |
| | 30-40% | | | |
| | 70-80% | | | |
| Reef relief | 1.4 | -1.5 | Levels estimated using a digital version of the consecutive substratum height difference methodology after McCormick (1994) | - |
| | 1.6 | -0.5 | | |
| | 1.8 | 0.5 | | |
| | 2 | 1.5 | | |
| Prey fish density | 44 | -1.43 | Estimated local densities and potential lionfish impacts based on existing data | Green et al. (2014), Smith et al. (2017) |
| | 74 | -0.44 | | |
| | 96 | 0.29 | | |
| | 135 | 1.57 | | |
| Excursion price change | -15% | -1.50 | Levels chosen arbitrarily, relative to average trip costs across Cozumel dive shops in 2014 ($50and100$ USD for snorkeling and diving trips, respectively) | - |
| | -5% | -0.30 | | |
| | 0% | 0.30 | | |
| | +10% | 1.50 | | |

choice behavior - in this case, their choice of hypothetical coral reefs to visit. Random utility theory (RUT) is the basis of the DCE approach. It postulates that the total 'utility' (i.e., sense of satisfaction) of a given alternative is a function of its deterministic and random components (McFadden, 1974; Ben-Akiva and Lerman, 1985). Based on RUT, the utility of a good chosen by individual $n$ can be described by the function $U_in = V_in + \epsilon in$, where $U_in$ is the overall utility of a good $i$, which is composed of $V_in$, a deterministic vector of attributes, and $\epsilon_in$, the random component of an individual's choice. An alternative i is chosen over alternative $j$ if $U_in > U_jn$ for all $j \neq i$. In other words, RUT assumes that individuals always act to maximize their utility or sense of satisfaction. I first defined the snorkeling or diving experience in Cozumel as the overall good. I then selected an array of environmental, economic and management attributes, with their respective levels, to create different reef profiles. Different combinations of scenarios with varying attribute levels constituted the choice sets presented to respondents.

I created coral reef profiles and choice sets by using a 420 orthogonal fractional factorial design, which allowed the systematic variation of all coral reef attribute levels in the choice sets (see Raktoe et al., 1981). The DCE consisted of 120 scenarios in 60 choice sets. Each scenario contained eight attributes presented in text or photographs, and each attribute had one of either two or four levels. The attributes described ecologically realistic aspects of the reef environment based on empirical data from the invaded range. Specifically, the attributes presented in digitally calibrated photographs included: lionfish density, native grouper density, native prey fish densities, reef relief, percentage coral cover, and the presence or absence of a Caribbean reef shark. Two attributes were presented in the text: a hypothetical lionfish control fee (in USD, to assess tourist willingness to pay the cost of removing lionfish), and percentage change in a hypothetical excursion price (Table 4.1). I digitally calibrated photographs of coral reef attributes in Adobe Photoshop CS5 (Table 4.1, Fig. C.1). Digitally calibrated images are powerful tools to represent complex systems (Orland et al., 2001). They have been used repeatedly in choice experiments (e.g. Arnberger and Haider, 2007; Landauer et al., 2012; Ryffel et al., 2014), and they present choice attribute levels in a format that is easy for respondents to evaluate (Bateman et al., 2009). During DCE construction I excluded scenarios that contained ecologically unrealistic combinations of attributes such as reefs with very high densities of lionfish and native predators, but very few prey fish, low coral cover and low vertical relief. I also always presented choice sets where the alternative with the most expensive control fee included at least one high-value of an ecologically desirable attribute (e.g., high native predator density) to ensure that the scenarios were realistic (Reed Johnson et al., 2013). My final experimental design had a D-efficiency score of 87.95.

### 4.3.2 Survey design and implementation

My survey consisted of four main sections: 1) questions to assess satisfaction with diving/snorkeling excursion; 2) questions to assess snorkeling/diving experience as well as environmental and lionfish invasion awareness; 3) questions to establish the socio-demographic characteristics of respondents; and 4) the DCE to determine tourist reef preferences under different lionfish invasion scenarios. While the fact that lionfish are invasive to the Caribbean was mentioned in the survey, there was no mention of the ecological impacts reported for this invasion. Prior to conducting my study, I tested (and subsequently modified) my survey questions and DCE in focus groups comprising coral reef ecologists, recreational dive shop owners, and tourist divers. I administered the DCE to respondents on electronic tablets using a web-based survey (fluidsurveys.com). I selected only adult respondents (i.e., 18 years or older) and administered only one survey per group to minimize pseudoreplication. I approached respondents haphazardly at the Cozumel International Airport in summer, and at dive stores, and dive tour docks in winter, immediately after their return from a diving/snorkeling outing. I asked whether respondents had engaged in snorkeling or diving in Cozumel, and people responding in the affirmative were invited to participate in my questionnaire. Each choice set presented consisted of a pair of hypothetical coral reef locations (Fig. C.1). Each choice set also included the option "not to dive on either reef if these were the only two reef sites available", to estimate potential economic losses to the local snorkeling and diving industry. I asked respondents to choose one of the two locations described or neither of them. Each respondent evaluated six choice sets.

Avidity bias is important to consider when studying visit behavior or recreational demand since probability distributions might differ between more frequent users and the general population (Moeltner and Shonkwiler 2005; Hynes and Greene 2013). I did not specifically ask respondents how many times they had visited Cozumel in the past. However, I did ask whether they had been to Cozumel before the arrival of lionfish in 2009. Approximately 39% of respondents had done so. This hints at a high return rate of snorkelers and divers to Cozumel, but is in line with the high level of loyalty (i.e., > 40% repeat visitors) reported by the Ministry of Tourism for Cozumel tourists in general (SECTUR 2009).

### 4.3.3 DCE data analysis

Based on RUT, it is possible to explain the behavior of respondents by estimating the probability of choosing alternative $i$ over $j$ for utility $V$:

$$Prob\left\{i \text{ chosen}\right\} = prob\left\{V_i + \epsilon i > V_j + \epsilon j; \forall j \in C\right\} \tag{4.1}$$

where $C$ is the set of all possible alternatives. Choice models can be analyzed using a multinomial logit model (MNL; McFadden, 1974; Boxall and Adamowicz, 2002; Train, 2003) to produce regression estimates (i.e., part-worth utilities) for each attribute, which when combined represent respondent choice probability $P$ as a whole:

$$P(i \mid i \epsilon M) = \frac{exp(X_{i,\beta})}{\sum_{j=M} exp(X_{j\beta})} \tag{4.2}$$

where $(M)$ indicates all scenarios present, $X$ is the vector of explanatory variables, and $\beta$ is the parameter vector to be estimated. I followed a mixed logit form extension of the MNL, the latent-class model (LCM), which explains preference heterogeneity in respondent choice. In latent-class models it is possible to estimate separate sets of choice model parameters for each latent class $c$, which will account for preference heterogeneity within one statistical model:

$$P(\text{choice } j \text{ by individual } n \text{ in choice situation } t \mid \text{class } c) = \frac{exp(X_{nt,j\beta_c})}{\sum_{j=M}^{J_n} exp(X_{nt,j\beta_c})} \tag{4.3}$$

where $\beta$ is the class-specific vector of the $jth$ alternative, chosen among $J_i$ alternatives by individual $n$ observed in $T_i$ choice situations, $i$ and $j$ (Eq. 4.1), $M$ and $X$ (Eq. 4.2) are defined above (see (Greene and Hensher, 2003), and (Morey et al., 2006) for a detailed explanation of LCM). Thus, the latent-class model divides the sample into classes characterized by relatively homogeneous within-class preferences, assessing the probability that individuals belong to a certain class as a function of their unobserved social, attitudinal and motivational characteristics (Birol et al., 2006).

I used the software Latent GOLD 4.5 (Vermunt and Magidson, 2005) to analyze the DCE results using a LCM analysis following the three-file system procedure. Given the need to better understand how management strategies affect different user groups (Légaré and Haider, 2008), I analyzed the DCE responses using (1) a MNL on all responses (Table C.1), (2) latent-class models LCM, exploring different number of classes (however models >2 classes did not converge so were not explored further; Table C.2) and (3) a modified latent-class analysis (Table C.3) that included two known classes defined a priori (i.e., snorkelers and divers) because of expected differences in motivation and behavior (Vermunt, 2003; Vermunt, 2008). I will refer to the latter model as the segmentation model. During model exploration, I used effects coding to examine the levels for all attributes, and I also examined the linear effects of continuous attributes (i.e., grouper and prey densities, reef relief, excursion price). The latter was done because levels of these continuous variables were not equidistant. To linearize attribute levels, I centered each level by subtracting from

Table 4.2: Hypothetical scenarios tested using the Decision Support Tool (DST). Status quo represents estimated attribute levels or linearized values for Cozumel reefs in 2014. No-management scenarios tested comprised a short (2 years) and long (5 years) time horizon with no management actions to control lionfish. The management scenario entailed the hypothetical implementation of a lionfish control fee charged to visitors during their diving or snorkeling trips. See Methods for full description of attributes, respective levels and experiment design.

| | | **No management** | | **Management** |
|---|---|---|---|---|
| Attributes | Status quo | ∼2 yr | ∼5 yr | Control fee |
| Lionfish density | 1 | 10 | 25 | $5 |
| Control fee (USD) | $0 | $0 | $0 | $5 |
| Grouper density | 1 | 1 | 0 | 1 |
| Reef shark | Absent | Absent | Absent | Absent |
| Coral cover | 5-15% | 5-15% | 5-15% | 5-15% |
| Reef relief | 1.8 | 1.8 | 1.8 | 1.8 |
| Native prey density | 96 | 74 | 44 | 74 |
| Excursion price change | 0% | 0% | 0% | 0% |

it the overall mean level value for that attribute, and then divided the centered value by the average interval between each pair of successive levels (Table 4.1). Lionfish density and control fee were not linearized because I were specifically interested in the effect of each specific level of these two attributes, rather than in the average effect across attribute levels. Given that control fee values could be correlated with lionfish numbers or with the reef attributes likely to be affected by lionfish management, I explored solutions with interacting attributes; however, these resulted in non-converging, uninformative models, which were not explored further. I used the BIC (Bayesian Information Criterion), and AIC (Akaike Information Criterion) as information criteria indicators to select the most parsimonious model, which is reflected by the lowest values of all of these indicators (Akaike, 1974; Vermunt and Magidson, 2005, p. 88). The segmentation model with the lowest information criteria indicators included linearized attribute levels.

Using Latent Gold, I then added to the most parsimonious model 15 covariates that could explain class membership. I obtained these covariates from survey sections 1-3. Sociodemographic covariates included general demographic information such as gender, country of residence, age groups (in three categories: 19-35, 35-50, and >50 years), yearly income (<20,20-39, $40-59$,60-79, $80-99$,100-149, $150-250, and$ >250, figures in thousands USD) and education (high school or less, trade technical or college education, university degree and postgraduate degree). I also explored covariates reflecting motivation and engagement in snorkeling or diving (i.e., number of snorkeling/diving trips per year, certification level, total number of logged dives, number of tropical regions of the world visited to snorkel/dive, ownership of snorkeling or diving equipment), and commitment to snorkeling/diving (assessed through a question asking the annual frequency and engagement level with snorkeling/diving). I explored perception covariates such as owning field identification guides, knowledge and involvement in environmental causes, awareness of invasive species and impacts, and awareness of the lionfish invasion and related impacts. Lastly, I assessed tourist satisfaction with their trip to Cozumel using a five-point Likert scale. To minimize the number of dimensions, related covariates (e.g., motivation and engagement in snorkeling/diving) were incorporated as principal components derived from a Principal Component Analysis (PCA). I kept in my final model only significant explanatory covariates that helped us to describe class membership (Vermunt and Magidson, 2005). Once I obtained my final model, I identified significant differences in part-worth utilities between attribute levels by interpreting z values, and between classes by using Wald II statistics (Vermunt and Magidson, 2005, p. 88).

Differences between the socio-demographic characteristics of respondents surveyed in the summer and winter months were assessed using unpaired t-tests. I evaluated the significance of these differences against a Bonferroni-adjusted critical alpha level of 0.014 (unadjusted alpha of 0.1/7 tests performed) to account for multiple testing (Armstrong, 2014) in R version 3.3.2 (R Core Team, 2016).

### 4.3.4 Assessing tourist support for lionfish management scenarios

I used the results of the DCE and segmentation model analysis to develop a Decision Support Tool (DST), in which the demand for different scenarios could be estimated for each tourist group based on segmentation model parameters. Such a tool can be used to estimate tourist support for hypothetical management scenarios - in this case, I modeled tourist support for various options to control lionfish density. To do this, I used the part-worth utility values from each attribute for each class in Equation 4.2 and then estimated the choice probability for a given class under a given scenario. The resulting values are probabilities interpreted as percentage of support by a class for a scenario (i.e., a given set of attribute levels), which I refer to as market shares (Hensher et al., 2005; Vermunt and Magidson, 2005). I structured my DST in the same way as the choice sets in the survey, thus estimating the probability of choice between two hypothetical alternatives (e.g., status quo and management actions) and neither of the two (i.e., dive elsewhere). By changing the levels for relevant attributes in each of the scenarios, one can calculate the likelihood of choice for many possible situations that could arise as lionfish continue to invade the region and management actions are implemented or not. Changes in probabilities based on the different part-worth utilities of two management scenarios result in changes in class market shares, which are then interpreted as changes in demand by a class for a given scenario.

Table 4.3: Model specification criteria for snorkelers and divers for multinomial logit model (MNL) for snorkelers and divers combined, latent-class model (LCM), and modified LCM (Segmentation model, with and without covariates; see Methods for details). I used information criteria indicators to select the most parsimonious model; the model with the lowest AIC (Akaike Information Criterion) and BIC (Bayesian Information Criterion) values is best supported by the data (Akaike, 1974; Vermunt and Magidson, 2005).

| | **Model type** | | | |
|---|---|---|---|---|
| Parameter | MNL (data combined) | LCM (2 classes) | Segmentation model (no covariates) | Segmentation model (with covariates) |
| Log likelihood | -1715.2963 | -1516.404 | -1413.9304 | -1277.1209 |
| Number of parameters | 25 | 43 | 41 | 49 |
| AIC | 3480.5926 | 3118.808 | 2909.8609 | 2652.2419 |
| BIC | 3576.9694 | 3284.5761 | 3063.7163 | 2834.0528 |
| Rho squared | 0.2286 | 0.3183 | 0.4105 | 0.4087 |

For my DST analysis, I assessed how the different classes of tourists reacted to four hypothetical lionfish invasion scenarios (Table 4.2). Scenario 1 was a status quo scenario, with coral reef and lionfish status as seen in Cozumel in 2014; Scenario 2 (short-term, no management) depicted coral reef and lionfish status expected after two years with no lionfish management; Scenario 3 (long-term, no management) considered coral reef and lionfish status expected after five years with no lionfish management; and Scenario 4 showed coral reef and lionfish status if management actions were in place to control lionfish.

I estimated the short and long-term no-management scenarios based on reported impacts of lionfish in The Bahamas by (Green et al., 2014) and Smith et al. (2017). I constructed the management scenario (Scenario 4) based on tourist preferences towards the smallest fee tested ($5 USD; see Results section), and on the assumption that this scenario would produce a substantial reduction in numbers of lionfish (i.e., I assumed lowest lionfish density tested on DCE) and positive effects on native prey and predator fishes (i.e., the intermediate prey and grouper densities tested on DCE) (Table 4.2). These effects, at least in terms of lionfish and native prey numbers, are consistent with empirical results of experimental lionfish removals by Green et al. (2014). Analysis of the four scenarios allowed us to compare tourist reaction to lionfish control fees being implemented or in consideration elsewhere in the Wider Caribbean region. I maintained reef relief value (1.8), percentage of coral cover (5-15%), reef shark absent, and no change in excursion price (i.e., snorkeling or diving trip) constant across the four scenarios. I performed a sensitivity analyses to assess how variation in these four attributes affected class-specific market shares when other attributes of interest were kept constant (Fig. C.2). I acknowledge that other management scenarios (e.g., the establishment of no-fishing areas, mooring buoys, coral aquaculture, etc.) could benefit coral reef attributes; however, given my lionfish management focus I did not explore these possibilities. All DST estimates were calculated in Excel.

## 4.4 Results

### 4.4.1 Descriptive statistics

I collected a total of 312 surveys, with a response rate of 74% and 72% in summer and winter, respectively. Of these, 302 respondents fully completed the DCE section. Snorkelers and divers surveyed in the summer and winter months did not differ in age, income, education level, motivational attitudes, commitment to snorkeling/diving, trip satisfaction, environmental awareness or awareness of the lionfish invasion (Bonferroni-adjusted alpha level: 0.014; Table C.4). Respondents were 42 years old, on average (range: 19 to 70 yr), and were mainly male (70%). The majority (84%) of respondents resided in the USA, with 7% hailing from Canada, 4% from Mexico, 3% from European countries, and the remaining 2% from other countries. The income of most respondents (40%) ranged from $60-100,000, with 24% having incomes above $100,000, and 17% below $60,000; the remaining 19% did not know or chose not to disclose their income. The majority of respondents (77%) held at least one university degree. The demographic profile of my respondents appears to be representative of Mexican Caribbean tourists (Güemes-Ricalde and Correa-Ruíz, 2010; SECTUR, 2009; Anaya-Ortiz and Palafox Muñoz, 2010; Table C.5)

### 4.4.2 Classes of marine tourists and their preferences

I obtained a three-class model for marine tourists visiting Cozumel (Table 4.3). It included an a priori identification of a snorkeling class, and divided divers in two latent classes: casual and committed divers (Table 4.4). Members of these three classes differed in age, outdoor activity commitment, and awareness of the lionfish invasion and its related impacts (Table 4.5). The other eight covariates examined did not differ systematically among classes. Part-worth utilities indicated that all but two of the reef attributes had an effect on excursion utility for all three classes. The exceptions are native prey density, which was important for committed divers only, and changes in excursion price, which had an effect on snorkelers only. Wald II statistics indicated that lionfish density, lionfish control fee, and percentage coral cover preferences were different among the three classes (Table 4.4). Casual divers differed significantly from committed divers in terms of their attitude towards lionfish presence on the reefs and willingness to pay control fees (see below), while snorkelers and casual divers behaved similarly to each other (Table 4.4).

Table 4.4: Part-worth utility of eight coral reef scenario attributes for three known-latent classes of tourists involved in marine activities in Cozumel, Mexico. This segmentation model included covariates (i.e. age, commitment to snorkeling/diving activity, and lionfish invasion awareness) to discern class membership (see Table 4.5 for details). Part-worth utility values are shown for every level of each attribute. In the case of continuous attributes, the estimate reflects the slope of the linear effect. Model intercept represents the likelihood of choosing a Cozumel dive site over the "Do not dive in Cozumel" option. Positive part-worth utility values indicate preference for an attribute level and negative values indicate dislike; the significance of within-class part-worth utilities is indicated with asterisks. The Wald II statistic was used to test differences among tourist groups. Significance for both within-class and between-class tests: *** $p < 0.01$, ** $p < 0.05$, * $p < 0.10$.

| | | **Parth-worth utility** | | | |
|---|---|---|---|---|---|
| **Attributes** | **Levels** | **Snorkelers** | **Casual divers** | **Committeed divers** | **Wald II** |
| Intercept | Program A or B | 2.34*** | 2.75*** | 1.88*** | 2.18 |
| Lionfish density | 0 | -0.53*** | -0.35** | 1.13*** | 35.13*** |
| | 1 | 0.36*** | 0.09 | 0.30 | |
| | 10 | -0.08 | -0.12 | 0.13 | |
| | 25 | 0.25** | 0.38** | -1.56*** | |
| Control fee (USD) | $0 | 0.03 | 0.01 | -1.08*** | 22.55*** |
| | $5 | 0.16 | 0.28** | -0.30 | |
| | $10 | -0.15 | -0.17 | 0.88*** | |
| | $15 | -0.03 | -0.12 | 0.51* | |
| Grouper density | Linear | 0.38*** | 0.26*** | 0.42*** | 1.93 |
| Reef shark | Absent | -0.05 | -0.22** | -0.30* | 4.00 |
| | Present | 0.05 | 0.22** | 0.30* | |
| Coral cover | 5-15% | -0.15** | -0.15** | -0.55*** | 5.91* |
| | 35-75% | 0.15** | 0.15** | 0.55*** | |
| Reef relief | Linear | 0.22*** | 0.20*** | 0.33** | 0.50 |
| Native prey density | Linear | 0.01 | 0.01 | 0.23* | 2.48 |
| Excursion price change | Linear | -0.10* | -0.05 | 0.08 | 1.77 |

Table 4.5: Parameter estimates for covariate values indicating how likely respondents of a tourist class are to be described by the respondent characteristics assessed. The significance of within-class probabilities is indicated with asterisks. The Wald statistic was used to test whether the set of parameter estimates are significantly different from 0, regardless of class. Significance for both within-class and between-class tests: *** $P = 0.01$, ** $P = 0.05$, * $P = 0.10$.

| **Variable** | **Levels** | **Snorkelers** | **Casual divers** | **Committeed divers** | **Wald** |
|---|---|---|---|---|---|
| Intercept | - | 1.08** | 0.24 | -1.32** | |
| Age groups | 19-35 | 0.21 | 0.07 | -0.28 | 12.20** |
| | 35-50 | 0.40** | -0.17 | -0.24 | |
| | >50 | -0.61*** | 0.10 | 0.51** | |
| Commitment to diving/snorkeling | Low | 0.79*** | -0.05 | -0.75** | 28.08 |
| | High | -0.79 | 0.05 | 0.75** | |
| Lionfish awareness | Linear | -0.44*** | 0.14 | 0.30** | 22.58*** |

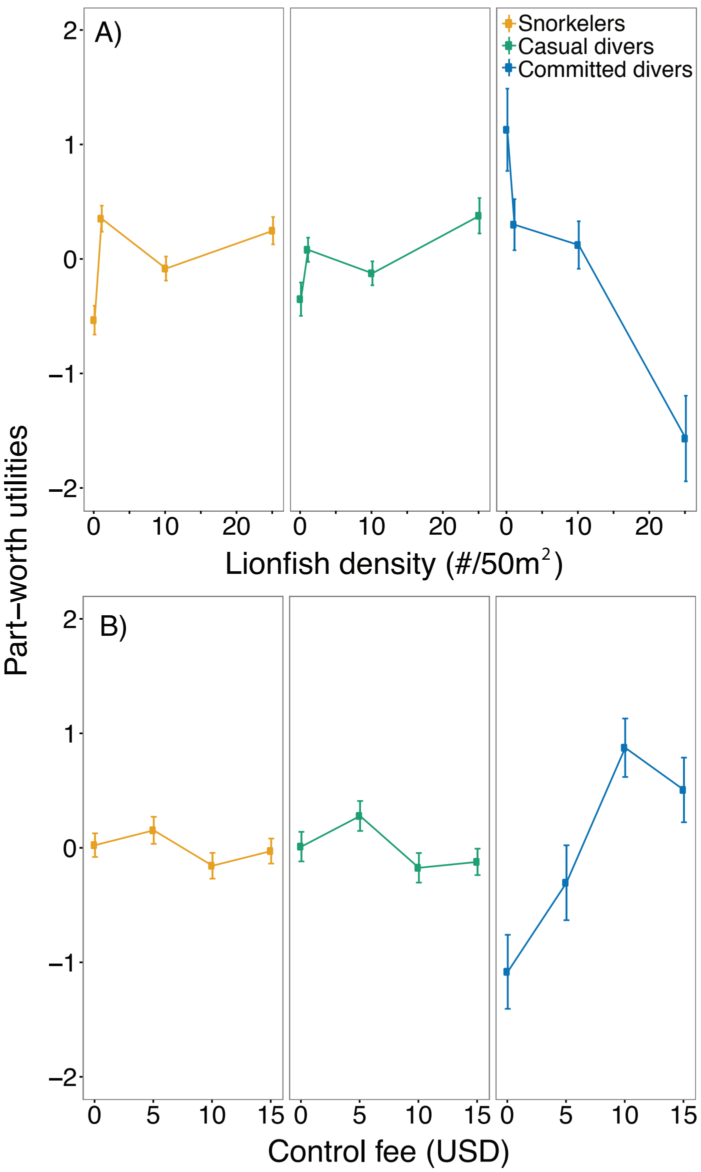

Figure 4.1: Part-worth utilities obtained in a three known/latent-class model of visitors to coral reefs of Cozumel, based on A) lionfish density and B) lionfish control fee attributes. Error bars represent standard errors for model coefficients.

### Class 1: Snorkelers

Snorkelers made up 33% of total respondents. The small sample size (n = 100) might have prevented us from identifying further latent classes, as I did for divers. Based on covariate analysis, snorkelers were most likely to be in the 36-50 yr age range. The majority (88%) considered snorkeling an enjoyable activity but practiced it infrequently. Most (75%) had little to no knowledge (i.e., scores = 1-2 out of 5) of the lionfish invasion and its ecological impacts (Table 4.5).

Snorkelers disliked reefs with no lionfish and were attracted to reefs with at least some or many lionfish (Table 4.4, Fig. 4.1A). This segment was not significantly influenced by the lionfish control fee (Table 4.4, Fig. 4.1B). Snorkelers also preferred reefs with high relief, high coral cover and high grouper density (Table 4.4). However, the model does not detect a significant snorkeler preference for changes in native prey density or for the presence or absence of a Caribbean reef shark (Table 4.4). Snorkelers were the only class that disliked excursion price increases (Table 4.4).

### Class 2: Casual divers

Casual divers were the largest class, accounting for 43% of all respondents. However, it was not possible to describe with high statistical confidence the casual diver class with the three informative covariates (Table 4.5). Casual divers were like snorkelers in terms of their preference for lionfish on reefs (Table 4.4, Fig. 4.1A). Casual divers preferred to pay the lowest lionfish control fee ($ 5 USD) but showed only mild, non-significant aversion towards higher fees (Table 4.4, Fig. 4.1B). Casual divers preferred high-relief reefs, high coral cover and high grouper density. Like snorkelers, casual divers did not exhibit a significant preference or dislike for changes in native prey density; however, they significantly preferred sites with a Caribbean reef shark (Table 4.4).

### Class 3: Committed divers

Committed divers made up the remaining 24% of respondents and were the smallest class (n = 72). Committed divers were older, on average, than the other two groups, with most being over 50 years old. The majority considered diving to be an important and probably their primary outdoor activity. Most importantly, they indicated that they were highly knowledgeable of the lionfish invasion and its ecological impacts (Table 4.5).

Committed divers disliked the presence of lionfish on reefs, particularly at high density, and would prefer to dive where lionfish are absent (Table 4.4, Fig. 4.1A). They were also willing

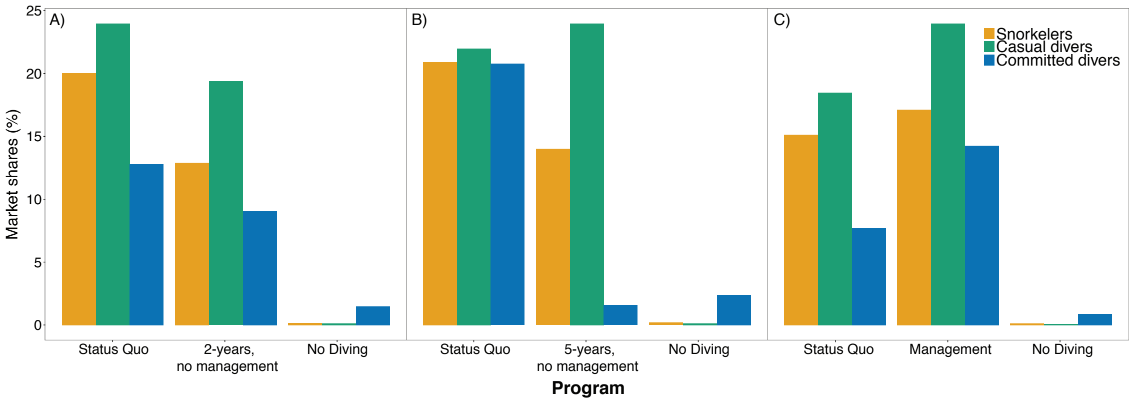

Figure 4.2: Tourist class market shares (%) from a decision support tool based on a three latent-class model of visitors to coral reefs in Cozumel. In all panels, "Status quo" represents reef conditions experienced by visitors in 2014, and "No diving" represents the option of not diving in Cozumel. The management scenario varies: (A) no management over the short term (~2 yr), (B) no management over a longer term (~5 yr), and (C) some management actions to reduce lionfish abundance and impacts, for which visitors pay a nominal control fee (US$5 per visit). Class percentages sum to 100% in each panel.

to pay moderate to high lionfish control fees (i.e., > $10 USD); in fact, they were against not contributing financially to lionfish management efforts (Table 4.4, Fig. 4.1B). Committed divers, like the other two classes, preferred high-relief reefs with high coral cover and high grouper density. Like casual divers, committed divers preferred to dive at sites where reef sharks are present (Table 4.4). Committed divers were the only class that reacted negatively to a reduction in native prey fish density. The part-worth utilities of committed divers are larger than those of snorkelers and casual divers for all attribute levels, suggesting strong preferences for the attributes presented by this group (Table 4.4).

### 4.4.3 Diver and snorkeler preferences under hypothetical management scenarios

Exploring the segmentation model results through a decision-support tool (DST) helped us to identify tourist class preferences for different lionfish management scenarios (Table 4.2). Market shares are based on class size (i.e., 33%, 44%, and 23% for snorkelers, casual and committed divers, respectively). The status quo scenario always represents the conditions that visitors could experience on Cozumel reefs in 2014.

In the absence of management action taken in the short term (i.e., two years), I would expect a large increase in lionfish density and a moderate decrease in native prey fishes (Table 4.2). These changes result in decreases in market shares for all three classes of marine tourists, compared to the status quo scenario (Fig. 4.2A). The market share of snorkelers would decrease by 7% - the largest decrease in market share - while those of casual and committed divers would decrease by 5% and 4%, respectively (Fig. 4.2A). Committed divers would experience a market share loss of 1% (i.e., 1% of divers would prefer not to dive in Cozumel at all; Fig. 4.2A).

If the lionfish invasion were allowed to progress unchecked for a longer period (i.e. ∼5 years.), a further moderate increase in lionfish abundance and now severe declines in native prey and grouper densities would be expected (Table 4.2). Market shares for snorkelers and committed divers would decrease by 7% and 19%, respectively, compared to the status quo scenario, with a market share loss of ∼2% for committed divers (Fig. 4.2B). On the other hand, casual divers show a small increase in market share (∼2%; Fig. 4.2B).

If a small control fee ($5 USD) were implemented to aid management actions, which would prevent increases in lionfish densities (compared to the status quo year) and minimize impacts on native prey and predator densities (Table 4.2), market shares for all three classes would increase when compared to the status quo scenario. Snorkelers and casual divers market shares would increase by 2% and 6%, respectively, while an increase of nearly 7% would be observed for the committed divers class (Fig. 4.2C). However, while implementing a higher control fee would benefit the reef environment even more and increase the market shares of committed divers, it would decrease the market shares of snorkelers and casual divers, given their unwillingness to pay >$5 USD per visit to control lionfish numbers (Fig. C.2).

## 4.5 Discussion

The lionfish invasion is a pressing conservation issue in the Caribbean region (Sutherland et al., 2010). However, while the ecological impacts of these non-native species are increasingly understood (Albins and Hixon, 2008; Green et al., 2012; Hixon et al., 2016), their effects on reef-dependent economies remain unclear (but see Johnston et al., 2015). I found that tourists taking part in recreational activities on coral reefs in the Mexican Caribbean hold widely divergent views of invasive lionfish. Committed divers favored ‘good reef conditions’ (i.e., high coral cover and reef relief, high abundance of groupers and other native fishes) and disliked seeing large numbers of lionfish. They also showed strong support for the implementation of relatively high fees to manage the lionfish invasion. The other two identified classes of tourists, casual divers and snorkelers, also preferred some aspects of ‘good reef condition’ (i.e., high coral cover and reef relief, presence of groupers), but they favored reefs with lionfish and did not support high management fees. A decision support tool, incorporating these stated preferences along with predicted ecological repercussions of the lionfish invasion, revealed that actions to manage the lionfish invasion, in the form of a

$5 USD lionfish control fee, seem to not deter divers and might be beneficial to the tourism industry of Cozumel.

### 4.5.1 Heterogeneity of preferences among reef tourists

Tourist groups visiting Cozumel reefs differed greatly in their reaction to lionfish. My study shows that seeing at least one lionfish adds to the experience of snorkelers and casual divers (Table 4.4, Fig. 4.1). This reaction is expected from tourists seeking to enjoy natural attractions when initially faced with an arguably beautiful and exotic fish (Moore, 2012; Hoag, 2014). In contrast, committed divers showed great aversion to lionfish, even in low numbers, and preferred reefs with no lionfish.

In spite of a key divergence in preference in relation to lionfish, snorkelers and divers shared an overall preference for reefs in good condition. This result is consistent with previous studies showing that various attributes correlated with reef state are important for snorkelers and divers (Rudd and Tupper, 2002; Uyarra et al., 2005; Dinsdale and Fenton, 2006; Shideler and Pierce, 2016). Indeed, snorkelers and casual divers value reef attributes such as high coral cover, high reef relief and high grouper abundance as much as, or more than, they value lionfish presence (Table 4.4). Perhaps not surprisingly, the preference for higher levels of all natural reef attributes was stronger for committed divers than for the other two classes. The non-significant attraction or dislike of some of the tourist classes to attributes such as changes in lionfish density, native prey density, reef shark presence and excursion price change might arise because of opposing attitudes within a class. For example, a subgroup of snorkelers might like to see sharks during their visit while the rest of their class might fear such encounters (Dobson, 2007) . It is possible that my sample size prevented me from identifying subgroups of snorkelers, which comprised a smaller class (33% of respondents) than divers.

The divergent preferences of different classes of marine tourists covaried with demographic and motivation characteristics. Environmental attitudes have been found to vary with age (Bremner and Park, 2007; Lee, 2011; Sharp et al., 2011), involvement in outdoor activities (Luo and Deng, 2007; Nisbet et al., 2009), and environmental awareness (Luo and Deng, 2007; Peters and Hawkins, 2009). Similar factors were useful to define my model and explain class divisions in my study. I expected to observe latent classes mainly as a result of diver specialization, as reflected by experience level and commitment to the diving activity (Dearden et al., 2007; Anderson and Loomis, 2011). Not surprisingly, commitment to snorkeling or diving did explain class membership, but age and knowledge of the lionfish invasion also contributed. These three covariates were useful to distinguish between snorkelers and committed divers, but were not useful to define casual divers. It is possible that the casual diver class was not well described because respondents within this class included people at the extremes of the covariates tested, but the low sample size prevented us from identifying further subgroups.

Tourists engaging in environmental activities are often sensitive to excursion prices (Dellaert and Lindberg, 2003; Saayman and Saayman, 2014). I found that this was not the case for divers. Only snorkelers reacted to changes in excursion price, stating a dislike for increases. It is possible that the sensitivity of snorkelers to higher excursion prices is a result of their average trip price, which is lower (∼$50 USD) than that of divers (∼$100 USD) (see below). While this finding is not directly relevant to the issue of lionfish control, it can have implications for the willingness of snorkelers to contribute to management actions that require financial contributions from users.

### 4.5.2 The potential for reef tourists to fund lionfish management

Individuals and groups who are actively involved in outdoor activities often display strong support for conservation initiatives. People who spend more time doing outdoor activities, such as visiting nature reserves or interacting with wildlife, generally show more environmental concern and endorse pro-environmental attitudes (Luo and Deng, 2007; Sorice et al., 2007; Nisbet et al., 2009; Semeniuk et al., 2009; Lee, 2011). This stance extends to the control of terrestrial invasive species. In the USA (Sharp et al., 2011), Scotland (Bremner and Park, 2007), and Spain (García-Llorente et al., 2011), individuals who are environmentally engaged, aware of the impact of invasive species and/or familiar users of terrestrial parks strongly support management actions against invasive species. In general, WTP and DCE studies focused on marine tourism indicate divers and snorkelers value healthy ecosystem attributes highly (Rudd and Tupper, 2002; Uyarra et al., 2005; Dinsdale and Fenton, 2006; Shideler and Pierce, 2016), and readily support the implementation of conservation management initiatives and management fees (Depondt and Green, 2006; Casey et al., 2010; Emang et al., 2016). My results show that this attitude also prevails in relation to marine invasive species, at least among some marine tourists.

Managing marine invasive species can be expensive (Bax et al., 2003; Williams and Grosholz, 2008). Culling is currently the most common form of lionfish control within the region (Malpica-Cruz et al., 2016), and it can effectively decrease lionfish abundances and limit their ecological impacts at local scales in some situations (e.g. Frazer et al., 2012; Green et al., 2014; but see Dahl et al., 2016). However, these interventions must be maintained over the long term to prevent lionfish populations from rebounding (Arias-Gonzalez et al., 2011; Barbour et al., 2011). Furthermore, culling is likely to be ineffective at large spatial scales and at depths beyond recreational diving limits (Andradi-Brown et al., 2017). Even if lionfish removals were limited to small, spatially discrete areas such as shallow-water coral reef patches, culling is time- and labor-intensive (Usseglio et al., 2017). As such, culling is likely to pose an undue financial burden on marine resource managers, unless sources of sustainable financing are identified.

My results suggest that some reef tourists would be willing to contribute to lionfish management. Committed divers, in particular, supported high lionfish control fees (US$10-15 per excursion) and disliked options without such fees. This support for control fee and aversion to lionfish presence on reefs by committed divers closely aligns with their keen participation in lionfish derbies - competitive events occurring throughout the Caribbean in which participants can gain monetary or material prizes for capturing lionfish (Malpica-Cruz et al., 2016). The majority of divers participating in these events are aware of the impacts of lionfish and willing to invest time and money in their management (Ali et al., 2013; Hoag, 2014; Trotta, 2014). In contrast, casual divers disliked high lionfish control fees and only supported the smallest fee (i.e., $5 USD). Snorkelers were the least supportive of implementing a control fee, perhaps because such a fee would represent a larger proportion of their total excursion price than it would for divers. It is worth noting that, given the strength of the preferences stated for various reef attributes, the support of snorkelers and casual divers for relatively low control fees appears to be driven more by the beneficial ecological effects of controlling lionfish on reefs, rather than by direct reductions in lionfish numbers. Nevertheless, the positive attitude towards a $5 USD control fee by snorkelers and casual divers, and the keen acceptance of higher fees by committed divers, indicates the potential willingness of many marine users to contribute financially to lionfish control. These findings add to the notion that snorkelers and divers are generally willing to contribute financially to the preservation and conservation of reef environments in marine protected areas (MPAs) (Arin and Kramer, 2002; Green and Donnelly, 2003; Depondt and Green, 2006), and to management actions to restore damaged reef ecosystems (Seenprachawong, 2003; Beharry-Borg and Scarpa, 2010).

To my knowledge, the possibility of charging a lionfish control fee to marine tourists visiting Caribbean marine protected areas (MPAs) has not been explored. Marine reserves and protected areas in the Caribbean are often poorly managed and have limited budgets to regulate recreational snorkeling and diving operations (Bustamante et al., 2014). A lionfish control fee would provide valuable additional financial resources that could be used, for example, to implement lionfish surveys and monitor the state of the invasion, undertake periodic removals in key locations within MPAs (e.g., core locations of high biological diversity) where large-scale derbies are not feasible, and mount awareness campaigns. While all tourists entering Cozumel Reefs National Park already pay a daily visitor fee ($\sim$$1.5 USD), these funds are distributed at the federal level among all terrestrial and marine protected areas in Mexico, yielding minimal funding for lionfish-focused interventions (Comisión Nacional de Áreas Naturales Protegidas, 2010). Rough estimates indicate that the funds raised through a lionfish control fee in Cozumel could be substantial. In 2014 $\sim$300,000 people paid a visitor fee to enter Cozumel Reefs National Park to take part in aquatic activities (Blanca Quiroga García, pers. comm.). If just 20% of these visitors engaged in snorkeling or diving, an acceptable, modest ($5 USD) lionfish control fee would result in $300,000 USD annually to be used for lionfish management. This estimate is equivalent to 50% of the authorized federal budget in 2014 for biological monitoring programs in all protected areas of Mexico (Comisión Nacional de Áreas Naturales Protegidas, 2016).

### 4.5.3 Potential impacts of lionfish on reef tourism industry

Marine tourism is arguably the most important economic activity in Cozumel. In 2012, 41% of the roughly 4 million tourists visitors to Cozumel indicated an interest in aquatic activities, 75% of which entailed diving or snorkeling (Mota and Frausto, 2014). There is no specific information available on the relative economic contributions of snorkelers and divers in Cozumel. All tourists incur accommodation and meal expenses during their 3-day (average) stay on the island, but the average excursion costs of snorkelers and divers differ ($50 vs $100 per trip, respectively). The fact that divers predominated (67% of respondents) in my sample, combined with the high diving excursion prices, suggests that factors that discourage visits by divers might have a larger impact on the industry than those that reduce appeal to snorkelers, if my sample is representative of the whole industry.

My study suggests that not implementing actions to mitigate the lionfish invasion could change the distribution of market shares of divers and snorkelers, with potential negative effects on the economy. In general, marine tourists across all three classes preferred the status quo (2014) reefs than reefs that remained unmanaged in the short and longer term. Lower market shares for unmanaged reefs are partly driven by a lionfish effect: most marine tourists tend to value seeing a few lionfish (e.g., 1 lionfish, in the status quo scenario) more than a higher abundance of lionfish (i.e., 10 lionfish in the 2-year no-management scenario, or 25 lionfish in the 5-year no-management scenario; Fig. 4.1). The single deviation from the overall trend - the higher market share of casual divers for the 5-year no-management scenario - is consistent with the high value they place on abundant lionfish (Fig. 4.1). The market share patterns are also partly attributable to a native fish effect: marine tourists tend to prefer the higher abundances of native groupers (and for committed divers only, native prey fish) in the status quo scenario than the lower abundances offered in the unmanaged scenarios. Unsurprisingly, committed divers showed the largest aversion to reefs that are unmanaged in the long term, with ∼20% fewer divers preferring those reefs than the status quo reefs (Fig. 4.2b), reflecting the strength of their preferences for reef attributes that reflect good condition. It was also the only class of users that would choose not to dive in Cozumel when lionfish impacts are large. Such a potential loss could be amplified if dissatisfied experienced divers, who focus on the environmental aspects of their visit, become less likely to recommend Cozumel as a destination to others (Chi, 2010; Morais and Lin, 2010).

Interestingly, more marine tourists of all three classes would prefer to visit managed than status quo reefs. My DST indicates that the driving force of these higher market shares is the control fee itself. Grouper density did not change between the managed (fee-paying) and the status quo scenarios. Small prey fish density decreased, but snorkelers and casual divers - unlike committed divers - are relatively insensitive to variation in abundance of small native fish. However, across all three classes of marine users, the preference for \$5 was higher (or, in the case of committed divers, the dislike was less intense) than the preference for no fee (Table 4.4). Given that more than two-thirds of respondents preferred lionfish on the reefs, their acceptance of even a small lionfish control fee seems counterintuitive. Nonetheless, this result might reflect the fact that snorkelers and casual divers, like many other tourists regardless of their outdoor involvement, are willing to contribute financially to conservation initiatives (Casey et al., 2010). However, given that snorkelers and casual divers do not tolerate control fees >\$5 USD, the implementation of higher fees would be likely to reduce market shares, and perhaps increase market losses, of tourists visiting Cozumel reefs.

It is important to note that the market share changes described here as a result of lionfish management (or lack thereof) cannot be safely extrapolated to predict economic impacts on the Cozumel tourism industry. My results are based on estimates of marine tourist preferences for various reef features and on potential impacts of the lionfish invasion on these attributes. Tourist preferences could change over time, and the potential impacts of lionfish may not come to pass as expected. I also cannot assess potential avidity bias, and hence the extent to which my pool of respondents represents “average” visitors to Cozumel. Lack of representativeness would weaken any attempt to forecast real economic impacts (Moeltner and Shonkwiler, 2005; Hynes and Greene, 2013). However, the high visitor return rate of my respondents, which is in line with official tourism statistics (SECTUR 2009), makes my estimated market share changes, especially market share losses, conservative because many respondents appear to be committed to revisiting Cozumel with or without changes in the state of coral reefs. Finally, local and global factors affecting tourism market growth, tourist return rates, travel security concerns, etc., which are beyond the scope of this study, will also affect market share changes such that the overall tourism industry might grow or shrink independently of coral reef state or management.

### 4.5.4 Conclusion

My study is the first to assess tourist willingness to pay for a lionfish control fee charged as part of a snorkeling or diving trip. Given their awareness of the consequences of the lionfish invasion and interest in diving, committed divers were supportive of the implementation of lionfish control fees. While the support for such fees was more muted among snorkelers and casual divers, my decision support tool indicated that implementing a \$5 USD fee in the Cozumel Reefs National Parks could offer an option that balances benefits to the reef and attribute preferences of users. To gain support, managers would need to work closely with the diving industry and establish awareness campaigns to inform tourists of the ecological effects of lionfish. Future studies should focus on whether such campaigns successfully change the attitudes of marine tourists in favor of management action to limit the effects of this invasion. The goals of management and any achievements stemming from the implementation of lionfish control fees should be assessed and conveyed to the public and stakeholders to guide future management strategies. The implementation of management fees might be relevant in other diving destinations throughout the Wider Caribbean Region.

# Chapter 5

# Managing marine invasive species through public participation: Lionfish derbies as a case study [1]

## 5.1 Abstract

The management of invasive species can be facilitated by public participation. The drivers of public involvement and success at invasive removal in tournaments (derbies) to catch Indo-Pacific lionfish (*Pterois volitans/miles*) in the Western Atlantic were examined. Information on 69 lionfish derbies held in the wider Caribbean region from 2010 - 2015 was compiled. Derbies attended mainly by artisanal fishers reported lower catches but higher participation than derbies dominated by recreational divers or attended by a mixed public. As predicted, the number of lionfish caught increased with effort and with time since lionfish were established in an area. In contrast, participation was best predicted by national wealth (GDP per capita) and number of local dive shops. For maximizing the number of participants, derbies should therefore be held in areas where lionfish are well established, and where the pool of potential participants is large. However, if the management goal is instead to slow the invasion, early detection is critical. The focus should then shift to areas where no or very few lionfish have been detected, and the derby approach modified to a more frequent or continuous, monitoring-like incentive scheme.

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[1] A version of this chapter appears as, Malpica-Cruz, L., Chaves, L.C.T., Côté, I.M. 2016. Managing marine invasive species through public participation: Lionfish derbies as a case study. Marine Policy. 74:158-164.

## 5.2 Introduction

Animal populations are often intentionally reduced for a variety of reasons unrelated to direct human consumption. For example, culling, i.e., the permanent removal of individuals from a population, has been used to prevent the spread of diseases (Tildesley et al., 2009), to protect crops (Geisser and Reyer, 2004), livestock (Berger, 2006), fisheries (Yodzis, 2001), and vulnerable habitats (Gordon et al., 2004), and to ensure public safety (McCagh et al., 2015). Culling has also been advocated or implemented to mitigate the impacts of a variety of invasive species in terrestrial (Brook et al., 2003), freshwater (McDonald et al., 2007), and marine ecosystems (Hewitt et al., 2009). In some cases, it is possible to eradicate invasive species (e.g. *Caulerpa taxifolia* in California; Anderson, 2005). However, in most cases the goal of natural resource managers is to decrease the abundance of invasive species to levels that minimize adverse ecological impacts.

The control of invasive species can add a serious burden to the task of managing natural resources. Stakeholders might hold divergent opinions about the value of invasive species (Estevez et al. 2015), and lethal strategies such as culling, especially of vertebrates, might be unacceptable to some land owners, thereby jeopardizing the collective action necessary for successful invasive species management (Wilkinson and Priddel 2011). The lack of ownership in marine systems might initially facilitate the implementation of invasive control programs, but the sheer scale of the habitat combined with chronic underfunding of marine conservation activities (Balmford et al. 2004) mean that reliance on public engagement and participation is often essential for successful outcomes (Granek et al. 2008).

Given the relative rarity of invasions by marine fish (Randall 1987; Baltz 1991; Cohen and Carlton 1998), there has been until now little need for use of culling to control vertebrate invaders in the ocean (but see Giddens et al. 2014). However, efforts to control the invasion by Indo-Pacific lionfish (*Pterois volitans/miles*), which is currently unfolding in large parts of the northwestern Atlantic, Gulf of Mexico and Caribbean (Schofield 2009, 2010), present a prime example of the use of culling by members of the public as a management tool to mitigate the effects of an invader on marine ecosystems. Lionfish have spread throughout the wider Caribbean region in just a decade (Whitfield et al. 2002; Whitfield et al. 2007; Freshwater et al. 2009; Côté et al. 2013). The impacts documented so far include reductions in richness, biomass and recruitment of native coral reef species (Albins and Hixon 2008; Green et al. 2012) and benthic community shifts to algal-dominated reefs (Lesser and Slattery 2011). Trophic cascades and fishery declines are expected in the longer term in some invaded areas, causing further negative ecological and potentially economic impacts (Arias-Gonzalez et al. 2011).

Natural resource managers now face the unprecedented challenge of dealing with a prolific and versatile invader that is unlikely to be eradicated from the region with currently available tools and technologies. Modeling studies have suggested that the exploitation rates necessary to considerably reduce lionfish populations are high (e.g., 27-65% per annum), and that once removals stop, lionfish populations will recover quickly (Arias-Gonzalez et al. 2011; Barbour et al. 2011). Culling of individuals by spearfishing or hand netting seems to be the only method to date that might mitigate the impacts of lionfish. For example, in a manipulative experiment, lionfish were repeatedly removed from patch reefs over a two-year period, and the decline of native fish biomass was stemmed on reefs maintained at low lionfish density (Green et al. 2014). Regular culling may therefore work as a lionfish control method, but it is time-consuming, requires considerable person-power, and is limited to the depths divers can reach (e.g. ~30 m for SCUBA divers and ~15m for free-divers).

Many countries have nevertheless adopted large-scale lionfish culling programs as a strategy to control lionfish (Barbour et al. 2011; Morris 2012). These efforts often take the form of lionfish derbies or tournaments in which concerned citizens, e.g., recreational divers and spearfishers, artisanal fishermen, and dive guides, attempt to catch the most, the largest, or the smallest lionfish over a given time period (usually a day) to claim various material and/or monetary prizes. The organizers of derbies include non-profit organizations, park managers, fishermen unions, and/or research institutions. These events are by far the largest initiatives to manage the lionfish invasion, and while some derbies are well established in some locations, many are occurring haphazardly throughout the region. There has been little monitoring of their effect on lionfish populations (but see Green et al. 2013). Notwithstanding any potential ecological benefits, derbies also play a valuable role in increasing public awareness and engagement in marine conservation (Trotta 2014), as well as providing data for research, market development and removal training (Akins 2012). Therefore, understanding what drives their success is important.

The aim of this study was to identify the factors associated with successful lionfish derbies at the Caribbean scale. The success of an invasive management intervention, such as derbies, should ultimately be measured in terms of the proportion of invasive individuals removed or the extent to which native fauna benefit from such removals. This information is not currently available at the regional scale. Therefore, derby success was defined in terms of catch (i.e., total number of lionfish captured) and participation (i.e., total number of participants), reflecting the social rather than ecological success of lionfish derbies. While other studies have examined the importance of volunteers in the context of the lionfish invasion (Morris 2012; Ali et al. 2013; Scyphers et al. 2015), or identified the socioeconomic correlates of diver attitudes towards and participation in lionfish management (Trotta 2014; Harvey and Mazzotti 2015), this is the first study to consider the social and economic drivers of this popular form of marine invasive control. The widespread implementation of lionfish derbies as tool to control the lionfish invasion makes the results of this study timely and relevant to better understanding and guiding management practices targeting lionfish and future marine fish invaders.

## 5.3 Methods

### 5.3.1 Data compilation

Information was compiled on lionfish derbies held in many countries across the tropical northwestern Atlantic, Gulf of Mexico and Caribbean from 2010 to 2015. Only derbies for which the following information was available were included in this study: location, date, duration, total number of participants, total number of lionfish captured, and type of participants. Data were obtained directly by emailing a survey requesting the above information to derby event organizers, including park managers, non-governmental organizations, and dive shops, as well as from an online summary of derby results maintained by the Reef Environmental Education Foundation (REEF; www.reef.org).

Two metrics of derby success were considered: catch, i.e. the total number of lionfish caught per day, and participation, i.e., the total number of participants registered in the derby. A suite of derby characteristics was identified, as well as attributes of the locality where the events took place, that could influence the success of derby events (Table 5.1). Hypotheses for each of these attributes in relation to each success metric were generated (Table 5.1).

Each derby was categorized into one of three groups, based on the type of participants. Some derbies were dominated by recreational divers, i.e. those who dive or fish mainly for recreational purposes. These participants would usually use self-contained underwater breathing apparatus (SCUBA) equipment. Some derbies were dominated by artisanal fishers, for whom fishing is the main source of income or food. Artisanal fishers usually dove without the aid of a SCUBA unit (i.e., apnea or free-diving). A third type of derby comprised a mixed public, including recreational divers, artisanal fishers, sport fishers, managers, and dive guides, with no participant type forming a clear majority.

### 5.3.2 Potential predictors of derby success

#### Effort

The total number of participants per day (i.e., participation) was used as the metric of culling effort. Catch was predicted to be positively correlated with effort (Table 5.1), perhaps reaching an asymptote where higher effort would no longer increase catch because of the limited number of lionfish available for capture within the derby area.

### Participant type

Catches should be most influenced by fishing experience. Therefore, derbies dominated by artisanal fishers should report larger catches than those dominated by recreational divers or attended by a mixed public (Table 5.1). On the other hand, participation should generally be higher in derbies dominated by recreational divers (Table 5.1), given their potentially large local populations and high commitment to marine conservation initiatives. It is possible that participation could interact with GDP per capita (see below; Table 5.1), if artisanal fishers represent the largest pool of participants in developing countries, while recreational divers predominate in developed countries.

### Time since lionfish invasion

Catch usually varies with fishing effort and with abundance of the target species (Cooke and Beddington, 1984; Jennings and Polunin, 1995; Halls et al., 2006). There were no data available from most derby sites to estimate pre-derby lionfish density. Instead, the number of years since invasion was used as a proxy of local lionfish abundance. Lionfish have invaded various parts of the Atlantic, Caribbean and Gulf of Mexico at different times, mirroring larval dispersion on oceanic currents (Freshwater et al., 2009), and lionfish populations have shown a recurring pattern of density increase over time (Green et al., 2012). All else being equal, time since invasion should therefore reflect roughly lionfish abundance, at least up to the potential carrying capacity of the area. Time since invasion at each derby site was obtained from published data (Schofield, 2009; 2010), and by asking derby organizers for the date of first lionfish sighting at their location. Larger catches were predicted at sites invaded longer ago, due to higher lionfish density (Table 5.1). Likewise, a larger number of derby participants at sites invaded earlier was expected, since awareness of the lionfish invasion and involvement of local or tourist population might grow over time (Table 5.1).

### Dive shops

Most derbies are organized in areas with a sizeable local or tourist diving community. The number of dive shops in each area (i.e., within ∼100 km from the derby location) was used as a proxy of the size of the potential pool of volunteer recreational divers. Data were obtained through an online search tool of the Professional Association of Diving Instructors' website (PADI, the largest diving school in the world; http://www.padi.com/scuba/locate-a-padi-dive-shop/, accessed 20 Feb 2015). It was predicted that the number of local dive shops would not directly affect catch, but that participation would increase with dive shop number (Table 5.1).

#### GDP per capita

Participating in lionfish derbies requires not only some fishing experience, but it also involves a potentially large investment of time and resources (money, gear, training, boat, etc.). Gross domestic product per capita (GDP; from www.worldbank.org, accessed 05 Mar 2015), of the nation where derbies took place, was used as a proxy of people's ability to invest and participate in conservation initiatives such as derbies. The limitation and coarseness of GDP per capita as metric are acknowledged, but it is the best indicator given the international scale of the analysis. Larger participation was predicted for derbies held in countries with a higher GDP per capita (Table 5.1). Alternatively, lower GDP per capita could indicate a greater financial need, which could make derby prizes an incentive to participate. The association between participation number and GDP per capita could therefore be negative (Table 5.1). GDP per capita was not expected to predict catch.

### 5.3.3 Analytical approach

Generalized linear models (GLM) with a negative binomial error distribution were used, because a Poisson error distribution indicated over-dispersion. Models were run using the package 'MASS' in R (Venables and Ripley, 2002; R Core Team, 2016). Participant type, time since invasion, and effort were included as fixed effects in the predictive model of lionfish catch. To model derby participation, participant type, time since invasion, number of dive shops, and GDP per capita were included. A priori models were developed using various combinations of main effects and their two-way interactions that corresponded to the specific hypotheses outlined in Table 5.1 (Burnham et al., 2010). Model uncertainty was incorporated using the Akaike's Information Criterion, corrected for small sample size (AICc). AICc identifies the best-supported model as a trade-off between model fit and model complexity, where the lowest value represents the best trade-off (Burnham et al., 2010). Models that differed by $< 2$ AICc points from the best-supported model were selected as top models, and coefficient estimates were averaged for each parameter across top models using the MuMIn R package (Barton, 2015). Model estimates were based on data from all three categories of participants combined, but for visual clarity, each category was depicted separately.

Table 5.1: Variables predicted to influence derby success, expressed as catch (total lionfish captured per day) and participation (total number of participants per derby).

| | Variables | Data type | Units/Levels | Predictions |
|---|---|---|---|---|
| Derby variables | Effort | Continuous | Number of derby participants | More participants = Larger catch |
| | Public invited | Categorical | Recreational divers, Artisanal fishers, Mixed public* | More artisanal fishers = Larger catch; More recreational divers = More participants |
| Local variables | Time since invasion | Continuous | Years since first report of lionfish in the area | Longer time since invasion = Larger catch; Longer time since invasion = Higher awareness = More participants |
| | Dive shops | Continuous | Number of dive shops in the area | More dive shops = Larger volunteer pool + higher capacity to promote events = More participants |
| | Gross domestic product per capita (GDP) | Continuous | US$ | Greater wealth = Greater capacity to invest = More participants Alternatively: Less wealth = Greater incentive to win prizes = More participants |

* 'Mixed public' refers participation by recreational divers, artisanal fishers, and other stakeholders such as dive guides, park managers, and recreational fishers.

Table 5.2: Results of model selection using AICc for generalized linear models (GLMs) of catch (number of lionfish caught), and participation (total number of participants) in lionfish derbies. $\Delta$AICc is the difference in AICc values between model i and the best-supported model (Rank = 1), Weight is the probability that model i is the best of the candidate set, and k indicates to the number of parameters in each model. Only models with $\Delta\text{AICc} < 2$ are shown. Check marks indicate the predictive variables included in each model (see Methods for predictive variable selection and description).

| | | **Predictive Variables** | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Response variable | Rank | Participant category | Effort | Time since invasion | Effort*Time since invasion | Number of dive shops | GDP per capita | AICc | $\Delta$AICc | Weight | k |
| Catch | 1 | | ✓ | | | | | 787.9 | 0.00 | 0.311 | 3 |
| | 2 | ✓ | ✓ | | | | | 788.1 | 0.20 | 0.282 | 5 |
| | 3 | ✓ | ✓ | ✓ | ✓ | | | 788.7 | 0.75 | 0.213 | 7 |
| | 4 | | ✓ | ✓ | ✓ | | | 788.9 | 0.95 | 0.194 | 5 |
| Participation | 1 | ✓ | | | | ✓ | ✓ | 506.0 | 0.00 | 0.724 | 6 |
| | 2 | ✓ | | | | | ✓ | 507.9 | 1.93 | 0.276 | 5 |

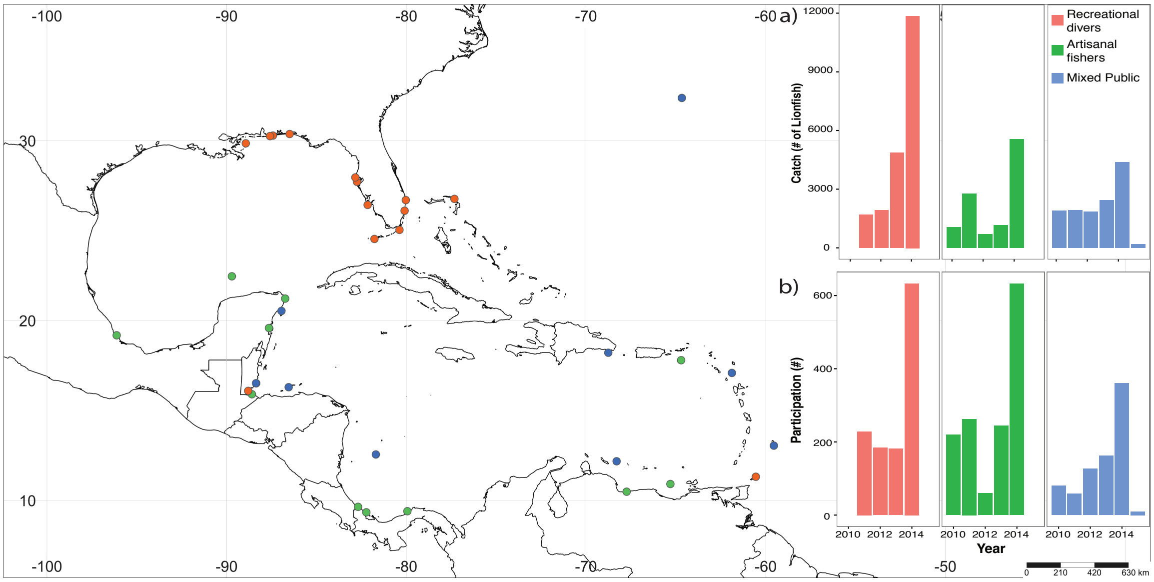

Figure 5.1: Lionfish derby locations across the northwestern Atlantic, Gulf of Mexico, and Caribbean. Locations are color-coded to show the main category of participants in each derby. Insets show a) total annual lionfish catch, and b) annual number of participants, from 2010 to 2015 for each category of derby participant.

## 5.4 Results

Information was obtained on 107 derbies that took place across the region, spanning the southeastern United States to Venezuela (excluding Nicaragua) and including several Caribbean Island States, from 2010 to 2015. However, complete data were available for 69 of these derbies, taking place in 17 countries from 2011 to 2014 (Fig. 5.1). Thirty derbies were attended mainly by recreational divers, 21 by targeted artisanal fishers, and 18 by a mixed public. Catches ranged from 6 to 1590 lionfish per day, while the number of participants varied from 3 to 150 per derby. These derbies were held in areas where lionfish first appeared 1 to 14 years ago (Fig. 5.1a,b).

### 5.4.1 Lionfish catch

Four models of lionfish catch were equally supported (Table 5.2). All predictive variables tested appear in these top models (Table 5.2), hence coefficients were averaged across models. As predicted, lionfish catch increased significantly with effort (Figs 5.2a, 5.3a), and with time since invasion (Figs 5.2a, 5.3b). Catch varied depending on the type of participants involved, and contrary to prediction, derbies dominated by artisanal fishers showed the lowest catches (Fig. 5.2a). Catches from derbies involving recreational divers and a mixed public did not differ, but were higher than those of derbies involving mainly artisanal fishers (Fig.

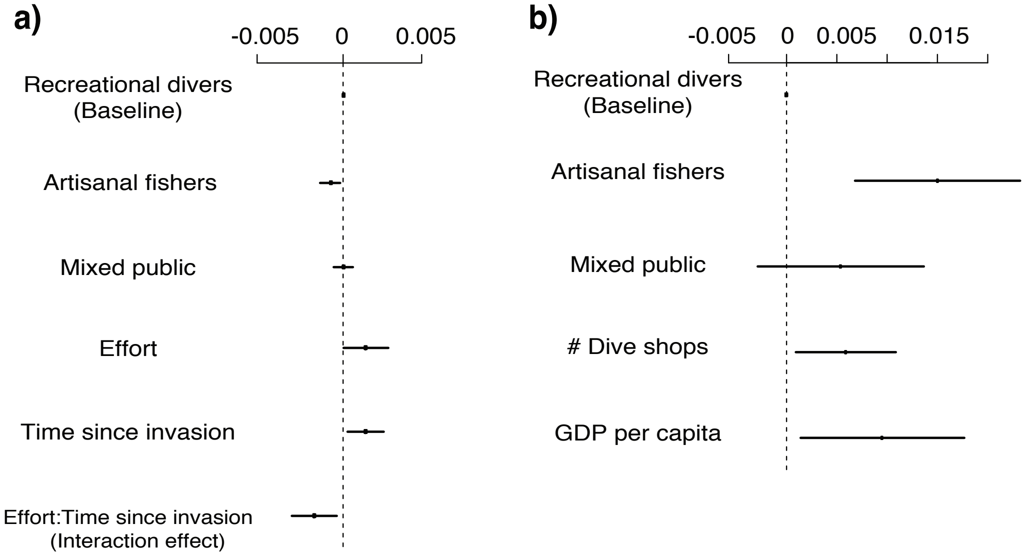

Figure 5.2: Model averaged coefficient estimates (logged) for explanatory variables retained in the best-supported generalized linear models of two metrics of lionfish derby success: a) catch (number of lionfish caught per day), and b) participation (total number of participants). See Methods section for details on model coefficient averaging procedure. The estimates of the effects of artisanal fishers and mixed public are expressed in relation to the recreational diver baseline (for catch = 5.53 (± 0.45); for participation = 2.96 (± 0.31)). Error bars represent 95% confidence interval.

5.2a). There was a negative interaction between effort and invasion timing (Table 5.2): at sites more recently invaded, catch increased with effort, but at sites invaded longer ago, catches reached an asymptote and subsequently decreased slightly with increased effort.

### 5.4.2 Participation

Two models of public participation were supported by the data (Table 5.2), although the top model obtained $\sim$1.93 more support than the second-ranked model. Contrary to predictions, the time elapsed since the start of the lionfish invasion at a locale did not predict derby participation and was not retained in any of the top models. Just like lionfish catch, participation varied among participant types (Fig. 5.2b). Participation was similar for derbies dominated by recreational divers and those attended by a mixed public, but derbies dominated by artisanal fishers were larger (Figs 5.2b, 5.3c, 5.d). As predicted, participation increased with the number of local dive shops and with GDP per capita (Figs 5.2b, 5.3c,d).

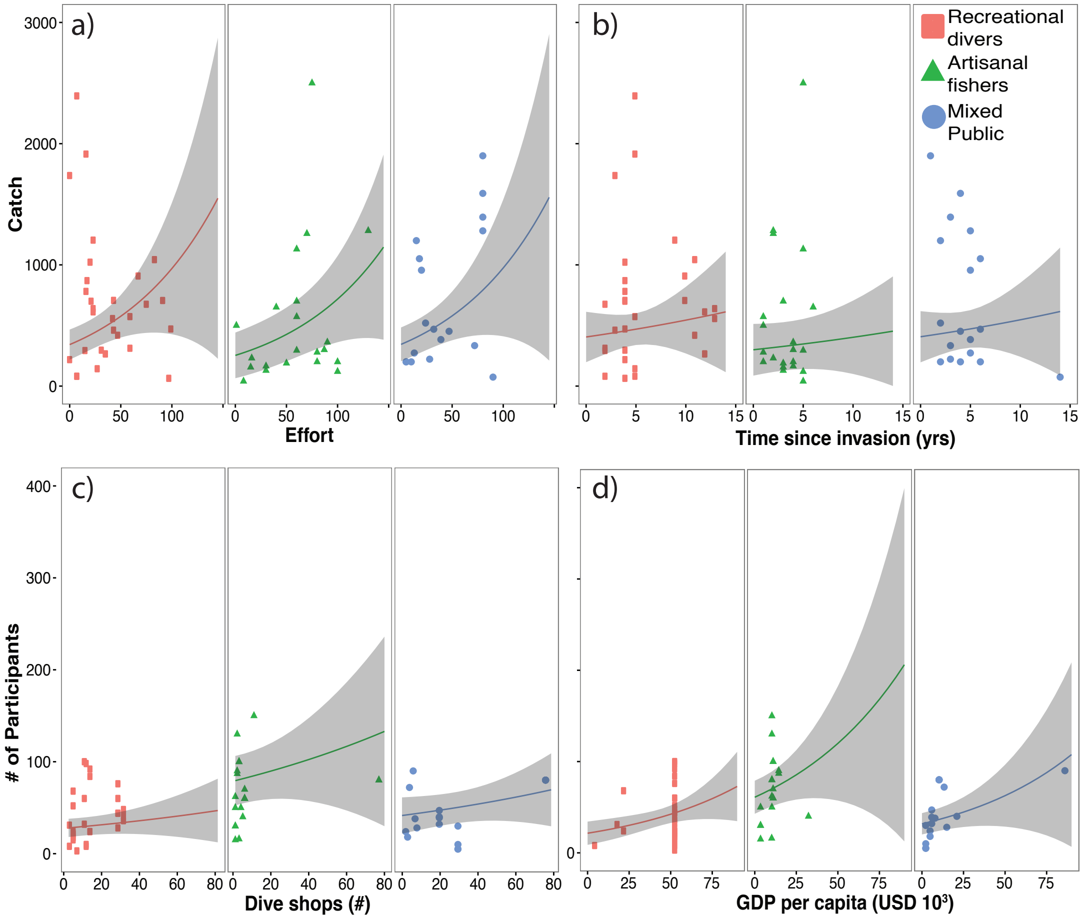

Figure 5.3: Relationships between key predictors and lionfish derby catch (i.e., total number of lionfish caught per day) (a and b), and derby participation (i.e., total number of participants per derby) (c and d) derived from generalized linear models. Relationships are shown separately for each category of participant. Points represent observed data, while continuous lines represent fits to each model's predicted values. Grey areas indicate 95% confidence interval of model fits. Note that model estimates were generated using all three categories of participants combined, but for visualization purposes results are presented separately for each category.

## 5.5 Discussion

Culling has been widely used as a tool to control wild populations of invasive species (Park, 2004; Hulme, 2006). In the case of lionfish, it is currently the most popular mitigation tool in areas where the species is established (Côté et al., 2014a), but it is one that depends heavily on continued public participation. Correlates of two metrics of lionfish derby success were identified. The number of lionfish caught increased with effort and time since lionfish establishment. In contrast, the number of derby participants covaried with the number of local dive shops and GDP per capita. Both catch and derby size varied depending on whether the main participants were recreational divers or artisanal fishers. The large geographic scale of the analysis and limited data from some areas generated large uncertainty in some of the model estimates, which warrants a cautious interpretation; however, most of the predictions made a priori were supported. Understanding the drivers of derby success can help design more effective lionfish culling campaigns.

### 5.5.1 Lionfish catch

Not surprisingly, more lionfish were caught when there were more derby participants. However, this relationship is weak, with each additional lionfish hunter in a derby resulting in only one additional lionfish caught. Note that the uncertainty around the catch-effort relationship is large, especially at high effort and for derbies dominated by artisanal fishers. Several factors likely contribute to this variability. For example, a larger number of lionfish catchers might not always reflect higher effort if people hunt in groups rather than individually. More lionfish catchers might also not translate into a larger number of boats participating in a derby if each boat carries more people, and ultimately, the number of boats might determine the size of the area covered during a derby and hence the catch. There were unfortunately no data on boat numbers. Likewise, the experience level of participants might affect this relationship. A participant experienced at spearing lionfish could be far more successful than several participants with little experience. Finally, variation among sites in lionfish abundance could introduce noise in the catch-effort relationship: at high lionfish abundance, adding hunters probably results in increased catch, whereas at lower abundance, it might not.

Time since the start of the lionfish invasion also plays an important role in determining catch. As predicted, catch was lower in recently invaded areas than in areas invaded longer ago, probably owing to the lower density of lionfish in the former locations. This observation supports the suggestion that harvest by recreational divers could be an efficient control tool at locations with high numbers of lionfish (Morris and Whitfield, 2009). However, the same observation raises the issue of whether implementing derbies in areas where lionfish have recently arrived (< 5 years) is wise. At several recently invaded locations, derbies were held in one year, yielded low catches (i.e., < 500 lionfish), and were not held subsequently. While this could indicate logistical difficulties in implementing derbies at these sites, it could also result from a lack of interest by participants and/or a low willingness of organizers to embark in another derby given low lionfish catches.

There was a negative interaction found between effort and time since invasion in predicting lionfish catch. This interaction is likely to be underpinned by an asymptotic relationship between catch and effort, as reviewed in (Hilborn and Walters, 1992). In recently invaded areas (i.e., the accelerating part of the curve) catch increases with effort, while in areas with a longer invasion history (i.e., the asymptotic part of the curve) catch stabilizes or decreases. Other factors that might have an effect on this interaction include the total area over which lionfish were captured, derby frequency, or the potential behavioural response of subjecting a population to a large-scale fishing effort (Côté et al., 2014b).

Finally, derbies dominated by artisanal fishers had the lowest catches, contrary to the expectation that this group, which has the most fishing experience, would be associated with high-catch derbies. More lionfish were caught daily in derbies dominated by recreational divers or with a mixed public. It could be that the lionfish-catching method preferred by artisanal fishers (i.e., usually free-diving) might be less effective than that used by recreational divers (i.e., SCUBA diving). It is also important to note that the areas where derbies were dominated by artisanal fishers tended to be areas invaded only recently by lionfish, potentially confounding the results and lowering the estimates of catch for artisanal fishers. The differences in daily catch between participant categories might therefore be driven largely by local lionfish abundance.

### 5.5.2 Participation

Time since invasion did not influence participation in lionfish derbies. It was expected that at sites where lionfish have been present for many years, public awareness of the problem and willingness to act locally would be heightened, leading to increased participation. Although awareness of lionfish appears to be higher in recently invaded than in non-invaded areas, at least among fishers (Ali, 2011), it is not clear that general awareness levels increase over time. For example, only about half of the members of the general public in Florida, where lionfish have been established for more than a decade and where outreach is extensive, are aware of the presence of lionfish in local waters (Harvey and Mazzotti, 2015). Moreover, recreational divers are generally very well informed, regardless of whether they dive in invaded or uninvaded areas (Ali, 2011; Harvey and Mazzotti, 2015), probably because of their first-hand experience with encountering lionfish. There may therefore be no link between time since lionfish invasion and public awareness, and other factors, such as promotion and awareness campaigns, might be better predictors of the number of participants attending a derby (Morris, 2012; Ali et al., 2013).

Interestingly, participation in derbies was highest when artisanal fishers dominated the pool of participants. It was expected that derbies targeting recreational divers would be the largest because of the appeal of partaking directly in coral reef conservation. It is likely that artisanal fishers were motivated to participate in derbies by the prizes (material and/or monetary), although a conservation interest should not be ruled out. Interviews with local artisanal fishers in developing countries indicate concern and interest in managing the lionfish invasion (Ali, 2011; personal observations). The apparent discrepancy between having lower catches but more participants when derbies are dominated by artisanal fishers might again be explained by the difference in time since invasion between areas with derbies involving mainly recreational divers (e.g., Florida, Bahamas, and other Caribbean Island States; > 5 years since invasion), and those with derbies involving mainly artisanal fishers (e.g., Mexico and Central America; < 5 years).

As expected, having more dive shops in an area and higher GDP per capita were associated with increased participation. The two factors are undoubtedly interrelated. The associations reflect not only the fact that diving is a relatively expensive recreational pursuit, but also a willingness by the diving community (composed of locals and tourists who dive recreationally) to pay to help mitigate the lionfish invasion. The cost of participation can be considerable: participants in Florida and The Bahamas spend $820 (USD) on average to participate in lionfish derbies (Trotta, 2014). More broadly, GDP per capita is a good predictor of willingness to pay for biodiversity conservation initiatives (Jacobsen and Hanley, 2009).

### 5.5.3 Implications for future derbies

The findings from this study can help to inform the design and implementation of future derbies. For example, to the extent that lionfish catch and participation are useful measures of success, derbies should be held in areas where lionfish are well established, and where the pool of potential participants is large (e.g., areas with several dive shops). The latter situation might more often, though not always, occur in developed than developing states. Although the results suggest that recreational divers might be more effective lionfish catchers, a wholesale targeting of recreational divers at the expense of artisanal fishers as derby participants is not recommended. In this study, the type of derby participant was geographically confounded with time since lionfish invasion, and it is currently not possible to disentangle these effects. There can be significant benefits to engaging artisanal fishers in local marine conservation efforts, e.g. as citizen scientists who can help with early detection of invaders (López-Gómez et al., 2013; Scyphers et al., 2015).

It is important to remember that the recommendations made here are intimately tied to the goal of management. Most lionfish derbies currently aim to provide intensive lionfish removal as well as to promote outreach and involve local communities in conservation (Akins, 2012). However, if the management goal is to slow the invasion, other metrics of success would be needed (e.g., harvest rate as a % of local abundance, and spatial extent of the harvest area). Such metrics, however, will require additional data (e.g., lionfish density) not currently available at the regional level. In this case, early detection is critical, because the longer invaders remain undetected, the lower the likely success of controlled interventions (Simberloff, 2003; Lodge et al., 2006). To keep lionfish populations in the lag phase that precedes exponential growth as long as possible, the focus should be on areas where no or very few lionfish have been detected, and the derby approach modified to a more frequent or continuous, monitoring-like incentive scheme.

Lionfish derbies are likely to remain an important strategy to control invasive lionfish populations locally and mitigate their effects on native fauna. Awareness campaigns and derby promotion should help increase participation, while judicious choice of the location and/or frequency of derbies should ensure large catches and continued interest by derby participants. Managers and organizers should also allocate resources to estimate lionfish population densities, before and after culls (Green et al., 2013). Only then will the true effectiveness of culling tournaments be understood.

# Chapter 6

# General Conclusions

My thesis combined approaches from ecology and socioeconomics to investigate the dynamics, impacts and responses of/to a specific stressor − the lionfish invasion − on a complex social-ecological system (Kittinger et al., 2012) − coral reefs. I used a combination of field surveys, micro-chemical analysis tools, interviews and quantitative modeling to gain insights into two major areas. First, I explored how an invasive predator can change trophic interactions and food web dynamics of coral reef communities. Second, I investigated how the impacts of an invasive predator can also affect the socioeconomic systems that depend on the natural systems. By focusing on a social-ecological system my thesis highlights the need for an interdisciplinary approach to fully understand the impacts of stressors, and particularly the need for research that goes beyond the direct consumption impacts of lionfish. This approach can provide the basis for sound decisions regarding control and mitigation actions to fight this invasion.

## 6.1 Unraveling the impacts of lionfish on ecosystem function and reconsidering management actions

The evidence to date suggests that the lionfish invasion is a major driver of change on coral reefs of the Wider Caribbean Region (Hixon et al., 2016). Studies have extensively documented the direct impacts of lionfish prey consumption (Albins and Hixon, 2008; Lesser and Slattery, 2011; Albins, 2012; Green et al., 2012; Benkwitt, 2014; Dahl and Patterson, 2014; Ballew et al., 2016; Smith et al., 2017), as well as showed how this invasion is changing the structure of communities (Lesser and Slattery, 2011; Green et al., 2012; Chapter 2). Despite the negative impacts of lionfish at many sites (e.g. Albins and Hixon, 2008; Lesser and Slattery, 2011; Green et al., 2012; Rocha et al., 2015), it is still not clear what the long-term ecological consequences of this invasion will be. Can Caribbean reefs cope with yet another stressor, or will their resilience (see Holling, 1973; Gunderson, 2000; Lade et al., 2013) be exceeded, leading to an ecological regime shift?

Changes in biodiversity – not only the loss but also the addition of species – can lead to changes in trophic interactions among species and trophic groups. Based on the scale and severity of these trophic changes, theory predicts that they could affect ecosystem function (Thébault and Loreau, 2005; Dobson et al., 2006). Therefore, in the case of predatory invaders, research should also focus beyond the impacts of direct consumption and assess potential impacts on ecosystem function. I show in Chapters 2 and 3 that lionfish have had impacts on the structure of fish communities as well as on the trophic interactions that are, to some degree, affected by this invasion. These latter impacts are complex: lionfish have potentially triggered inter- and intraspecific competition interactions, as well as behaviourally mediated effects on native species.

The stable isotope information I obtained and analyzed suggests that changes have occurred not only to the trophic niches of the lionfish population but also of the reef fish community. Therefore, while I propose different mechanisms to explain the trophic niche metric patterns observed in Chapters 2 and 3, it is possible that some of the changes observed to the trophic niche of the lionfish population could be explained by the changes to the trophic niche of the fish community. As lionfish predation has potentially changed the trophic niches of the reef fish community and thus its trophic niche metrics, these isotopic changes could be transferred up to the lionfish population and hence be reflected in its trophic niche metrics. However, untangling the contribution of these different mechanisms – lionfish tracking prey availability versus changes in the trophic niche of the fish community – would be impossible with the data at hand and would require a study that ideally incorporates stomach content analysis as well as stable isotope prey data. Such information would allow estimating the contribution of the different prey items to lionfish diet and pinpointing the main drivers behind the lionfish trophic niche shifts.

As direct and indirect impacts of lionfish change trophic interactions between prey and consumers, these effects reverberate throughout the community, and key ecosystem functions such as the transfer of energy and nutrients could be altered, with unknown consequences for coral reefs functioning. The changes observed in trophic niche metrics of invaded reef fish communities suggest that deep alterations to the structure and dynamics of food webs on coral reefs are already underway. Unless ecosystem processes such as reef productivity, biomass turnover, and species recruitment can help the reef ecosystem to cope with these large impacts, changes to the structure and biodiversity of reef communities will continue and likely change the way coral reef ecosystems work in the invaded region. Also, the addition of the lionfish invasion to the long list of anthropogenic stressors currently impacting coral reefs in the Wider Caribbean Region could further degrade coral reef ecosystems and drive them to new equilibrium states (Gutiérrez et al., 2014). Therefore, more studies are needed both to assess tipping points in the resilience of coral reefs in the context of this invasion, as well as to evaluate management strategies that can not only mitigate the impacts of this invasion but enhance overall ecosystem resilience.

Practical and ecological factors have raised concern regarding the appropriateness of lethal control of invasive species (Doherty and Ritchie, 2017). In Chapter 3 I found evidence that the recurrent removal of lionfish through culling, which is widely used to mitigate the negative impacts of this invasion, might have unexpected consequences on direct and indirect predation interactions. This is likely due to the disruption of spatial (movement) processes related to density-dependent intraspecific competition (Benkwitt, 2013; Tamburello and Côté, 2015; Smith et al., 2017). However, at the moment it is not clear whether the changes observed in trophic metrics as a result of lionfish removal would result in negative impacts on fish community structure or ecosystem function. Questioning the efficacy of lionfish culling would be particularly concerning given its widespread use to control this invasion, and reported positive impacts on native communities (Green et al., 2014). However, other studies have also pointed out logistical limitations (e.g. high and sustained effort needed; Barbour et al., 2011) and unexpected consequences (e.g., changes in lionfish behaviour that could make further captures difficult; Cote et al., 2014b; but see Cote et al., 2014a) of this control strategy. Therefore, further studies are needed not only to explore whether culling can mitigate the direct predatory impacts of lionfish (see Green et al., 2013), but also to assess the net benefits of implementing or not implementing removal action.

## 6.2 Beyond the ecological impacts of the lionfish invasion

While the study of the ecological impacts of invasive species is warranted, researchers should also assess the potential and real impacts to ecosystem services. Coral reefs provide many important services to people, some of which will undoubtedly be affected to some degree by the lionfish invasion (Albins and Hixon, 2011; Johnston et al., 2015; Hixon et al., 2016). These include declines in commercially or recreationally important species (Morris and Akins, 2009; Green et al., 2012; Ballew et al., 2016), but also changes in the experience of marine tourists (e.g., divers and snorkelers) as a consequence of lower densities of reef fishes and reduced coral cover if trophic cascades are unleashed (Albins and Hixon, 2011; Lesser and Slattery, 2011). In Chapter 4 I find evidence that the ecological impacts of the lionfish invasion can reduce the attractiveness of sites to some marine tourists. These findings are relevant given the economic importance of snorkeling and diving tourism in the Wider Caribbean Region (European Commission, 2002; Cesar et al., 2003). Moreover, the results from Chapter 4 also indicate that stakeholders such as marine tourists appear to be willing to contribute to the financing of conservation and management initiatives. This is good news, given that lionfish eradication is virtually impossible with current technologies, and the large costs associated with managing this invasion will therefore have to be borne in the long term.

There is no doubt that anthropogenic activities are the major causes of species invasions globally (Carlton, 1999; Carlton, 2003). In the case of lionfish, the aquarium trade and a subsequent release of fish on coral reefs off Florida caused this invasion (Whitfield et al., 2002; Semmens et al., 2004). While human actions such as these ones can have large negative impacts we must ultimately also turn to the human component of the social-ecological system to find solutions to human-made problems. By creating lionfish derbies, which I explore in Chapter 5, managers have not only attempted to tackle lionfish proliferation, but have also involved local communities as "underwater conservation soldiers", making them key actors in the management effort. Involving communities into preserving their natural resources in this way greatly increases the likelihood of successful conservation results (Granek et al., 2008). However, while the perceived goals of lionfish derbies throughout the invaded range are the same, the local conditions where these events occur are strikingly different and as such, so could the outcomes. Managers planning derbies should pay close attention to the fishing effort exerted per derby and the local time since invasion, as these are key factors that will drive lionfish catch, while national wealth (GDP per capita) and number of local dive shops will determine the pool of participants. Therefore, managers should ideally implement derbies only when and where their likelihood of success is high. Lionfish derbies are an example of how interactions between ecological and social systems change in the face of an ecosystem stressor, in this case providing economic, conservation, and research opportunities.

Given the exceedingly low likelihood of lionfish eradication, control strategies with a different perspective should be explored. Beyond the immediate benefits expected from lionfish derbies, their widespread implementation could ultimately help to motivate local commercial fishing initiatives that could help to curtail the reported exponential growth of lionfish populations in some invaded areas (Whitfield et al., 2007; Schofield, 2009; Côté et al., 2013). As the social-ecological system adapts to this invader, and despite the evident negative impacts to the ecosystem, new approaches such as those that advocate the use of the invasive species as a resource should be explored (Shaanker et al., 2010; Kannan et al., 2014). While several calls have been made to exploit lionfish (Gallagher, 2013; Lund, 2015; Carrillo-Flota and Aguilar-Perera, 2017), a fishery is still in its early stages in just a few localities in The Bahamas, Haiti, Costa Rica and Mexico (personal observation; Carrillo-Flota and Aguilar-Perera, 2017). However, concerns exist that establishing a lionfish fishery would shift the management goal from controlling and limiting lionfish populations to ensuring their continued harvesting for profit (Aguilar-Perera, 2013). Therefore, the implementation of any lionfish fishery, while providing an economic alternative to local fishing communities, should ideally be implemented as part of an ongoing fishing operation that could target lionfish with a minimal investment in fishing gear, as well as with awareness campaigns addressed to the fishing community explaining the long-term benefits of maintaining low lionfish densities at the local scale. Ideally, an enterprise such as this should also assess ongoing potential negative interactions with established fisheries (e.g., competition for habitat and prey with native predators that are the target of traditional fisheries, predation on juvenile stages of target species, etc.), and have clear management goals that ultimately aim to minimize the negative impacts of this invasion.

## 6.3 Global stressors and the need for a unified front

The different levels at which the lionfish impacts are taking place will ultimately test the resilience of the complex social-ecological system that is created by coral reefs in the invaded region. Whether the lionfish impacts – combined with other damaging anthropogenic stressors affecting coral reefs – could push the system to a new equilibrium state is yet to be seen; however, current literature and results from this thesis indicate that changes at both the ecological and social levels are already taking place.

As coral reef ecosystems in the Wider Caribbean Region change as a consequence of the lionfish invasion, both the natural and the social component of the large socio-ecological system adjust to the presence of this invader, either with negative or positive consequences. This dissertation sheds light on the need to study and manage the impacts not only of the lionfish but also of other invasive species and perhaps also of other stressors, from a multidisciplinary and integrated perspective since impacts will rarely be limited to the natural system. Adopting a social-ecological system approach to tackle the lionfish invasion can help to advance our understanding and provide solutions that might ensure the persistence of both natural and social systems.

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# Appendix A

# Supporting material for Chapter 2

Table A.1: Individual and cumulative contributions of individual species to dissimilarity in prey fish community structure between 2008 and 2010 on Bahamian reef sites invaded by Indo-Pacific lionfish. Only species that contributed disproportionately (i.e., > 1.8%; see Methods in main text) are shown. * Denotes species that have been confirmed as prey of lionfish at my study sites during the study period through analyses of lionfish stomach contents.

| Family | Species name | Individual contribution (± SD) | Cumulative contribution |
|---|---|---|---|
| Gobiidae | **Coryphopterus personatus* | 0.0912 (0.0725) | 0.1721 |
| Labridae | **Clepticus parrae* | 0.0851 (0.0686) | 0.3326 |
| Atherinidae | **Atherinomorus sp.* | 0.0479 (0.0990) | 0.4228 |
| Inermiidae | **Haemulon vittatum* | 0.0421 (0.0878) | 0.5023 |
| Pomacentridae | **Chromis cyanea* | 0.0320 (0.0213) | 0.5627 |
| Carangidae | *Selar crumenophthalmus* | 0.0240 (0.0407) | 0.6079 |
| Labridae | **Thalassoma bifasciatum* | 0.0196 (0.0144) | 0.6448 |

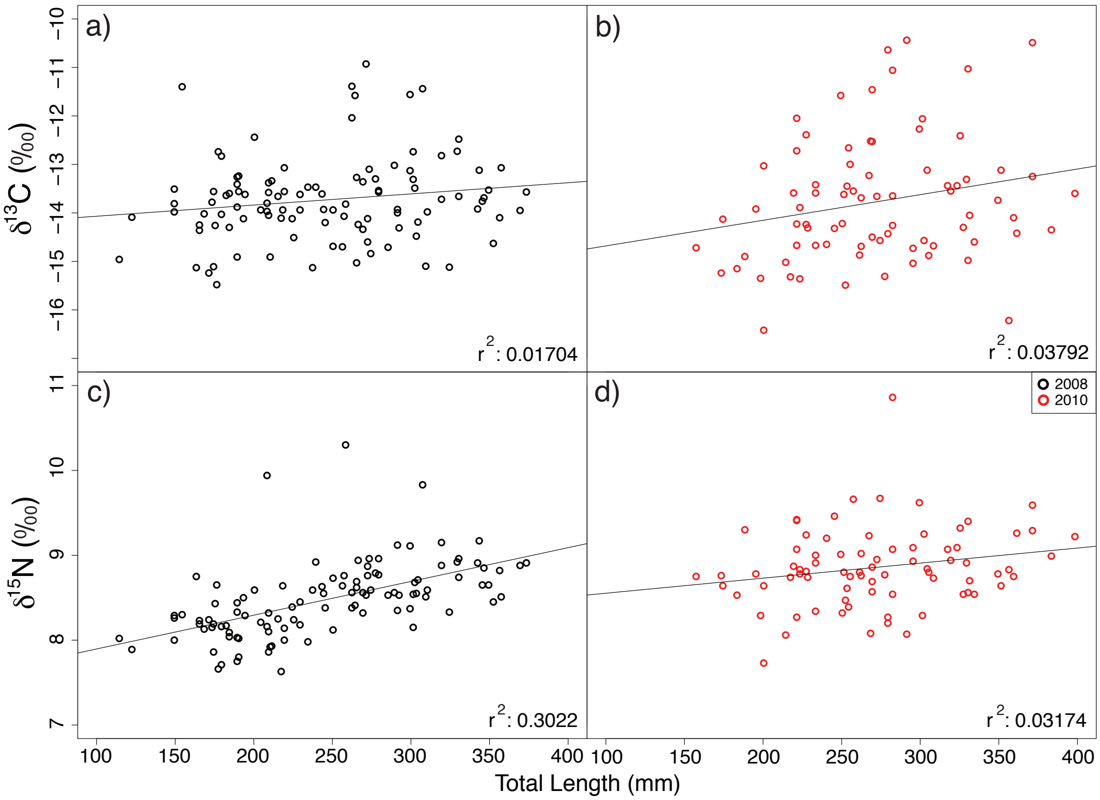

Figure A.1: Nitrogen (a and b) and carbon (c and d) stable isotope ratios as a function of total length for lionfish collected off New Providence, The Bahamas, in 2008 (a and c) and 2010 (b and d). Linear regression model results suggest that the values of $\delta^{15}$N increased with lionfish length, although the relationship was marginally non-significant in 2010 (2008: $F_{(1,104)} = 46.48$, $p < 0.001$; 95 % C.I. = 0.0023 − 0.0051; 2010: $F_{(1,76)} = 3.52$, $p = 0.06$; 95 % C.I. = -0.0001 − 0.0037). The values of $\delta^{13}$C also increased significantly with fish length but only in 2010 (2010: $F_{(1,76)} = 4.04$, $p = 0.04$; 95 % C.I. = 0.00004 − 0.01; 2008: $F_{(1,104)} = 2.82$, $p = 0.09$; 95 % CI = -0.0004 − 0.005). Fitted regression lines (solid lines) and $r^2$ values are shown for each isotope and year.

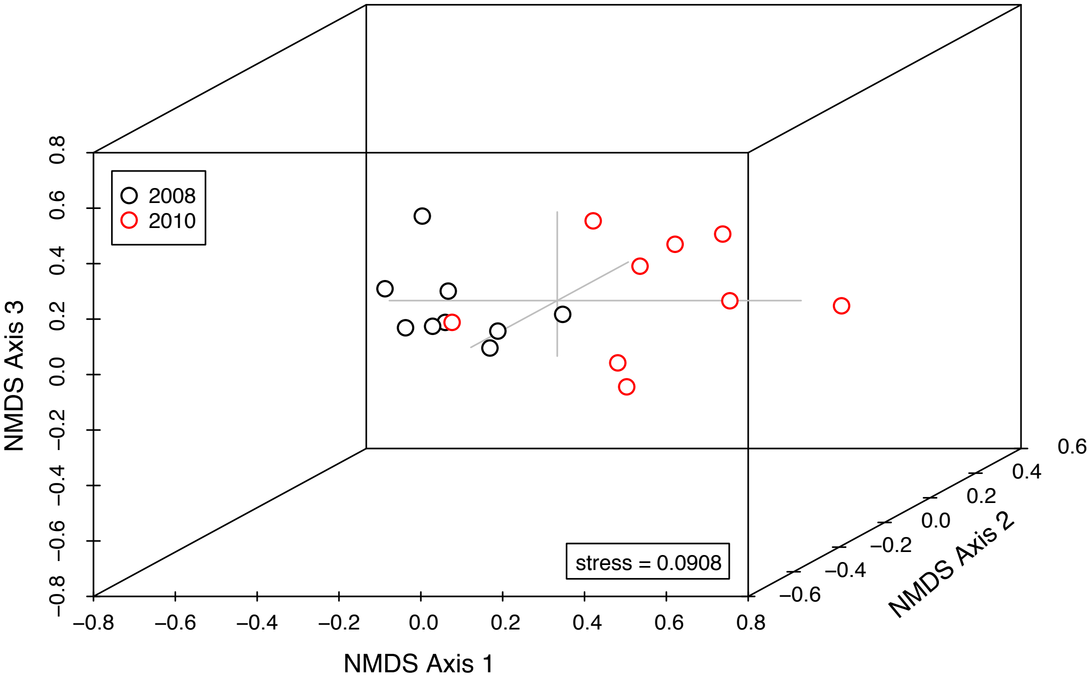

Figure A.2: Non-metric MDS visualization of mean lionfish prey community structure (all reef fish individuals <15cm TL) surveyed at nine reef sites off New Providence, The Bahamas, in 2008 and 2010.

# Appendix B

# Supporting material for Chapter 3

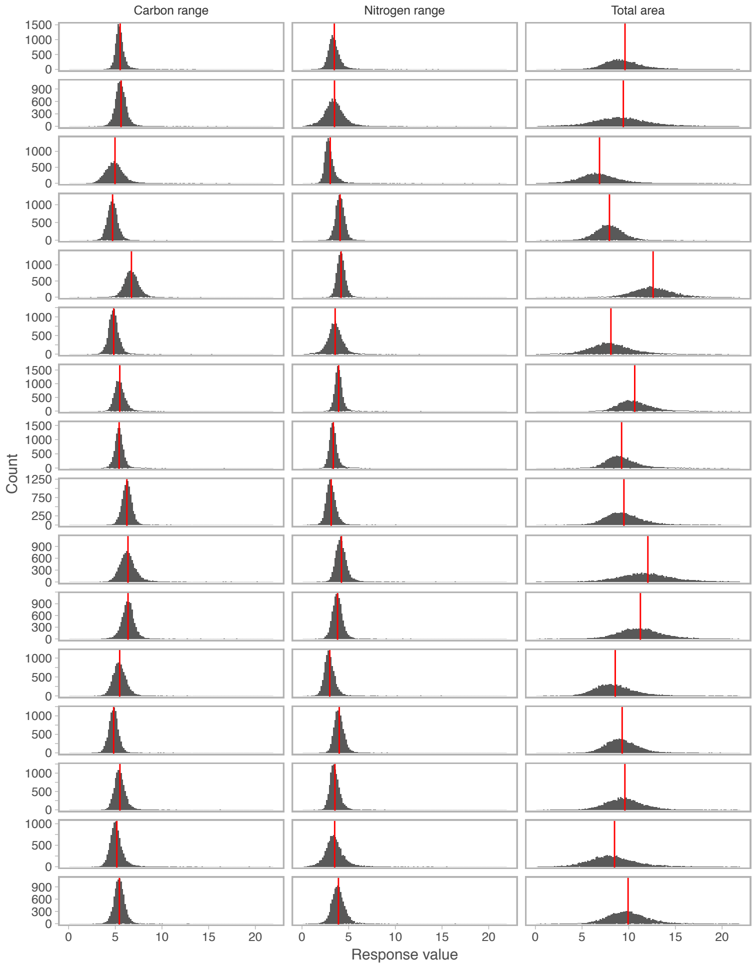

Figure B.1: Posterior distributions for trophic niche metrics (CR: carbon range, NR: nitrogen range, TA: total area) inferred from stable isotope analysis of carbon and nitrogen estimated from reef fish in 16 reef patch communities in Rock Sound, Eleuthera Island, The Bahamas. Response values for CR, NR and TA are in ‰.

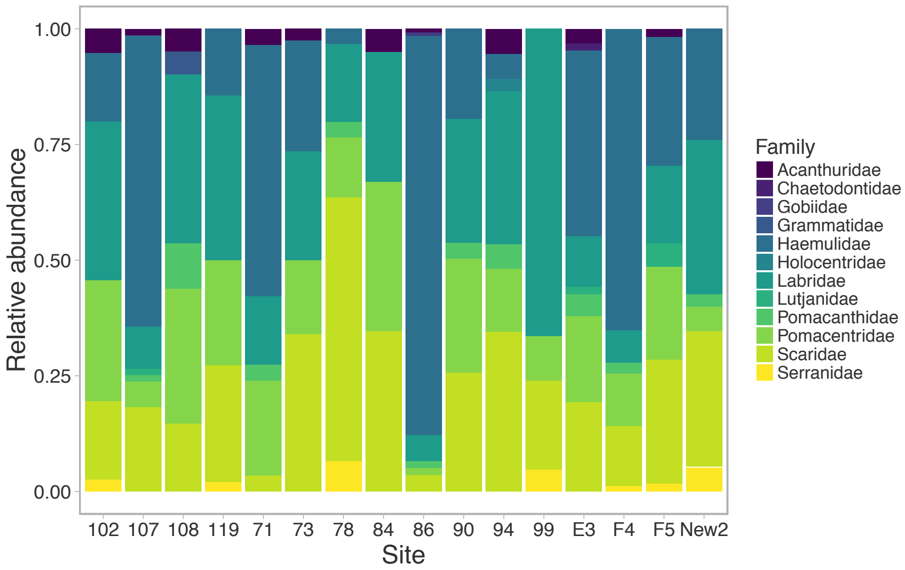

Figure B.2: Relative abundance (as % of total fish counted on each reef) of fish families sampled in summer 2013 at 16 reef patches in Rock Sound off Eleuthera Island, The Bahamas.

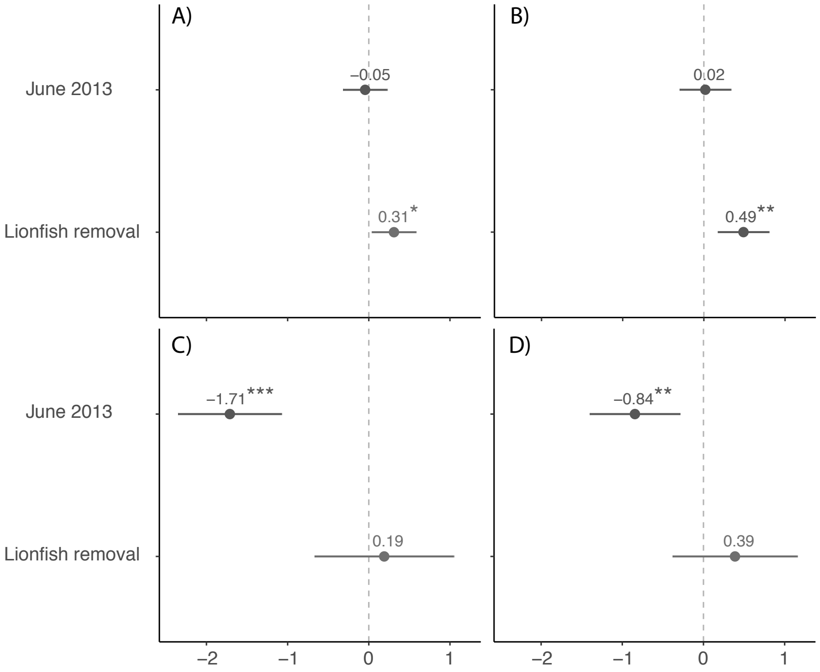

Figure B.3: Coefficient estimates for linear mixed-effects models (LMM) of the effect of time (shown: June 2013 against June 2012 baseline) and lionfish removal (shown: lionfish removed vs no removal baseline) on density of (A) obligate reef fish species (all sizes), (B) small obligate reef species (i.e., prey fish < 15 cm TL), (C) lionfish, and (D) native predators (i.e., snappers and groupers). Error bars around the estimates indicate 95% confidence intervals. Significance levels: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$.

# Appendix C

# Supporting material for Chapter 4

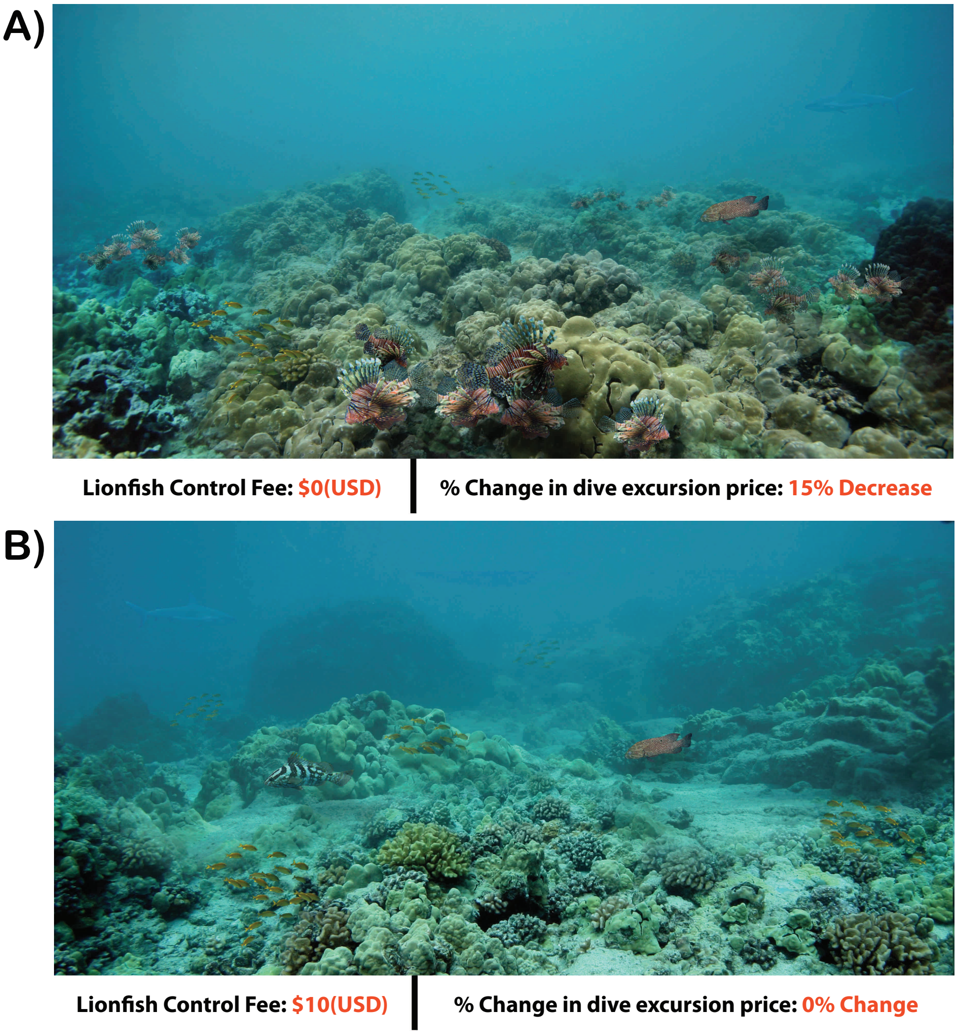

Figure C.1: Choice set example of two reef scenarios (A and B) showing different combinations of attribute levels.

Table C.1: Part-worth utility of eight coral reef scenario attributes for a multinomial logit model (MNL) of tourists involved in marine activities in Cozumel, Mexico. Part-worth utility values are shown for every level of each attribute. In the case of continuous attributes, the estimate reflects the slope of the linear effect. Model intercept represents the likelihood of choosing a Cozumel dive site over the “Do not dive in Cozumel” option. Significance for within-class tests: *** P = 0.01, ** P = 0.05, * P = 0.10.

| | | **Parth-worth utility** |
|---|---|---|
| **Attributes** | **Levels** | **Class 1** |
| Intercept | Program A or B | -1.00*** |
| Lionfish density | 0 | -0.10 |
| | 1 | 0.17* |
| | 10 | -0.01 |
| | 25 | -0.05 |
| Control fee (USD) | $0 | -0.05 |
| | $5 | 0.06 |
| | $10 | -0.01 |
| | $15 | -0.01 |
| Grouper density | 0 | -0.42*** |
| | 1 | -0.16** |
| | 2 | 0.19** |
| | 4 | 0.39*** |
| Reef shark | Absent | -0.19*** |
| | Present | 0.21*** |
| Coral cover | < 5% | -0.20** |
| | 10-20% | -0.15** |
| | 30-40% | 0.15** |
| | 70-80% | 0.20*** |
| Reef relief | 1.4 | -0.30*** |
| | 1.6 | -0.5 |
| | 1.8 | 0.18*** |
| | 2 | 0.17** |
| Native prey density | 44 | 0.02 |
| | 74 | -0.02 |
| | 96 | -0.06 |
| | 135 | 0.06 |
| Excursion price change | -15% | 0.09 |
| | -5% | 0.04 |
| | 0% | -0.05 |
| | +10% | -0.08 |

Table C.2: Part-worth utility of eight coral reef scenario attributes for a two latent-class model (LC) of tourists visiting Cozumel, Mexico. Part-worth utility values are shown for every level of each attribute. In the case of continuous attributes, the estimate reflects the slope of the linear effect. The Wald II statistic is used to test differences among tourist classes. Model intercept represents the likelihood of choosing a Cozumel dive site over the "Do not dive in Cozumel" option. Significance for within-class tests: *** P = 0.01, ** P = 0.05, * P = 0.10.

| | | **Parth-worth utility** | | |
|---|---|---|---|---|
| **Attributes** | **Levels** | **Class 1** | **Class 2** | **Wald II** |
| Intercept | Program A or B | 2.04*** | 2.23*** | 0.04 |
| Lionfish density | 0 | 0.09 | -0.46*** | 17.13*** |
| | 1 | 0.12* | 0.29** | |
| | 10 | -0.02 | -0.07 | |
| | 25 | -0.19** | 0.24** | |
| Control fee (USD) | Linear | 0.02** | -0.01 | 5.52** |
| Grouper density | 0 | -0.39*** | -0.63*** | 3.05 |
| | 3 | -0.21** | -0.16 | |
| | 6 | 0.20** | 0.26* | |
| | 9 | 0.40*** | 0.54*** | |
| Reef shark presence | Absent | -0.20*** | -0.04 | 2.87* |
| | Present | 0.20*** | 0.04 | |
| Coral cover | 5% | -0.26** | -0.22 | 0.36 |
| | 15% | -0.19** | -0.15 | |
| | 35% | 0.22** | 0.14 | |
| | 75% | 0.23*** | 0.22 | |
| Reef relief | 1.4 | -0.31*** | -0.29 | 0.5 |
| | 1.6 | -0.06 | -0.13 | |
| | 1.8 | 0.21** | 0.18* | |
| | 2 | 0.16** | 0.24* | |
| Native prey density | 44 | -0.04 | 0.07 | 3.18 |
| | 74 | -0.06 | 0.12 | |
| | 96 | 0.01 | -0.19 | |
| | 135 | 0.09 | -0.01 | |
| Excursion price change | Linear | -0.25 | -0.86 | 0.51 |

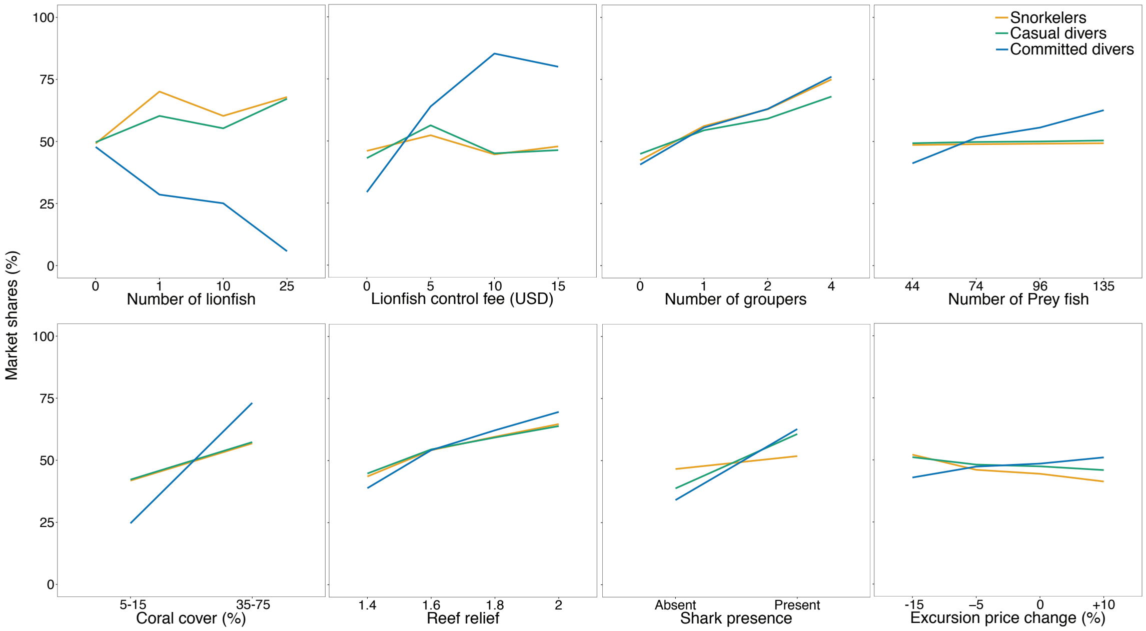

Figure C.2: Sensitivity of market shares to changes in attribute levels for three classes of marine tourists: snorkelers (yellow), casual divers (green) and committed divers (blue). Comparisons are made to the lowest value for all numeric attributes or arbitrary levels for nominal attributes.

Table C.3: Part-worth utility of eight coral reef scenario attributes for three known/latent classes of tourists involved in marine activities in Cozumel, Mexico. This model specification does not include covariates. Part-worth utility values are shown for every level of each attribute. In the case of continuous attributes, the estimate reflects the slope of the linear effect. The Wald II statistic is used to test differences among tourist classes. Model intercept represents the likelihood of choosing a Cozumel dive site over the "Do not dive in Cozumel" option. Significance for both within-class and between-class tests: *** P = 0.01, ** P = 0.05, * P = 0.10.

| | | **Parth-worth utility** | | | |
|---|---|---|---|---|---|
| **Attributes** | **Levels** | **Snorkelers** | **Casual divers** | **Committed divers** | **Wald II** |
| Intercept | Program A or B | 2.21*** | 2.14*** | 2.23*** | 0.04 |
| Lionfish density | 0 | -0.52*** | -0.35** | 1.32*** | 36.72*** |
| | 1 | 0.33*** | 0.05 | 0.36 | |
| | 10 | -0.08 | -0.10 | 0.07 | |
| | 25 | 0.27** | 0.40** | -1.74*** | |
| Control fee (USD) | $0 | 0.06 | 0.04 | -1.26*** | 25.08*** |
| | $5 | 0.15 | 0.20 | -0.06 | |
| | $10 | -0.15 | -0.20** | 1.00*** | |
| | $15 | -0.07 | -0.03 | 0.31 | |
| Grouper density | Linear | 0.38*** | 0.24*** | 0.56*** | 3.41 |
| Reef shark | Absent | -0.04 | -0.21** | -0.25 | 3.64 |
| | Present | 0.04 | 0.21** | 0.25 | |
| Coral cover | 5-15% | -0.16** | -0.17** | -0.54*** | 6.20* |
| | 35-75% | 0.16** | 0.17** | 0.54*** | |
| Reef relief | Linear | 0.21*** | 0.15*** | 0.49** | 2.93 |
| Native prey density | Linear | -0.02 | 0.01 | 0.16 | 1.21 |
| Excursion price change | Linear | -0.09 | -0.08 | 0.15 | 1.77 |

Table C.4: Sociodemographic differences between snorkelers and divers surveyed in Cozumel in summer and winter of 2014 tested with unpaired t-tests. Significance levels were compared against a Bonferroni-adjusted critical alpha level of 0.014 (unadjusted alpha of 0.1/7 tests performed). See Methods for explanation of levels used for Education, Motivation for snorkeling or diving, Satisfaction, Environmental awareness and Lionfish invasion awareness.

| | **Snorkelers** | | | | | **Divers** | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | $\bar{x}$ | | | | | $\bar{x}$ | | | | |
| Variable | Summer | Winter | $t$ | df | $p$ | Summer | Winter | $t$ | df | $p$ |
| Age (years) | 36 | 35 | 0.18 | 102 | 0.86 | 39 | 42 | -2.20 | 203 | 0.03 |
| Income (Thousands USD) | 110 | 70 | 1.8 | 91 | 0.08 | 130 | 110 | 1.79 | 162 | 0.08 |
| Education | 2.80 | 2.86 | -0.21 | 104 | 0.83 | 3.10 | 3.00 | 0.68 | 183 | 0.50 |
| Motivation | 1.13 | 1.29 | -1.18 | 100 | 0.24 | 1.68 | 1.73 | -0.68 | 206 | 0.50 |
| Satisfaction | 4.53 | 4.86 | -1.41 | 104 | 0.16 | 4.75 | 4.67 | 1.04 | 208 | 0.30 |
| Environmental awareness | 3.00 | 3.29 | -0.91 | 104 | 0.36 | 3.12 | 2.86 | 1.96 | 207 | 0.05 |
| Lionfish invasion awareness | 1.92 | 2.14 | -0.47 | 104 | 0.64 | 3.28 | 3.48 | -1.16 | 207 | 0.25 |

Table C.5: Socio-demographic characteristics of tourists surveyed in Cozumel in summer and winter of 2014 in the current study and in previously published studies or official reports of tourists to the Mexican Caribbean (Güemes-Ricalde and Correa-Ruíz, 2010), and to Cozumel (Anaya-Ortíz and Palafox Muñoz, 2010; and SECTUR, 2009).

| Variable | | This study | Güemes-Ricalde and Correa-Ruíz (2010) | Anaya-Ortíz and Palafox Muñoz (2010) | SECTUR (2009) |
|---|---|---|---|---|---|
| Country of residence (%) | USA | 84 | 40 | 88 | 78 |
| | Canada | 7 | 8 | 8 | 6 |
| | Mexico | 4 | 3 | - | - |
| | Europe | 3 | 38 | - | - |
| | Other | 2 | - | - | 16 |
| Age (mean years) | | 42 | 35 | - | 36 |
| Gender | Female (%) | 31 | 42 | - | 37 |
| | Male (%) | 69 | 55 | - | 63 |
| Education (%) | University degree | 77 | - | 84 | - |
| Income (%) | >$60,000 USD | 64 | - | - | 67 |