Predation by Invasive Indo-Pacific Lionfish on Atlantic Coral Reef Fishes: Patterns, Processes, and Consequences

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Stephanie Jane Lee Green

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Examining Committee:

Chair: Wendy J. Palen, Associate Professor

Isabelle M. Côté
Senior Supervisor, Professor, Dept. of Biological Sciences
Simon Fraser University

Nicholas K. Dulvy
Supervisor, Professor, Dept. of Biological Sciences
Simon Fraser University

Mark A. Hixon
Supervisor, Professor, Dept. of Zoology
Oregon State University

Jonathan W. Moore
Internal Examiner
Assistant Professor, Dept. of Biological Sciences
Simon Fraser University

John F. Bruno
External Examiner
Associate Professor, Department of Marine Sciences
University of North Carolina Chapel Hill

Date Defended/Approved: November 30, 2012

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Ethics Statement

Abstract

Invasive species cause significant ecological impacts, ranging from the homogenization and reduction of biodiversity to changes in ecosystem function. In marine systems, where predation is a key force shaping demographic processes, predatory invaders are predicted to have particularly severe effects. My thesis focuses on the patterns, processes and consequences of the recent invasion of Western Atlantic coral reef habitats by predatory Indo-Pacific lionfish (*Pterois volitans and P. miles*). I first investigate the rate and timing of predation by lionfish through *in situ* observations on invaded Bahamian coral reefs, and find that lionfish primarily consume prey during crepuscular periods and at higher rates than reported from their native range. Next, I examine trends in the biomass of 42 native fishes found in the stomach contents of lionfish on invaded reefs, and find declines of ~65% in just two years likely owing to lionfish predation. Through field observations of predation and stomach contents analyses, I identify morphological and behavioural drivers of prey selection by lionfish: small size, shallow body depth, demersal habit, and not cleaning all contribute vulnerability to predation. Using these insights, I model the effect of lionfish predation on the biomass of their fish prey, taken as the difference between rates of lionfish prey consumption and prey fish production on invaded reefs, the latter estimated from community size-spectra data using metabolic scaling relationships. My model accurately predicts the magnitude of prey depletion observed on Bahamian reefs, and reveals that lionfish are likely to continue depleting native fishes unless culled by 30-95%. Finally, I conduct a removal experiment on 24 natural patch reefs over 18 months to test the model's predictions, and find that the lionfish density reductions predicted by the model are sufficient arrest native fish biomass declines. My thesis reveals the important role that invasive lionfish now play in structuring Atlantic coral reef fish communities, and quantifies the threat of invasion for the persistence of fish diversity in the region. However, by demonstrating that lionfish removal can limit the severe ecological impacts of this invasive predator, my research offers strategic targets and much needed hope for local marine management action.

Keywords: Exotic species; predator-prey interactions; diet selection; behavioural observations; size-based model; coral reef conservation

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Chapter 1

General Introduction

As rapid globalization continues to foster world-wide biotic exchange, many species are establishing populations outside of their native range, where they may become invasive and interfere with the ecological functioning of native communities (Elton 1958, Mack et al. 2000). Species invasions cause significant ecological and economic impacts, ranging from the homogenization and reduction of biodiversity to the loss of local food security (Chapin et al. 2000, Goodell 2000). With biological introductions occurring at an increasing pace (Mooney and Cleland 2001), there exists an urgent need for scientific information to aid in the prevention and mitigation of these effects. Researchers endeavour to deduce general principles that describe and predict patterns and processes of invasion, but the identity of the invader, circumstances surrounding its introduction, and the ecology of the community into which it is introduced complicate the formulation of widely applicable theory (Davis et al. 2000, Kolar and Lodge 2001, Sakai et al. 2001, Diez et al. 2008).

Of particular importance to the outcome of an invasion is the life history of the introduced species and its position within the trophic structure of the invaded system. While the majority of successful invaders occupy low trophic levels and impact invaded ecosystems by altering bottom-up processes (GISD 2012), the successful establishment of exotic predators can, in contrast, have direct top-down effects by altering feeding relationships (e.g. Reinthal and Kling 1997). In fact, predation is the sole cause of the majority of invasion-mediated extinctions of vertebrate species in terrestrial systems (Sax and Gaines 2008). In the marine realm, where predator-prey interactions are largely governed by body size (Kerr and Dickie 2001, Jennings 2005) and predation is a major force structuring community assemblage (Hixon and Carr 1997, Almany and Webster 2004), predator invasions are predicted to have particularly extreme consequences.

Invasions by marine predators are exceedingly rare, but one is currently occurring. The recent invasion of Indo-Pacific lionfish (*Pterois volitans* and *P. miles)* into the Western Atlantic and Caribbean represents the first marine vertebrate predator invasion of the region and is one of only a handful of successful vertebrate invasions across the world's oceans. First reported off the coast of Florida in the early 1980s, lionfish have rapidly established populations throughout the region via the transport of buoyant eggs and larvae in surface currents (Morris and Green 2012). Accompanying this rapid range expansion are exponential increases in abundance on many invaded reefs (REEF 2012; USGS 2012). Lionfish are stalking predators that prey on a large number of Caribbean species over a broad range of body sizes (Morris and Akins 2009), yet they are largely protected from predation by their venomous dorsal fin spines. Of all anthropogenic threats to reefs in the region, the invasion of lionfish is the least well understood, and there are serious concerns about their potential ecological impacts on native Atlantic fish communities (Sullivan-Sealey 2008, Sutherland et al. 2010, Albins and Hixon 2011).

Studying the interactions between Indo-Pacific lionfish and the diverse assemblage of native fishes they now consume on invaded Atlantic coral reefs provides an opportunity to simultaneously gain a better understanding of the forces shaping communities of marine predators and their prey, and increase the accuracy of our predictions about the consequences of vertebrate predator invasions in marine systems. Focussing on invaded coral reefs in the Bahamas, my thesis examines the ecological factors driving patterns of predation by lionfish on coral reef fishes, and the effect of their predation on fish community assemblages. Coral reefs in the Bahamas were first colonized by lionfish in 2004 and now support densities which exceed those reported from the native range (Green and Côté 2009, Darling et al. 2011). The relatively long invasion history for coral reefs across the Bahamian archipelago makes these reefs an excellent study system to quantify the effects of lionfish on native ecosystem structure and function, and the potential for management intervention to successfully halt these effects.

In Chapters 2, 3 and 4 of this thesis, I elucidate patterns of predation by lionfish on native fishes occupying invaded Bahamian coral reefs and explore the ecological processes that underpin them. Specifically, in Chapter 2, I conduct *in situ* observations of behaviour to quantify the rate and daily pattern of predation by lionfish in the invaded range. Then in Chapter 3, I examine trends in the biomass of 42 native fishes identified in the stomachs of lionfish, to determine whether there has been significant change to fish community composition as a result of lionfish predation. In Chapter 4 I identify morphological and behavioural characteristics of prey that drive vulnerability to lionfish predation. I achieve this by considering two separate data sets: *in situ* observations of predation (Chapter 2) and *ex situ* stomach contents analyses and environmental prey availability (Chapter 3). I then compare prey fish features identified as important determinants of vulnerability to lionfish predation identified by both analyses.

In the last section of my thesis, I use the ecological insights gained from Chapters 2, 3 and 4 to develop and test a predictive model of the effect of lionfish predation on the biomass of native fish assemblages. In Chapter 5, I construct an empirical model in which the effect of lionfish predation on fish prey biomass is measured as the difference between two fundamental rates: lionfish prey consumption, estimated from *in situ* observations and stomach contents analyses, and prey fish production, estimated from community size-spectra data using metabolic scaling relationships. In Chapter 6, I explicitly test the predictions of my predation model by conducting a lionfish removal experiment on 24 natural patch reefs in the Bahamas over an 18 month period to determine whether the magnitude of lionfish density reductions required, as predicted by the model, is sufficient to protect native fish communities from predation-induced declines. In the final chapter, I pull the findings of my thesis together and consider their implications for the future of coral reef communities in the Caribbean as well as the novel insights they provide for understanding marine invasions.

Chapter 2

Foraging behaviour and prey consumption in the Indo-Pacific lionfish on Bahamian coral reefs[1]

Abstract

Predicting and mitigating the effects of invasive Indo-Pacific lionfish on Caribbean fish communities requires a thorough understanding of the species' predation behaviour in the invaded range, including the types and amounts of prey consumed and how foraging patterns vary in relation to extrinsic conditions. We studied the activity levels and prey consumption rates of lionfish on 12 shallow coral reefs in the Bahamas in relation to time of day and prey availability. Lionfish predation rates and activity levels were significantly higher during crepuscular (dawn and dusk) periods than at mid-day. Available prey fish biomass was highest at dawn but lower at mid-day and dusk, suggesting that lionfish predation activity is not limited by prey availability alone. Our calculated average daily mass-specific prey consumption rates, which incorporated daily variation, was ~3 times the estimates obtained from studies of captive lionfish in their native range and of invasive lionfish observed only during the day. Our results will help to predict more accurately the effect of predation by invasive lionfish on native reef fish communities.

Introduction

Species invasions are emerging as a top threat to marine systems globally and are occurring at an ever increasing pace (Mooney and Cleland 2001, Goldberg 2004). There

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[1] A version of this chapter appears as, Green S. J., J.L. Akins and I.M. Côté (2011) Foraging behaviour and prey consumption in the Indo-Pacific lionfish on Bahamian coral reefs. Marine Ecology Progress Series 433, 159-167.

is growing concern that one recent invasion—that of the Indo-Pacific lionfish (*Pterois volitans* and *P. miles*) across coral reefs in the Western Atlantic and Caribbean—will have extreme effects on regional biodiversity and fish production (Albins and Hixon 2008, Green and Côté 2009, Morris and Whitfield 2009, Sutherland et al. 2010, Albins and Hixon 2011). Lionfish regularly prey on a wide array of native Caribbean fish species, including several of commercial importance (Morris and Akins 2009). Efforts to predict and mitigate the effects of lionfish predation on Caribbean fish communities require a thorough understanding of the type and amount of prey they consume on invaded reefs. Many extrinsic factors, such as prey size, density and predation risk, influence patterns and rates of predation (Vincent 2008). These factors are in turn influenced by spatial and temporal variation in abiotic environmental conditions (e.g. Sweatman 1984, Yamashita et al. 2005). In the marine realm, the daily cycle of light availability has a particularly strong influence on the foraging activities of most predators, with many species foraging most actively during low-light dawn and dusk ‘crepuscular’ periods (Hobson 1973, Helfman 1978, Galzin 1987). Species feeding under these conditions may benefit from increased prey availability, increased capture success or decreased detection by visual predators (Fishelson 1975, Helfman 1993, Connell 1998).

To date, variation in lionfish foraging behaviour and predation rates across the day has not been investigated, but may have important consequences for estimating daily and annual prey consumption. For example, while lionfish are believed to hunt primarily during low-light crepuscular periods in their native range (Fishelson 1975, 1997), daytime observations of lionfish on Bahamian reefs have yielded estimates of prey consumption that far exceed anecdotal reports from the native range (Côté and Maljković 2010). If the rates at which invasive lionfish consume prey are highest during crepuscular periods, a question not examined by (Côté and Maljković 2010), then lionfish prey consumption in their introduced range has been under estimated. In addition, a thorough understanding of the timing of lionfish foraging activity is important for the design of future diet studies so that sample collection may be conducted around times of high foraging activity.

The objectives of this study were to document the foraging patterns, activity levels and prey consumption rates of lionfish, as well as their available prey, at different times of the day on invaded Bahamian coral reefs. We addressed 2 specific questions: (1) Are lionfish prey consumption rates and activity levels significantly higher during low-light (crepuscular) hours than during mid-day periods? (2) Do high predation rates and activity levels by lionfish coincide with periods of higher prey availability? Accurate estimates of mass-specific prey consumption rates are important because they can be used to examine the effect of lionfish on native prey populations. However, the only available estimates of lionfish prey consumption derive from daytime-only estimates (Côté and Maljković 2010), and from bioenergetics studies of captive specimens (Fishelson 1997, Cerino 2010). To illustrate the importance of incorporating daily variation in behaviour into estimates of prey consumption, we compared our own estimates of daily mass-specific prey consumption rates by lionfish to estimates from these 2 published studies.

Methods

Study sites and data collection

In September 2008 and December 2009 we conducted detailed observations of lionfish behaviour, and estimated prey availability at dawn, mid-day and dusk, on 12 invaded coral reef patches off the Bahamian island of Eleuthera (25°22.5’N, 76°49.0’W). Lionfish were first sighted around Eleuthera in 2005 (USGS 2012), and are now abundant on reefs around the island (REEF 2012). The 12 sites were similar in terms of location and structure. Reefs were roughly circular, with similar areas (from 80 to 100 m^2) and depths (from 3 to 5 m). Each site was separated by at least 500 m of sand and seagrass from any other reef structure. Benthic structure was provided primarily by living and dead hard corals (from 60 to 80% of benthic composition) at all sites. Vertical relief, measured as the total height of the reef structure (to the nearest cm) at 6 points per site (Luckhurst and Luckhurst 1978), did not vary among sites (1-way ANOVA; F = 0.56, df = 11,66, p = 0.72). We observed lionfish on 6 reefs in September 2008 and on 6 other reefs in December 2009. In each season, we observed lionfish on 2 reefs at dawn, 2 at mid-day and 2 at dusk. Taking both seasons together, this resulted in 4 reefs being observed in each of the 3 time periods. Dawn observations covered the period from 1 h before to 1 h after sunrise, while dusk observations covered the period from 1 h before to 1 h after sunset.

All mid-day observations occurred between 11:00 and 15:00 h. In September 2008, sunrise was at ~07:00 h and sunset at ~19:00 h, and in December 2009, sunrise and sunset were at ~07:00 and ~17:00 h, respectively. Because lionfish were not individually marked, it was not possible to knowingly observe the same individual across different time periods, nor was it possible to observe only some individuals in one time period and the remainder in other periods. For this reason, all lionfish on a patch were observed in a single session during one of the 3 pre-determined periods of day. The number of lionfish on each patch varied between 5 and 12. Two or 3 trained observers, depending on the number of lionfish present, simultaneously observed different focal fish on a reef. Because prey consumption rates can be influenced by fish size (i.e. Fonds et al. 1992), we compared mean lionfish total length (TL) on reefs observed at the 3 times of day using a 1-way analysis of variance, and found no significant difference. Mean ± SD at dawn was 22 ± 6 cm; at mid-day, 20 ± 6 cm; at dusk, 24 ± 9 cm ($F = 2.72$, df = 2, 89, $p = 0.08$).

All observations were conducted while on SCUBA at a distance of 2 to 3 m from focal lionfish. During a pilot study, observers at this distance appeared not to affect fish behaviour, yet still had an unobstructed view of the focal lionfish and its potential prey. Before observations began, we noted the distribution of lionfish at each study site to ensure that no individual was observed twice. Each lionfish was observed for 30 min. At the beginning of each observation period, we estimated the TL of the fish to the nearest cm. We noted all predation attempts during each 30 min period and identified the target of each attempt to the lowest taxonomic level possible. Hunting lionfish typically hove closely above a single prey item, often for several minutes, before striking, allowing ample time to identify the targeted species. Predation attempts were categorised as successful if the focal lionfish unambiguously consumed the prey fish, or unsuccessful if the prey fish either escaped or if the outcome of the attempt was uncertain. We also estimated and recorded the TL (to the nearest cm) of each prey item consumed.

Using an instantaneous sampling method (Altmann 1974), we also recorded lionfish activity at 30 s intervals during each 30 min observation. Lionfish activity was categorised as either resting (i.e. in contact with the reef, with dorsal spines typically held flat along the dorsal midline) or active. We distinguished 3 categories of ‘active’ behaviour: hunting, hovering or swimming. Hunting lionfish displayed a stereotypical posture: head down and hovering near prey, pectoral fins spread out and angled forward, dorsal spines erect and tail undulating. Hovering lionfish were nearly motionless above the substratum, but without exhibiting a hunting posture. Swimming lionfish were actively in transit from one part of the reef to another. We also recorded the distance moved (to the nearest 0.5 m) by each fish in 30 s intervals during each observation. The sum of all distances recorded at 30 s intervals yielded the total distance moved by each lionfish. To assess variation in prey availability across the day, we conducted a point count of reef fish abundance every 5 min during each 30 min observation. We estimated and recorded the species, number and TL (to the nearest cm) of all fishes, including cryptic fishes, within a 1 m radius of the focal lionfish. This survey method may have overlooked potential prey items that were hidden within the reef framework; however, such prey items were most likely unavailable to lionfish, which prey by stalking in generally open habitats. We therefore assumed that the potential prey recorded by the divers reflect the minimum prey availability to lionfish. During the 2 darkest observation periods (the first 30 min of ‘dawn’ and the last 30 min of ‘dusk’), indirect lighting was used to ensure accurate observations of lionfish behaviour and prey availability. Indirect lighting was achieved by partially shielding a dive light with a hand and aiming it at the substratum, ~1 m away from the focal lionfish. This small amount of lighting could have affected lionfish behaviour and prey availability, thus reducing our ability to detect a relationship between lionfish activity or prey availability and natural changes in ambient light. However, during the 2 periods when lighting was used, lionfish were less active and fewer prey were available as compared with adjacent observation periods (see ‘Results’), suggesting that the effect of lighting was limited.

Daily patterns of behaviour and prey consumption

To address the question of whether lionfish prey consumption rates and activity levels are significantly higher during crepuscular hours than at mid-day, we examined dawn-to-dusk variation in 4 aspects of lionfish behaviour. We first assessed the effect of time of day on 2 metrics of lionfish activity, namely active behaviour and hunting behaviour. Fish behaviour was scanned every 30 s across the 30 min observation period for each fish. For each fish, we calculated the proportions of scans per 30 min in which active or hunting behaviour occurred. Then, for each response variable, we created a generalized linear mixed-effects model (Bolker et al. 2009) in which reef sites—a random effect—were nested within time of day (3 categories: dawn, mid-day and dusk)—a fixed effect—specifying binomial distributions for both behaviours. We conducted Bonferroni-corrected Wald *Z* tests to evaluate differences between the 3 periods of the day by the mass of the corresponding lionfish, and expressed prey consumption as mass of prey consumed (g) per mass of lionfish (g) per 30 min period. Finally, we examined whether high predation rates and activity levels by lionfish coincided with periods of higher prey availability. Based on the distribution of prey sizes consumed by lionfish during our observations, we defined potential prey fish as those individuals ≤6 cm TL. We converted prey TL (cm) to weight (g), and calculated the density of prey fish biomass (g m^{-2}; referred to as available prey biomass) as our measure of prey availability. Available prey biomass was modelled with a normal error distribution following a log (x + 1) transformation. We sought to compare the available prey biomass at different times of the day, but the risk of predation by active lionfish could reduce the number of prey fish observed. Alternatively, active lionfish may seek out patches of high prey density.

To consider both the effects of time of day and lionfish behaviour on available prey biomass, we created a linear mixed-effects model where time of day (3 categories: dawn, mid-day and dusk) and lionfish behaviour (2 categories: active and inactive) were fixed effects for measures of available prey biomass associated with each lionfish (random effect), nested within reef site (random effect). We tested for temporal autocorrelation between our point counts by comparing a model that included a residual correlation structure (corAR1) with one that did not, and found that fit was significantly better for the model with the residual correlation structure (ANOVA; df = 7,8, p = <0.001, $AIC_{\text{no correlation}} = 347$ and $AIC_{\text{correlation}} = 335$). We then conducted Bonferroni-corrected pair-wise comparisons to evaluate the differences in available prey biomass between pairs of time periods. We conducted all analyses in R (R Core Team 2008), using the package nlme (Pinheiro et al. 2011) for linear mixed-effects models and MASS (Venables and Ripley 2002) for generalized linear mixed-effects models. We estimated overdispersion for each dependent variable using Pearson's residuals (Zuur et al. 2009) and found none. Visual validation of each model (i.e. plots of residual versus fitted values, and boxplots of residuals; (Zuur et al. 2009) confirmed that errors were homogeneous and normally distributed.

Daily prey consumption calculation

We estimated the average daily mass-specific rate of prey consumption for lionfish in our study, taking into account daily variation in predation activity. We assumed that lionfish consume prey at rates measured during dawn observations for ~2 h of the day and, similarly, during dusk observations, for ~2 h of the day. We assumed that lionfish consumed prey at rates similar to that of our mid-day observations (conducted between 11:00 and 15:00 h) during all non-crepuscular daylight hours (~9 h per day). Finally, given the fact that lionfish are visual predators (Fishelson 1997) and that lionfish were completely inactive at night (i.e. between 22:00 and 05:00 h) on 2 reefs where pilot observations were made (L. Akins unpublished data), we assumed that no predation events occurred at night. Given the frequency of hunting activity observed between dawn and dusk, a low rate of nocturnal predation would lead to only a marginal underestimation of total daily prey consumption. We constructed a 95% CI for our estimate of mean daily mass-specific prey consumption from a weighted estimate of variance in the daily rate, which we calculated from our estimates of variance in the rate for each defined period of the day, using the number of hours of prey consumption at each rate as weighting factors.

Results

On Eleuthera reefs, 92 lionfish ranging in size from 8 to 36 cm (mean ± SD: 21 ± 6 cm) were observed during 46 h of underwater observation. Activity levels and prey consumption rates closely tracked the daily light cycle (Figure 2.1A-D), with all measured aspects of lionfish activity and predation behaviour peaking around sunrise and sunset, and decreasing during mid-day hours (Figure 2.1A-D). Available prey biomass in the vicinity of lionfish followed the same pattern, particularly at dawn (Figure 2.1E).

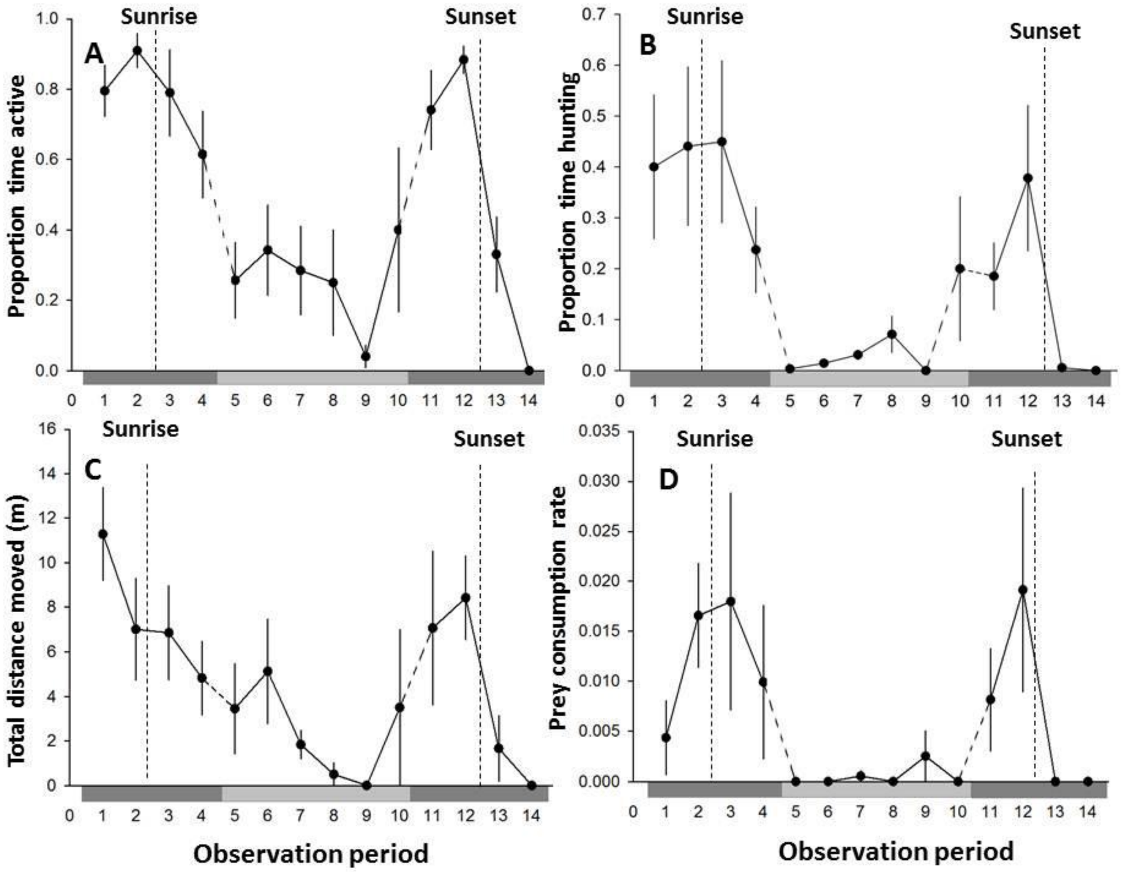

Figure 2.1. Pterois volitans. Foraging behaviour and prey consumption rates on patch reefs near Eleuthera, Bahamas, by observation period. (A) Proportion of time active, (B) proportion of time spent hunting, (C) total distance moved (m) per 30 min, (D) mass-specific consumption rate (g prey per g lionfish per 30 min) and (E) biomass (g m–2) of prey-sized (≤6 cm TL) reef fishes in the vicinity (<1 m distant) of lionfish across the day. Each of the 14 observation periods lasted 30 min. Long dashed lines: breaks in observations between crepuscular and mid-day periods. Short-dashed lines indicate the timing of sunrise and sunset within dawn and dusk crepuscular periods, respectively. All means ±SE, with n = 3 to 10 lionfish per 30 min period; (E) n = 18 to 50 lionfish centred prey counts per 30 min period.

All aspects of lionfish behaviour varied significantly among time periods (Figure 2.2A-D). Lionfish spent more time active during both crepuscular periods than at mid-day (Table 2.1, Figure 2.2A). Fifteen lionfish observed during mid-day remained inactive throughout their entire observation period, compared with only 5 individuals during dusk observations and none at dawn. Lionfish also travelled significantly greater distances during the dawn crepuscular period than at mid-day, with distance travelled during the dusk crepuscular period being intermediate to that travelled between dawn and mid-day, and not significantly different from either (Table 2.1, Figure 2.2C). During one dusk observation, a 31 cm lionfish was observed following and herding a 24 cm lionfish in apparent courtship across the reef and adjacent sand, travelling at least 23 m.

Table 2.1. Pterois volitans. Results of post hoc pair-wise comparisons (Bonferroni- corrected Wald Z or t-tests) generated for generalized linear mixed models (GLMM) and linear mixed models (LMM) comparing foraging behaviour and available prey biomass at dawn, mid-day, and dusk on coral reefs off Eleuthera, Bahamas. Foraging behaviour was measured through 4 response variables: proportion time active, proportion time hunting, total distance travelled (m^2) and mass- specific prey consumption rate (g prey per g lionfish per m^2) for lionfish observed over a 30 min period during one of the 3 time periods. Available prey biomass (g m^{-2}) was measured as the biomass of prey-sized reef fishes within 1 m of each lionfish. The model for available prey biomass also included lion fish behaviour (Active or Resting) as an explanatory variable. Bold values indicate significant differences between pairs (i.e. $p_{adjusted} < 0.017$)

Response variable	Model type	Test type	Pair-wise comparison	P-value
Proportion time active	GLMM	Wald Z	Dawn: Mid-day	**0.014**
			Dawn: Dusk	0.463
			Mid-day: Dusk	**0.008**
Proportion time hunting	GLMM	Wald Z	Dawn: Mid-day	**0.001**
			Dawn: Dusk	0.272
			Mid-day: Dusk	**0.007**
Total distance travelled	LMM	T test	Dawn: Mid-day	**0.013**
			Dawn: Dusk	0.449
			Mid-day: Dusk	0.087
Mass-specific prey consumption rate	LMM	T test	Dawn: Mid-day	**0.005**
			Dawn: Dusk	0.225
			Mid-day: Dusk	**0.017**
Available prey fish biomass	LMM	T test	Dawn: Mid-day	**0.002**
			Dawn: Dusk	**0.002**
			Mid-day: Dusk	0.769
			Active- Resting*	0.142
			Resting: Active	0.188

On several occasions, lionfish were observed to move away from the reef, where they were initially observed, to hunt over open sand and seagrass. One individual observed at dusk travelled 130 m away from the reef, and was still swimming away at the end of the observation period. Lionfish spent a significantly greater proportion of time hunting, and showed higher mass-specific rates of prey consumption at dawn and dusk than during midday (Table 2.1, Figure 2.2B,D). We observed a total of 45 predation attempts from 25 of the 92 lionfish observed. Of these attempts, only 2 were documented at mid-day, and one of these occurred while the lionfish was stationary on the substratum. Of all strikes at prey, 85% were successful. The majority of strikes were on reef fishes, with the exception of 3 strikes at small crustacean prey (Table 2.2). Of the 26 species from 11 families of reef fishes hunted by lionfish, we observed successful captures of individuals from 12 species (Table 2.2). The average TL of captured prey was 4 ± 1 cm, with a mean body mass of 1.47 ± 1.58 g. Time of day had a significant effect on the density of prey-sized reef fishes recorded in the vicinity of lionfish (Table 2.1, Figure 2.2E), while lionfish behaviour (active or resting) did not (Table 2.1). The biomass of prey-sized fish was significantly higher at dawn than at either mid-day or dusk (Table 2.1, Figure 2.2E). Taking into account the variable rates of predation observed throughout the day, we estimated that lionfish in our study consumed, on average, 0.089 g prey per g lionfish per day (95% CI: from 0.076 to 0.102 g prey per g lionfish per day). Given the average size of lionfish in this study (148 ± 145 g), and the average size of prey, this mass-specific daily consumption rate amounts to, on average, 13 g prey per lionfish per day (95% bootstrapped CI: from 12 to 15 g prey per day).

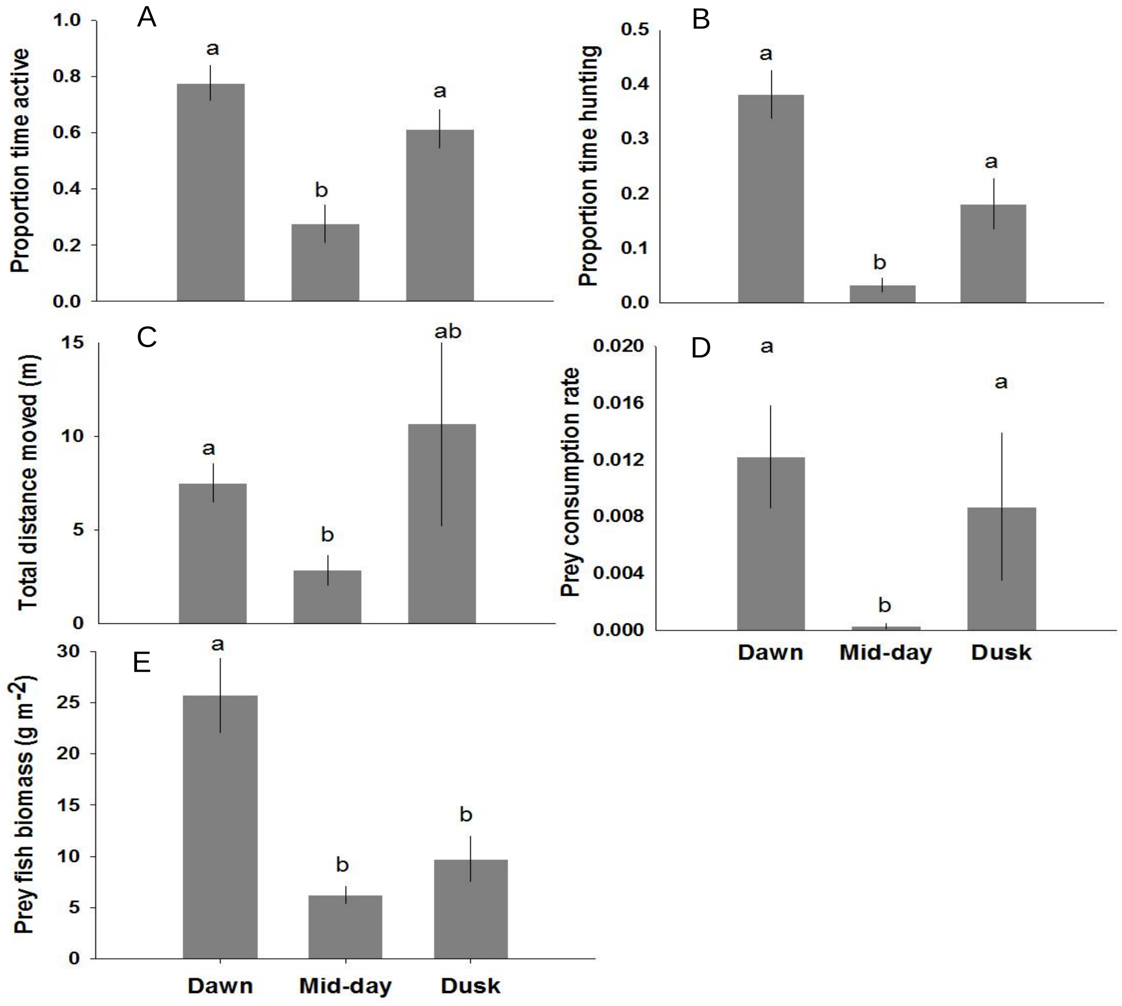

Figure 2.2. Pterois volitans. Foraging behaviour and prey consumption rates on patch reefs near Eleuthera, Bahamas, by period of day. (A) Proportion of time active, (B) proportion of time spent hunting, (C) total distance (m) moved per 30 min, (D) mass-specific prey consumption rate (g prey per g lionfish per 30 min) and (E) biomass (g m^{-2}) of prey-sized (≤6 cm TL) reef fishes in the vicinity (<1 m distant) of lionfish during each period. Means ± SE, with N_{dawn} = 32 lionfish, $N_{mid\text{-}day}$ = 37 lionfish, N_{dusk} = 23 lionfish; (E) N_{dawn} = 216 lionfish-centered prey counts, $N_{mid\text{-}day}$ = 222 lionfish-centered prey counts, N_{dusk} = 138 lionfish-centered prey counts. Within each panel, means with different superscripts were significantly ($p < 0.017$) different from each other in Bonferroni-corrected post hoc tests

Table 2.2. *Pterois volitans*. Reef fish species and life stages hunted by lionfish on 12 coral reefs off Eleuthera, Bahamas. juv: juvenile fish

Order	Suborder	Family	Species	Life stage	Captured
Perciformes	Acanthuroidei	Acanthuridae	*Acanthurus bahianus*	juv	
			Acanthurus chirurgus	juv	
			Acanthurus coeruleus	juv	
	Blenniodei	Labrisomidae	*Malacoctenus gilli*	adult	
	Gobioidei	Gobiidae	*Coryphopterus dicrus*	adult	
			Coryphopterus eidolon	adult	x
			Coryphopterus glaucofraenum	adult	
			Gnatholepis thompsoni	adult	x
			Prolepis hipoliti	adult	x
	Labroidei	Labridae	*Halichoeres bivittatus*	juv	x
			Halichoeres garnoti	juv	
			Thalassoma bifasciatum	juv	x
			Xyrichtys spp	juv	x
		Pomacentridae	*Stegastes diencaeus*	juv	
			Stegastes leucostictus	juv	
			Stegastes partitus	adult	
		Scaridae	*Scarus iserti*	juv	x
			Sparisoma aurofrenatum	juv	x
			Sparisoma viride	juv	x
	Percoidei	Apogonidae	*Apogon binotatus*	adult	
		Chaetodontidae	*Chaetodon capistratus*	adult	
		Grammatidae	*Gramma loreto*	adult	
		Haemulidae	*Haemulon aurolineatum*	juv	x
			Haemulon flavolineatum	juv	x
			Haemulon plumierii	juv	
Tetraodontiforme	Tetraodontoidei	Tetraodontidae	*Canthigaster rostrata*	adult	x

Discussion

Lionfish predation behaviour varies significantly throughout the day and across the fish's invaded range. Lionfish observed during our study were most active during crepuscular times. The peak in activity during the dawn crepuscular period was associated with high densities of available prey. These observations are consistent with the anecdotal observation of Fishelson (1975), who reported that lionfish in the Red Sea foraged at dawn and dusk, and were mostly inactive during the day, sheltering under coral ledges. We also found that all aspects of activity, including the proportion of time spent active, time spent hunting, total distance moved and mass-specific prey consumption rates, were depressed at mid-day on Eleuthera reefs. Taking into account this daily variation in predation behaviour yields a much higher prey consumption rate than previously estimated for lionfish.

A number of mechanisms could explain the temporal variation in lionfish predatory activity. First, lionfish may hunt only when prey are available. The variation in prey-sized fish biomass documented here, with a peak at dawn, is consistent with daily trends in abundance of coral reef fishes in other regions, where the change-over between diurnal and nocturnal fish communities has been shown to be strongly linked to light level (Hobson 1972, Helfman 1978, Galzin 1987). However, while we did not observe a similarly large peak in prey biomass at dusk, lionfish observed during this period nevertheless consumed prey at rates similar to those observed over the dawn period. This mismatch may indicate that lionfish prey consumption rates were not limited by access to prey.

A second possible mechanism is that lionfish predatory activity is higher during crepuscular periods because their hunting success is relatively high at low light levels. Better hunting success might result from good visual acuity among lionfish or poor ability by prey fish to detect the presence of these predators under low light conditions. In either case, we would expect the proportion of prey captured by lionfish to be higher during crepuscular periods than at mid-day and to be equally high at dawn and dusk at equivalent low-light levels. While the scarcity of predation attempts by lionfish during mid-day observations prohibits a thorough comparison of capture success between crepuscular and mid-day conditions, capture success was indeed high and similar at dawn (85% of attempts successful) and dusk (88% successful). Studies quantifying capture success by fish predators in relation to light availability are needed to elucidate the importance of this mechanism for explaining variation in hunting activity across the day. However, the observation of frequent daytime hunting by lionfish on overcast days (Côté and Maljković 2010), when light levels may have approximated crepuscular conditions, suggests that light levels are an important factor controlling lionfish activity.

A third possible mechanism is the contribution of satiation to daily variation in lionfish hunting patterns. Satiation has been shown to affect the predation rates of piscivorous fish because short-term storage capacity in the stomach has been exceeded (Essington 2000). However, preliminary laboratory studies of lionfish digestion rates of the Atlantic pinfish *Lagodon rhomboides* have revealed that prey are not substantially broken down after 8 h in the gut (J. A. Morris pers. comm.). If prey digestion time is longer than the interval between crepuscular periods, the high rates of prey consumption we observed at both dusk and dawn suggest that lionfish may not feed to satiation in a single foraging bout. Instead, they may partition their feeding activities between the 2 crepuscular periods each day, in which case their prey consumption is limited by other factors, such as prey availability (perhaps at dawn) and capture success.

A final explanation for the patterns of foraging behaviour we observed may be that lionfish time their activities to escape detection by visually oriented predators. However, we did not observe any encounters between lionfish and potential predators (e.g. sharks, large groupers or eels). Given that lionfish have venomous spines and are a relatively novel species in the Caribbean, it is unlikely that predation threat in their invaded range controls their foraging behaviour.

Our study highlights the importance of considering daily environmental variation when assessing prey consumption rates. Our estimate of daily mass-specific rate was 0.089 g prey per g lionfish per day (95% CI: from 0.076 to 0.102 g prey per g lionfish per day). Prior to our study, 2 estimates of lionfish prey consumption rates were available. A bioenergetics experiment with Red Sea lionfish *Pterois miles*, fed ad libitum, reported such lower average daily mass-specific prey consumption rates than ours, viz. from 0.02 to 0.06 g prey per g lionfish per day (Fishelson 1997), suggesting that captivity affects energy requirements and may result in under-estimates of prey consumption. In contrast, observations of Bahamian lionfish in the wild but taken only during mid-day periods yielded 0.038 g prey per g lionfish per day (Côté and Maljković 2010). Our estimate is therefore ~3 times larger than that of the previous *in situ* study. Although some of the difference between the 2 *in situ* estimates may be attributed to differences in average lionfish mass (148 g in our study versus 340 g in Côté & Maljković [2010]) and water temperature (on average, 26°C in our study versus 23°C in Côté & Maljković [2010]), most is likely explained by our consideration of crepuscular peaks in hunting activity. Increasing the accuracy of prey consumption estimates will allow ecologists to better predict the impacts of lionfish on native fish communities. Our study thus provides valuable estimates of mass-specific predation rates of lionfish on native Caribbean fishes that can be used in conjunction with estimates of prey production to quantify the effect of lionfish predation on Caribbean reef fish.

Chapter 3

Invasive lionfish drive Atlantic coral reef fish declines[2]

Abstract

Indo-Pacific lionfish (*Pterois volitans* and *P. miles*) have spread swiftly across the Western Atlantic, producing a marine predator invasion of unparalleled speed and magnitude. There is growing concern that lionfish will affect the structure and function of invaded marine ecosystems, however detrimental impacts on natural communities have yet to be measured. Here we document the response of native fish communities to predation by lionfish populations on nine coral reefs off New Providence Island, Bahamas. We assessed lionfish diet through stomach contents analysis, and quantified changes in fish biomass through visual surveys of lionfish and native fishes at the sites over time. Lionfish abundance increased rapidly between 2004 and 2010, by which time lionfish comprised nearly 40% of the total predator biomass in the system. The increase in lionfish abundance coincided with a 65% decline in the biomass of the lionfish's 42 Atlantic prey fishes in just two years. Without prompt action to control increasing lionfish populations, similar effects across the region may have long-term negative implications for the structure of Atlantic marine communities, as well as the societies and economies that depend on them.

Introduction

The successful invasion of a marine ecosystem by vertebrate predators is exceedingly rare (GISD 2012). Nevertheless, one such invasion is currently unfolding. Indo-Pacific

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[2] A version of this chapter appears as, Green S.J., J.L. Akins, A. Maljković and I.M. Côté (2012) Invasive lionfish drive Atlantic coral reef fish declines. PLoS One. e32596

lionfish (*Pterois volitans* and *P. miles*) have spread rapidly across the Western Atlantic, Caribbean and Gulf of Mexico, producing a marine predator invasion of unparalleled speed and magnitude. Lionfish were first reported off the southeast coast of Florida in the 1980s and have since become established to varying extents across the entire Caribbean region via larval dispersal in ocean currents (Betancur-R et al. 2011). These stalking predators consume a wide variety of native fish and invertebrate species at high rates, and are well defended from predation by venomous fin spines (Morris and Akins 2009, Green et al. 2011).

There is growing concern, largely based on the results of small-scale experiments (Albins and Hixon 2008), that lionfish will affect the structure and function of invaded marine ecosystems (e.g. Sutherland et al. 2010, Albins and Hixon 2011) but detrimental impacts on natural communities have yet to be measured. To determine whether predation by lionfish is having negative effects on native reef fish communities, we studied nine sites along a 15 km stretch of continuous reef off the southwest coast of New Providence Island, Bahamas (24º59.072 N, 77º32.207 W), where lionfish were first sighted in 2004. We conducted visual transect surveys of both native fish and lionfish, and identified lionfish prey through stomach contents analysis of 567 lionfish collected from the study reefs in 2008 and 2010. Standardized roving diver surveys conducted at the sites each year since 2004 were used to assess changes in lionfish abundance over time within the study area.

Materials and Methods

Our study took place at nine locations, each separated by at least 1km, along a continuous stretch of coral reef bordering the Tongue of the Ocean trench off southwest New Providence, Bahamas. We estimated the size (total length (TL) to the nearest 1 cm) and density of all small-bodied and cryptic fishes (i.e. < 15 cm TL) during detailed searches of 6-12 30 m x 2 m (length x width) transects at each site in summers of 2008 and 2010. Size and density of larger-bodied (i.e. >15 cm TL) fishes were assessed on 2-6 30 m x 4 m transects during the same periods. All transects were laid parallel to the reef crest at depths between 10-20 m at each site. Fish lengths (cm) were converted to body mass (g) using published species-specific allometric scaling constants obtained from FishBase (Froese and Pauly 2000) and verified in the primary literature. When species-specific constants were not available, we used allometric constants for closely related species with a similar body shape.

To test whether fish biomass (g 100m^{-2}) had changed significantly between 2008 and 2010, we created linear mixed-effects models, comparing the biomass of fish between years (fixed effect), while nesting transects within sites (random effects; Zuur et al. 2009). To calculate the median percent change in fish biomass between 2008 and 2010 across the study system and 95% confidence intervals which incorporate variation among transects within sites, we first specified log-normal distributions for fish biomass at each site in 2008 and 2010. The mean and standard deviation of each distribution was calculated from transect data at each location. We next calculated the percent change in biomass between 2008 and 2010 for each site. To incorporate variation in our estimates of percent change, we conducted 1000 iterations of the calculation, using Monte Carlo simulation to draw from the distributions of biomass for each site (Vose 2008). We then calculated the average system-wide change in biomass from the medians of the site-specific percent-change distributions. We performed 500 replicates of this latter procedure to generate a distribution of values for system-wide percent change in biomass. Figure 2 displays the median of this bootstrapped distribution, with the 2.5 and 97.5 percentiles as our confidence limits. Between 2004 and 2010, lionfish abundance was recorded during roving diver surveys at the study sites by trained observers on SCUBA as part of the Reef Environmental Education Foundation (REEF) fish survey project (Schmitt and Sullivan 1996). Each survey consisted of a 30-60 min roving search of the site, during which the observer recording all species observed (including lionfish) as well as the categorical abundance of each species on a four-point $\log_{10}$ scale [single (1), few (2-10), many (11-100), and abundant (>100) (REEF 2012). Data were entered into REEF's on-line data base at www.reef.org, where they passed through both an automated electronic and program manager review to ensure accuracy and completeness. Automated electronic checks included comparison to existing data from the site and flagging of species identification or abundance parameters outside existing data boundaries. All potential species/abundance outliers were confirmed with the observer by the program manager before processing was completed. Surveys which did not pass this quality assurance process were not included in the database.

Prey species for lionfish were determined from the stomach contents of the 567 lionfish specimens collected from the study sites between 2008 and 2010. Lionfish were collected using hand nets and euthanized at the surface in a clove oil and sea water solution. Stomach contents were then extracted and identified visually to the lowest taxonomic resolution possible.

Results and Discussion

Lionfish abundance increased swiftly between 2004 and 2010 off southwest New Providence, Bahamas (Figure 3.1). Between 2008 and 2010, abundant lionfish populations coincided with rapid declines in native fishes. During this period lionfish increased from 23% to nearly 40% of the total biomass of predators residing in the study area, which included 16 ecologically-similar native fishes, in terms of body size and diet [8,9]. Ninety percent of the prey consumed by lionfish were small-bodied reef fishes from 42 species (Appendix A) Between 2008 and 2010, the combined biomass of these 42 species declined by 65%, on average, across the study reefs (Figure 3.2; linear mixed-effects model (LMM); *P* <0.001, t = 4.5, df = 105). Since lionfish were already abundant within the study area in the year prior to our observations (Figure 3.1), the cumulative decline in prey fish biomass since lionfish first colonized the area undoubtedly exceeds what we observed between 2008 and 2010.

Aside from predation by lionfish, at least three alternative factors could cause such a rapid decline in the abundance of so many species: recruitment failure, increased predation by native species, or disease. Wholesale recruitment failure, owing to unfavourable oceanographic conditions for the pelagic larvae of reef fish, is unlikely to be a factor in the decline of lionfish prey, since the biomass of several species of small-bodied gobies (*Elacatinus* spp.; Appendix A), which also have pelagic larvae but have never been recorded in diet of lionfish (Albins and Hixon 2008, Morris and Akins 2009, Green et al. 2011, Côté et al. in press) and may contain a chemical defense against predation (Lettieri and Streelman 2010), remained stable over the two-year period (Figure 3.2; LMM; *P* = 0.45, t = 0.78, df = 105).

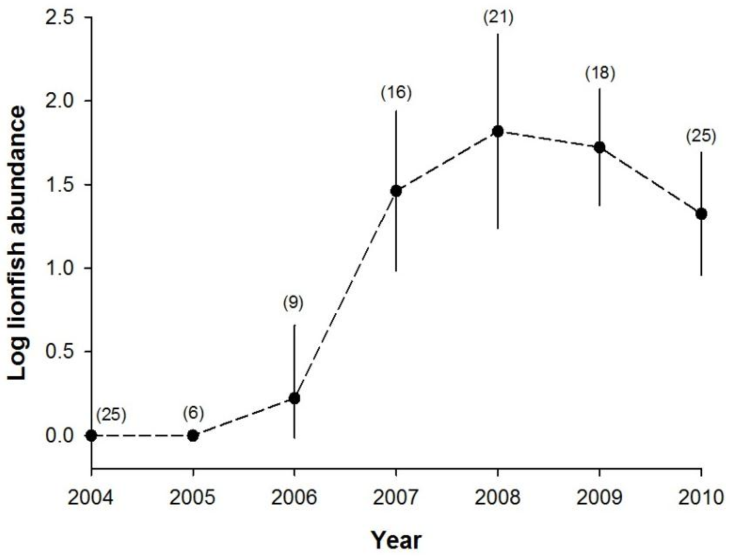


Figure 3.1. The abundance of Indo-Pacific lionfish (Pterois volitans and P. miles) on coral reefs off southwest New Providence, Bahamas. Abundance is the number of lionfish sighted during each roving survey, recorded in $\log_{10}$ scale. Points represent log-scale means, bounded by 95% confidence intervals. The yearly number of surveys is given in parentheses.

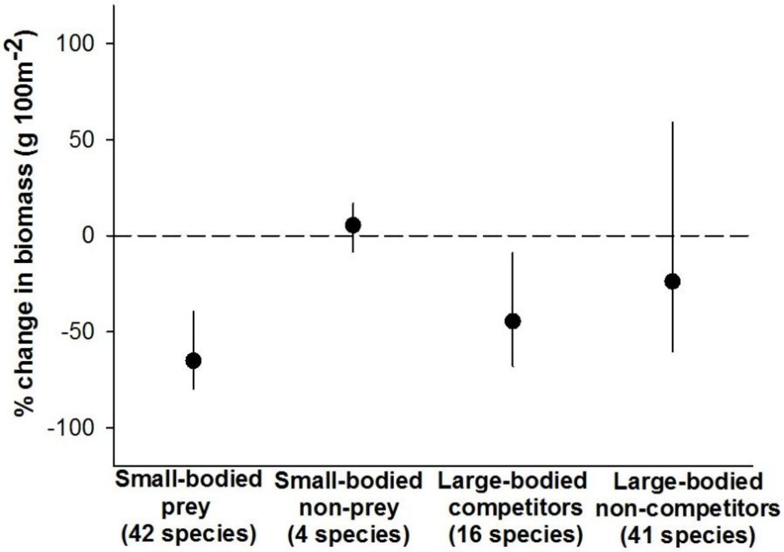


Figure 3.2. The percent change in biomass of native fishes between 2008 and 2010 on New Providence, Bahamas coral reef sites. Points represent medians, bounded by parametric bootstrapped 95% confidence intervals. The dashed line indicates no change in biomass.

The decline in prey species was also not caused by an increase in native predators, as the biomass of the 16 'lionfish-analogous' species also declined by 44% (Figure 3. 2; LMM; P = 0.02, t = 2.1, df = 55), a change likely attributable to fishing pressure and/or competition with lionfish. By contrast, the biomass of non-predatory but large-bodied fishes, which were not vulnerable to lionfish predation (because they were already too large to be lionfish prey in 2008) or competition over this period but many of which are exploited to some degree, remained unchanged (Appendix A; Figure 3.2; LMM; P = 0.13, t =1.54, df = 55). Finally, no fish disease epidemic was reported during the study period, leaving lionfish predation as the most likely cause of the changes in prey fish abundance documented here.

Without prompt action, increasing lionfish populations are likely to have similar impacts on prey fish biomass across the region. The impacts of lionfish may not be limited to small-bodied prey species. In time, the abundance of large-bodied fishes which are consumed as juveniles by lionfish may be also be affected; these prey species fulfill important functional roles on coral reefs (Appendix A). Given the broad geographic extent of the invasion, complete eradication of lionfish from the Atlantic appears unlikely (Barbour et al. 2011). However, lionfish control programs, which are being initiated across the Caribbean, may successfully mitigate the effects of lionfish at local scales within high-priority areas, such as Marine Protected Areas and fish nursery habitats (Akins 2012). In the absence of effective local action, the effects of the lionfish invasion may have long-term implications for the structure of Atlantic marine communities, as well as the societies and economies that depend on them.

Chapter 4

Behaviour and morphology determine vulnerability of native fishes to an invasive marine predator

Abstract

Predation is a key force shaping demographic rates in aquatic ecosystems, which are often composed of myriad predator-prey relationships. However, studying the drivers of prey selection in a natural, multi-species context is challenging because predation usually cannot be directly observed. We use the recent invasion of Bahamian coral reef fish communities by predatory Indo-Pacific lionfish (*Pterois volitans*) to test hypotheses about the morphological and behavioural drivers of prey selection across a community-wide array of fish prey using *in situ* visual observations of prey consumption and availability for individual lionfish, and comparisons of prey abundance in lionfish stomach contents to availability on invaded reefs at large. Both approaches reveal that prey size, body shape and position in the water column are important determinants of prey vulnerability to predation by gape-limited lionfish, with small and fusiform fishes found just above reefs being the most vulnerable. Moreover, cleaning species experience a significantly lower risk of predation compared with non-cleaning fishes. Over time, prey types which are selectively consumed by lionfish on invaded Atlantic coral reefs may post more rapid and substantial declines as the invasion progresses. Our study shows that evaluating the contribution of variation in traits such as behaviour and morphology, versus body size alone, has major implications for modelling predator-prey interactions within ecological communities.

Introduction

Understanding prey selection is a key step in addressing questions about the structure and function of ecological food webs (Juanes et al. 2001, Almany and Webster 2004). Optimal foraging theory predicts that predators should select prey items in a manner which maximizes energetic gain while minimizing energy expenditure in locating, handling and processing the item (Pyke et al. 1977). If all prey types are equal in energetic profitability, then predators should consume prey in proportion to their abundance in the environment, so that diet composition will track changes in prey community composition across space and time (Beukers-Stewart and Jones 2004). However, particular prey types may be consumed in quantities disproportionate to their availability when differences exist between prey in their nutritional value, or when prey types vary in one or more morphological or behavioural characteristics that affect their encounter rate and handling time by predators (Hambright 1991, Scharf et al. 2003, Almany et al. 2007).

Quantifying the determinants of prey selection is particularly important in aquatic food webs, where predation is a key driver of demographic rates and processes (Caley 1993, Hixon and Beets 1993). While there is both experimental and observational evidence that prey morphology and behaviour affect prey selection, studies are usually limited to selection among a few focal prey species, or among trait variants within a single prey species (Savino and Stein 1982, Wahl and Stein 1989, Wahl 1995, Link 2004). However, given that the majority of aquatic food webs are composed of numerous predator-prey relationships, there is a need to understand the role of morphology and behaviour in determining vulnerability to predation across a community-wide array of potential prey. A major challenge to the study of prey selection in a multi-species context is the impracticality of directly observing prey selection under natural conditions.

Here we use the rapid invasion of western Atlantic coral reefs by predatory Indo-Pacific lionfish (*Pterois volitans* and *P. miles*) to examine the importance of a suite of morphological and behavioural characteristics of native fish prey in conferring vulnerability to predation. First reported from the coast of Florida in the 1980s, lionfish have become established in marine habitats across the western Atlantic, Caribbean and Gulf of Mexico (Betancur-R et al. 2011). Lionfish are gape-limited stalking predators capable of consuming prey that are almost half their total length, yet lionfish are themselves largely protected from predation by venomous fin spines (Fishelson 1975, Morris and Whitfield 2009). Lionfish display several behaviours that make them an ideal model predator for studying drivers of prey selection. First, lionfish exhibit bold behaviour and have little fear of divers, which facilitates a close approach without altering behaviour (Côté and Maljković 2010, Green et al. 2011). Second, they hunt prey via a slow hovering stalking strategy which affords an observer easy view of the target prey, as well as the success of strikes at prey (Côté and Maljković 2010, Green et al. 2011). Finally, the wide array of fish species consumed by lionfish on invaded coral reefs (Morris and Akins 2009), and the high level of redundancy in behavioural and morphological traits within reef fish communities (Bellwood et al. 2004), allow us to evaluate the role of prey morphology and behaviour in conferring vulnerability to predation independently from species identity.

In this study we use two methods to test hypotheses about the morphological and behavioural drivers of fish vulnerability to lionfish predation on invaded coral reefs in the Bahamas. We conduct visual observations of lionfish hunting, in which we document the prey consumed by and available to individual lionfish. We also compare the abundance of prey items in lionfish stomach contents to prey abundance on invaded reefs at large. Predation by lionfish has been implicated in the significant decline of reef fish biomass in parts of their invaded range (Green et al. 2012). Identifying prey traits that confer vulnerability to predation will aid in forecasting species-specific prey declines elsewhere in the region, and will ultimately provide insights into the roles played by prey morphology and behaviour in structuring marine communities.

Methods

Direct observations of prey selection

To quantify lionfish prey selection *in situ*, we conducted detailed visual observations of lionfish on shallow coral patch reefs off Eleuthera Island, Bahamas (22º22.500 N, 76º49.000 W) in September 2008 and December 2009. Individual lionfish were observed continuously for 30 min by a SCUBA diver from a distance of 2-3 m (Green et al. 2011).

Only individuals that were actively hunting (i.e., oriented with head down, pectoral fins spread and actively stalking prey fishes) and consumed at least 1 prey item during the 30 min observation period were included in this study. At the onset of observations, we estimated the size of the focal lionfish (total length [TL] to the nearest 1 cm). During each observation period, we recorded the identity, abundance and size (total length [TL] to the nearest 1 cm) of all fishes within a 1 m radius of the hunting lionfish every 5 min (hence, six point counts per observation). We also recorded the identity and size of all prey items consumed by lionfish during the 30 min period, as well as the fishes within a 1 m radius of the focal lionfish immediately following each prey capture. Lionfish are visual predators that primarily hunt in the open over the top of coral reefs or sand/seagrass beds. We thus assumed that only prey within visual sight of the lionfish (i.e., not those in crevices or under ledges) were available for consumption. We classified all fishes of less than 15 cm TL as potential prey items, based on physiological limits on predator: prey size ratio set by gape size (Nilsson and Brönmark 2000).

Indirect observations of prey selection

We also inferred lionfish prey selection by comparing the abundance of prey items in the stomachs of lionfish collected from eight sites along a continuous coral reef system off southwest New Providence Island, Bahamas (24º59.072 N, 77 º 32.207 W), with the abundance of prey identified during visual surveys of the same sites. Lionfish collections and prey visual surveys were conducted at depths of 10-20m between May and July 2008. Lionfish were collected using hand nets, and euthanized in a clove oil and seawater solution at the surface. We then measured TL to the nearest 1 cm, extracted stomach contents from each specimen and identified all fish prey items visually to the lowest taxonomic resolutions possible. For whole fish prey (i.e., items for which TL could be estimated) which could not be identified to species because of degradation of key skin pigments and colouration, we obtained species identity via DNA barcode analysis (Côté et al. in press). To minimize potential identification bias, we only included in our analyses lionfish stomachs from which all of the fish items could be identified to species (either visually or via DNA barcoding).

To estimate the abundance of prey available to lionfish, we conducted detailed surveys of prey-sized fishes (i.e. <15 cm TL) on 6-12 30 m x 2 m belt transects at each of the eight lionfish capture locations. Along each transect a trained observer carefully searched in all holes and crevices for cryptic fishes, using a dive light as needed. The identity and TL of all fishes was recorded to the nearest 1cm. We assumed that any prey hidden within the reef framework and not recorded in our visual surveys would not be available to lionfish to consume.

Transect surveys of prey-sized fishes were conducted immediately prior to lionfish collections at each site. We assumed that the assemblage of prey-sized fishes observed on our transect surveys matched the assemblage of prey fishes available to lionfish during hunting bouts at the sites within ~24 hr of capture, based on lab-derived times to digestion for lionfish prey (J.A. Morris, unpublished data) and preliminary results from external tagging and tracking on lionfish on the study reefs (S.J. Green unpublished data).

Prey trait hypotheses

To simultaneously examine the effects of prey morphology and behaviour on lionfish diet selection, we compiled information on a suite of traits that are likely to influence vulnerability to predation (Table 4.1), and generated hypotheses for each. We then assigned a score or value for each trait to each fish species encountered on our Bahamian study reefs (see Appendix B for detailed species table), based on published descriptions of each species (Böhlke and Chaplin 1993, Deloach 1999, FAO 2002b, a, Humann and Deloach 2002).

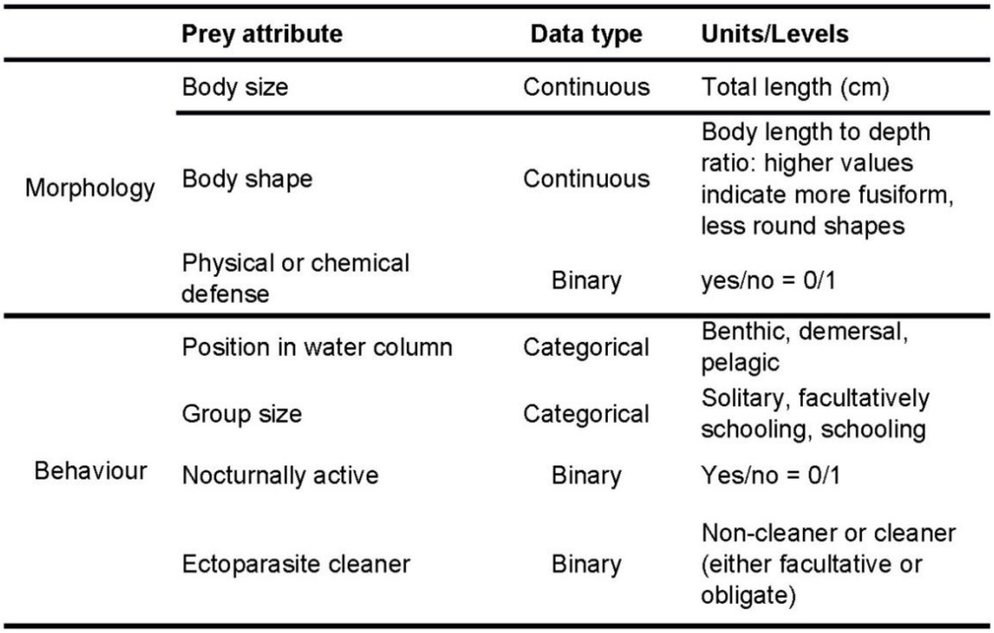
Behaviour

Lionfish are gape-limited predators which employ a stalking predation strategy (Côté and Maljković 2010, Green et al. 2011). Several aspects of prey behaviour should confer variable vulnerability to this hunting style. In particular, we predicted that the position of a species in the water column and whether it tends to aggregate with conspecifics (i.e., schooling behaviour; (Pitcher 1993) may significantly influence the frequency and outcome of predatory interactions with lionfish. Lionfish are demersal, visual predators that generally approach their prey by hovering slowly; we therefore predicted that demersal (i.e., living < 2m from the bottom) fishes would be more vulnerable to predation than benthic species (i.e., those living on or in the benthos), which may be less visible, or pelagic fishes occupying the water column above reefs (i.e. > 2m above the benthos), which may be less accessible. While many studies suggest that schooling behaviour is an effective anti-predator strategy because aggregations can dilute individual risk of predation (Pitcher 1993), we hypothesized that lionfish, whose slow movements afford them a close approach to potential prey, may in fact target schooling fish species because the conspicuousness of schools may reduce predator search time. We recognised three categories of aggregation behaviour: solitary, facultatively schooling and schooling. We defined 'facultative schooling' as an intermediate state, based on the observation that many fish species tend to form loose feeding aggregations as juveniles (e.g., wrasses and parrotfishes). We also hypothesized that fishes that are nocturnally active and whose emergence from sheltered reef habitats overlaps with the timing of lionfish foraging behaviour at crepuscular times (Green et al. 2011) would be more vulnerable to lionfish predation than their diurnal counterparts because this strategy may result in increased encounters with hunting lionfish (Hobson 1973, Fishelson 1975, Green et al. 2011). Finally, we anticipated that fishes that exhibit cleaning behaviour, either facultatively (i.e., only as juvenile) or obligately (i.e., throughout their lifespan), may be less readily consumed by lionfish, because such species often experience lower mortality rates from predation, possibly because of recognition by fish predators of the service cleaners provide (e.g. Côté 2000).

Morphology

We considered three major aspects of prey morphology which may affect vulnerability to predation by lionfish. For gape-limited predators, the costs of prey consumption (in terms of energy and time for capture and handling) have been shown to increase with prey body depth (Hambright 1991, Nilsson and Brönmark 2000). We thus anticipated that prey body shape plays an important role in prey selection by gape-limited lionfish, with vulnerability to predation decreasing with increasingly deep-bodied (i.e., increasingly round) shapes. We quantified shape as the ratio of TL to maximum body depth, such that higher values indicate less round (more fusiform), and hence more vulnerable, shapes. We calculated the average ratio of fish TL to the widest body depth (in cm), measured from lateral images of 3-5 specimens (available in Humann and Deloach [2002] and on FishBase [www.fishbase.org]) of each Bahamian fish species encountered on the study reefs. Second, we hypothesized that fishes possessing a chemical or physical defense (e.g., a toxic or distasteful compound, sharp spine(s) or barb) would be less vulnerable to predation compared with their undefended counterparts (e.g. Hoogland et al. 1956). Finally, studies of lionfish stomach contents report the average size of prey relative to their lionfish predator as ~15% (much smaller than the maximum of 48%; Morris and Akins 2009). However, it is unclear whether this result simply reflects the abundance of various prey sizes on invaded reefs. However, there is ample experimental evidence that gape-limited predators tend to selectively consume prey which are far smaller than their maximum gape limits, likely because larger prey are better at evading predators, and smaller prey are less costly to capture and handle by predators (Einfalt and Wahl 1997, Nilsson and Brönmark 2000). We therefore hypothesized that vulnerability to predation would decrease with increasing prey size (quantified as body length [TL to the nearest 1cm]).

Table 4.1. Morphological and behavioural traits of prey fish predicted to influence vulnerability to predation by invasive lionfish (Pterois volitans/miles)



	Prey attribute	Data type	Units/Levels
Morphology	Body size	Continuous	Total length (cm)
	Body shape	Continuous	Body length to depth ratio: higher values indicate more fusiform, less round shapes
	Physical or chemical defense	Binary	yes/no = 0/1
Behaviour	Position in water column	Categorical	Benthic, demersal, pelagic
	Group size	Categorical	Solitary, facultatively schooling, schooling
	Nocturnally active	Binary	Yes/no = 0/1
	Ectoparasite cleaner	Binary	Non-cleaner or cleaner (either facultative or obligate)

Statistical analysis

In the absence of prey selection, our null expectation is that lionfish will consume prey types in proportion to their environmental abundance. Our analyses of direct and indirect observations of lionfish predation tested whether the consumption by lionfish of prey types varying in morphology and behaviour deviated significantly from this null expectation. Specifically, we used generalised linear mixed-effects model (GLMM) to assess the effects of prey morphology and behaviour on lionfish prey selection from our direct observations of predation. We scored each potential prey fish within 1 m of a hunting lionfish as either consumed or not consumed (binary response: 0 or 1). As potential predictors of prey selection, we included individual prey TL, species-specific body shape, position in the water column, whether the prey species was nocturnal, physically or chemically defended, and a cleaner (Table 4.1). We specified three nested random effects, so that each potential prey was nested within the point count on which it was observed, the focal lionfish that was being observed, and the body length of the lionfish (TL to the nearest 1cm). The latter was included because we expected that prey size limits would increase with increasing predator size. We created our model using the glmer() function in the package lme4 for the statistical software R (R Core Team 2008). Parameter estimates for each fixed and random effect were obtained using the Laplace approximation with a binomially distributed error and cloglog-link function because the proportion of zeros in our data set greatly exceeded the proportion of ones (Bolker et al. 2009, Zuur et al. 2009). We conducted multiple Bonferonni-corrected Wald Z tests to obtain pair-wise comparisons of the relative selection probabilities for all levels of all categorical variables.

To identify the drivers of lionfish prey selection from our indirect observations of lionfish stomach contents and prey availability on New Providence reefs, we first calculated the proportion of each fish prey type (species and TL [in 1cm bins] combination) consumed by lionfish sampled from the study area, by dividing the abundance of each type, summed across the stomach contents of all lionfish, by its abundance estimate from our visual surveys of availability on the reef. Next, we constructed a generalised linear model (GLM) where the proportion of each prey type consumed was predicted by its morphological and behavioural characteristics (Table 4.1), and weighted by its abundance on surveys of the study area (Zuur et al. 2009). We created our model using the glm() function in the package AED for the statistical software R (R Core Team 2008). Again, we conducted multiple Bonferonni-corrected post-hoc Wald Z tests to obtain pair-wise comparisons of the relative selection probabilities for each categorical predictor.

Results

Prey selection from direct observations

On Eleuthera reefs we observed 22 hunting lionfish capture a total of 32 prey fishes from 22 species and 12 families (Appendix B). Lionfish size ranged from 10-36 cm TL (26 ± 6 cm; mean ± SD), while their captured prey ranged from 2- 7 cm TL (4 ± 1 cm; mean ± SD). The maximum number of prey consumed by a single lionfish during our observations was 4; twelve lionfish consumed a single prey fish. There were 32 species from 16 families recorded in point counts of fish prey availability (i.e., all individuals within 1 m radius of the focal lionfish and less than 15 cm TL; Appendix B).

Vulnerability to predation, measured as the individual likelihood of being consumed, decreased significantly with prey length and increased with more fusiform body shapes (Table 4.2; Figures 4.1 and 4.2). Cleaning behaviour was also a significant predictor of consumption by lionfish, with cleaners being significantly less vulnerable to predation than their non-cleaning counter parts (Table 4.2; Figure 4.1). Non-cleaning fishes were almost twice as less likely to be consumed by lionfish than non-cleaning species of a similar size and body shape (Figure 4.2). Living near the bottom tended to make native fishes more likely to be consumed by lionfish than occupying positions higher up in the water column (Table 4.2), but aggregation behaviour, nocturnality, and morphological defenses of prey did not influence vulnerability to predation by lionfish on Eleuthera reefs (Table 4.2; Figure 4.1).

Table 4.2. Results from A) a generalised linear mixed-effects model (GLMM) of lionfish diet selection from in situ observations on coral reefs off Eleuthera, Bahamas, and B) a generalised linear model (GLM) of lionfish diet selection inferred from lionfish stomach contents and visual surveys on coral reefs off New Providence, Bahamas. Levels of variables indicated in parentheses represent the baseline level against which the other level was compared.

Model	Response	Prey aspect	Variable	Level	Estimate	SE	*P*
A. GLMM	Individual prey consumed (0/1)		Intercept	-	-3.1	1.98	0.12
		Morphology	Body shape	-	0.7	0.23	0.002
			Length	-	-0.35	0.23	<0.001
			Defense	-	-23.15	123	0.99
		Behaviour	Water column position (Baseline: benthic)	Demersal	1.55	0.83	0.062
				Pelagic	-25.01	231	0.99
			Cleaner	-	-0.86	0.45	0.05
			Aggregation behaviour (Baseline: facultative)	Schooling	0.6	0.45	0.19
				Solitary	-0.69	0.62	0.26
			Nocturnal	-	-25.93	164	0.99
B. GLM	Proportion prey consumed		Intercept	-	-6.98	0.61	<0.0001
		Morphology	Body shape	-	0.48	0.059	<0.0001
			Length	-	-0.46	0.055	<0.0001
			Defense	-	0.29	0.5	0.57
		Behaviour	Water column position (Baseline: benthic)	Demersal	1.56	0.39	<0.0001
				Pelagic	-10.8	480	0.98
			Cleaner	-	-0.77	0.22	<0.0001
			Aggregation behaviour (Baseline: facultative)	Schooling	2.34	0.22	<0.0001
				Solitary	-1.15	0.26	<0.0001
			Nocturnal	-	4.07	0.44	<0.0001

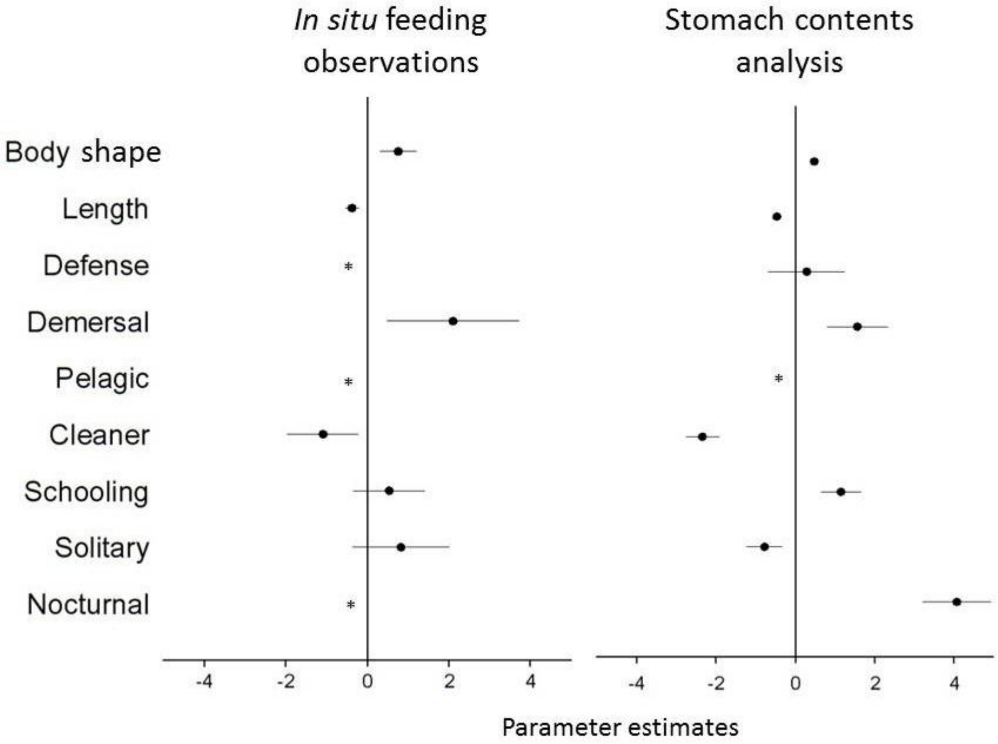


Figure 4.1. Coefficients from the generalised linear mixed-effects model (GLMM) of lionfish prey selection on Eleuthera coral reefs ('*in situ* observations') and the generalised linear model (GLM) of lionfish prey selection on New Providence coral reefs. Points represent mean values bounded by 95% confidence intervals. Levels 'Demersal' and 'Pelagic' are compared against the base level 'Benthic', and 'Schooling' and 'Solitary' are compared against the level 'Facultatively schooling'.* indicates parameter estimated with high variation by the model (i.e. standard error [SE] >100; Table 4.1) as a result of low proportion of fishes possessing the specific trait form within the data set (i.e. < 3% of observations).

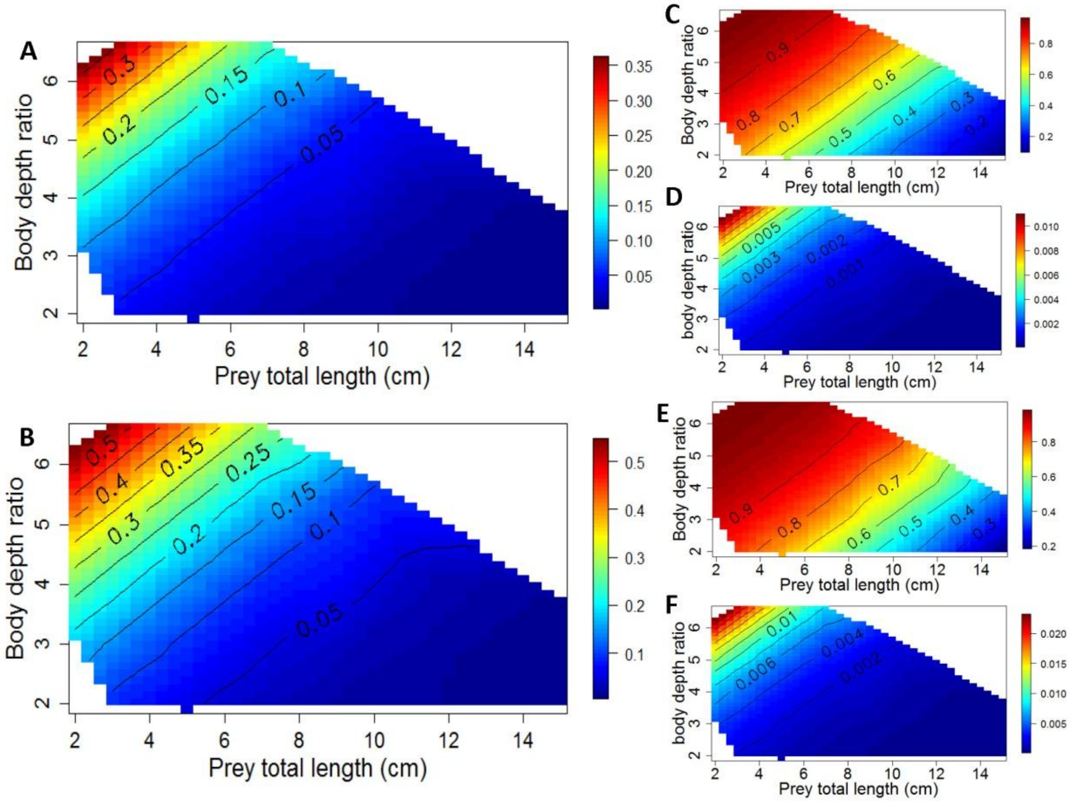


Figure 4.2. Contour plots of predicted mean vulnerability to predation by lionfish on coral reefs off Eleuthera, Bahamas, for A) fishes that clean (either facultatively or obligately) and B) non-cleaning species for various combinations of prey fish total length (cm) and body shape (quantified as the ratio of fish length to body depth; lower values indicate rounder shaper whereas higher values denote fusiform shapes), and corresponding upper and lower 95% confidence limits for cleaners (C and D, respectively) and non-cleaners (E and F, respectively). Black bands denote a change in predation probability of 0.1. Cooler colours denote the combinations of prey fish size and body depth ratio yielding low vulnerability to predation, while warmer colours denote scenarios in which vulnerability to predation is high.

Prey selection from indirect observations

Of the 637 lionfish collected from the New Providence reef system, 108 of contained whole fish prey that could be identified to species, either visually or through DNA barcode analysis. From these specimens, we documented a total of 258 prey fishes from 38 species and 16 families (Appendix B). The lionfish examined ranged in sizes from 10 – 38 cm TL (25 ± 5cm; mean ± SD) and their fish prey ranged from 2-13 cm TL (4 ± 2cm;

mean ± SD). The maximum number of prey fishes observed in a single lionfish stomach was 15; more than half (57 of 108) of the lionfish stomachs contained only one prey fish. We recorded 103 species from 30 families during the visual surveys of potential prey (i.e., all fishes < 15cm TL; Appendix B).

On New Providence reefs, the vulnerability of prey fishes to lionfish predation again decreased with prey length and increased with more fusiform body shapes (Table 4.2; Figures 4.1 and 4.3). Again, we found that cleaning behaviour was a significant predictor of consumption by lionfish, with cleaners being selected relatively less frequently than non-cleaners (Table 4.2; Figure 4.1). However, prey position in the water column, aggregation behaviour and nocturnal activity also significantly influenced lionfish prey selection (Table 4.2; Figure 4.1). On New Providence reefs demersal fishes were significantly more vulnerable than their pelagic and benthic counterparts, which were equally likely to be selected by lionfish (Table 4.2; Figure 4.1). Schooling fishes were also significantly more vulnerable than solitary fishes, as were nocturnal prey compared to diurnal fishes (Table 4.2; Figure 4.1). When the traits are considered in combination, fishes which potentially exhibit vulnerable forms of each morphological and behavioural trait are ~200 times more likely to be consumed by lionfish than their ‘invulnerable’ counterparts of the same size and body shape on New Providence reefs (Figure 4.3).

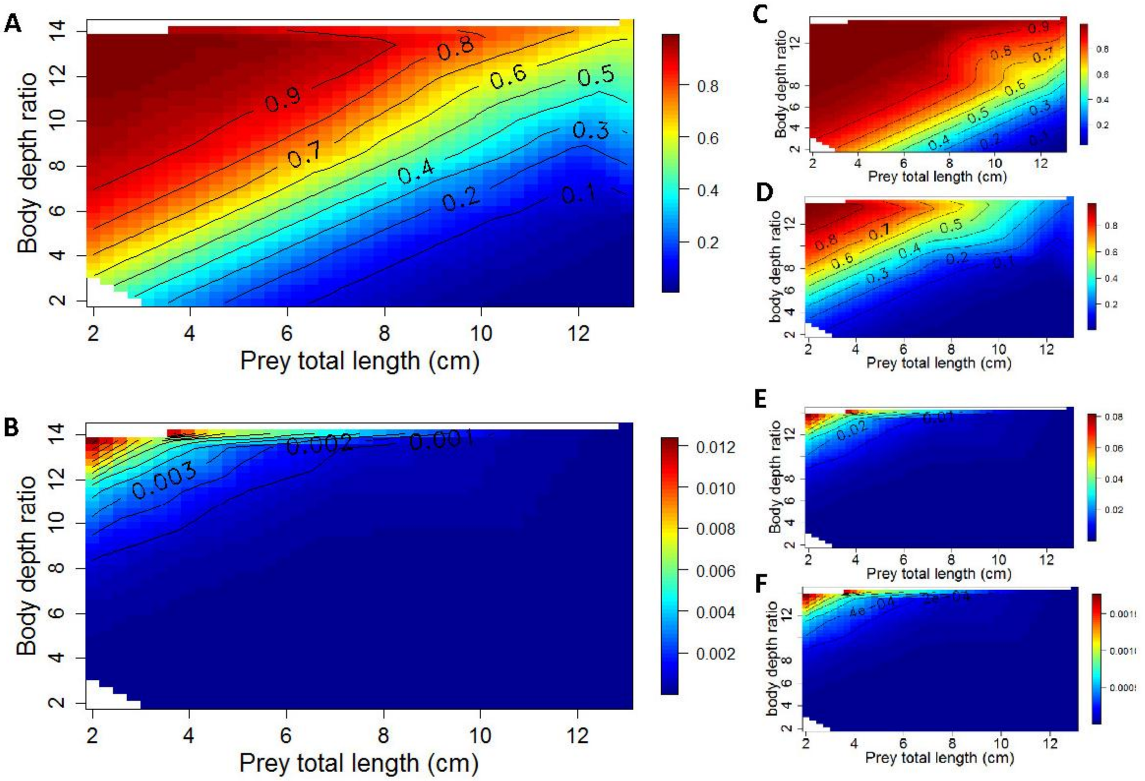


Figure 4.3. Contour plots of predicted mean vulnerability to predation by lionfish on coral reefs off New Providence, Bahamas, for A) fishes which are demersal schoolers that do not exhibit cleaning behaviour (facultatively or obligately) and are nocturnally active and B) cleaning species which are pelagic, solitary, and diurnally active, for various combinations of fish total length (cm) and body shape (quantified as the ratio of fish length to body depth) and corresponding upper and lower 95% confidence limits for each site of traits (C and D, and d and f, respectively). Black bands denote a change in consumption probability of 0.1. Black bands denote a change in predation probability of 0.1. Colour scheme is as described in Figure 4.2.

Discussion

Our study reveals that several aspects of prey morphology and behaviour confer vulnerability to predation by invasive lionfish. In particular, our analyses of both *in situ* behavioural observations and ex situ stomach contents reveal that prey size, body shape and position within the water column are important determinants of vulnerability to predation, with small and fusiform fishes occupying the water just above reefs most vulnerable to predation by lionfish. Furthermore, both approaches identify cleaning behaviour as a significant correlate of vulnerability to predation, with cleaning species at a significantly lower risk of predation compared with non-cleaning fishes. Sociality and nocturnality also significantly influenced lionfish prey selection on New Providence but not on Eleuthera reefs.

Interestingly, we found that schooling behaviour increased the vulnerability of fish prey to lionfish predators on New Providence reefs. This situation may arise if schooling fishes do not perceive the slow, hovering approach of lionfish as a predation threat, or if search time by lionfish for prey is reduced due to the aggregation of similar prey types. While our observations indicate that, on the whole, schooling prey are more vulnerable than solitary fishes, the success of schooling behaviour as an anti-predator strategy has been shown to depend on a combination school size, prey vigilance and predator detection strategy, which are thought to be species and context dependant (Bednekoff and Lima 1998). Further work is needed to tease apart the effects of school size and prey vigilance on vulnerability to lionfish predation.

The majority of our predictions for the behavioural and morphological features of native fish which affect their vulnerability to lionfish predation were confirmed by data collected at two very different spatial scales. However, there were two exceptions. While pelagic prey were on average far less likely to be consumed than their demersal or benthic counterparts, as was expected, (Table 4.1), their likelihood of being eaten was surrounded by large uncertainty for both study regions. This may be due to the fact that very few prey-sized pelagic fishes were observed on Eleuthera and New Providence reefs (i.e. <0.004% of fishes observed in both locations). For example, *in situ* observations of potential prey close to hunting lionfish on Eleuthera reefs yielded only 4 observations of pelagic fishes. If the spatial distribution of prey-sized pelagic fishes rarely overlap with demersal lionfish, then such fishes are largely unavailable for lionfish to consume, and should not in fact be considered among the set of fishes lionfish choose among (e.g. hierarchical resource selection [Johnson 1980]). Another prey feature which unexpectedly had little influence on vulnerability to lionfish predation was the presence of a physical or chemical defense. One possible explanation is that the manner in which prey use physical defenses (e.g. spines or barbs) may be ineffective against the hunting strategy of lionfish; during many of our direct observations, prey appeared largely unaware of their lionfish predator immediately prior to a capture.

Alternatively, defenses of small-bodied prey may simply be ineffective against relatively large-bodied lionfish predators (on average, prey were 15% of the lionfish's TL).

We show that lionfish predation mortality will be greatest for prey possessing a particular suite of behavioural and morphological characteristics on invaded Atlantic coral reefs. As lionfish can reach densities allowing the rapid depletion of prey biomass (Green et al. 2012), prey types which are selectively consumed may post more rapid and substantial declines over time, with potentially serious implications for local population persistence. Time-series data documenting the relative change in biomass of prey types over time, in relation to lionfish predation pressure, are needed to test these predictions. Moreover, selective predation by lionfish may have repercussions on invaded marine food webs if vulnerability to lionfish predation correlates with functional role of prey. For example, if many herbivores are small, fusiform and demersal, the high rate of lionfish-induced mortality could impair the process of herbivory, which suppresses algal growth on coral reefs (Mumby et al. 2006). Because our analyses focus on prey characteristics and not species identity, our findings may provide useful insight into the potential effects of lionfish predation on fish communities elsewhere in the invaded region; data on fish assemblages from pre- and early- invasion regions may be used to establish spatial priorities for management action. For example, locations where native fish communities are composed of a high proportion of vulnerable individuals (i.e., small-bodied, fusiform, demersal and nocturnal species) could be targeted for lionfish culling.

Accurately quantifying predator-prey interactions is integral to understanding ecological patterns and processes within marine communities, particularly within the context of increasing levels of anthropogenic change (Myers and Worm 2003). Our findings provide important insights into current thinking about predator-prey interactions, which can be broadly characterized into two prevailing paradigms: a species-based view, in which food webs are constructed by quantifying the interaction strength between pairs of predators and prey (Paine 1980, Polis and Strong 1996), and a size-based approach which classifies predator-prey interactions based on body size, largely ignoring species identity (Jennings 2005, Blanchard et al. 2011). Our study shows that evaluating the contribution of variation in traits such as behaviour and morphology, versus body size alone, has major implications for modelling predator-prey interactions within ecological communities (e.g., (Hartvig et al. 2011).

Chapter 5

Predicting the effects of an invasive predator on marine fish communities: A size-based approach[3]

Abstract

Accurately predicting the ecological effects of invasive species on recipient communities is a major challenge because it requires knowledge of the mechanisms of impact, as well as the population levels of the invader that elicit negative effects. This challenge is well illustrated by the invasion of Indo-Pacific lionfish (*Pterois volitans* and *P. miles*) into marine habitats across the Western Atlantic, Caribbean and Gulf of Mexico. Here, we draw on size-based metabolic scaling theory to develop an empirical model of the effect of lionfish predation on the biomass of their fish prey, and find that it accurately predicts observed declines in lionfish prey assemblages on invaded coral reefs in the Bahamas. Looking ahead, we forecast that populations of lionfish will continue to remove prey at rates far greater than they can replenish, with lionfish prey consumption outstripping prey production by an order of magnitude across the nine study sites. To halt further declines in native fish biomass, we estimate that lionfish densities must be reduced by a minimum of 28-82% on invaded reefs.

Introduction

Invasive species are altering the structure and function of ecosystems across the globe, with concomitant impacts on economies and societies (Manchester and Bullock 2000, Mooney and Cleland 2001). The scale and magnitude of many invasions preclude

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[3] A version of this chapter is in preparation for publication and co-authored by N.K Dulvy, A.B. Cooper and I.M Côté.

eradication. The management of these invasions must therefore rely on the suppression of populations, ideally below levels that cause negative ecological or economic effects (Van Driesche et al. 2008). However, the identification of such threshold population levels is challenging because it requires a thorough understanding of the mechanisms by which an invader affects the recipient communities, and particularly of the links between invader populations levels and negative ecological effects.

Indo-Pacific lionfish (*Pterois volitans* and *P. miles*) offer a prime example of a broadly distributed, highly abundant invader which is beginning to cause severe negative ecological effects. Lionfish have rapidly spread over more than 4,000,000 km^2 of marine habitat across the Western Atlantic, Caribbean and Gulf of Mexico, and are now undergoing exponential increases in abundance at many locations (Betancur-R et al. 2011; REEF 2012). Well defended from predation by venomous spines, invasive lionfish occupy a range of habitat types and depths, where they consume an array native fishes and crustaceans at high rates (Schofield 2009, Green et al. 2011). There is growing concern that predation by lionfish will nullify efforts to protect vulnerable fish populations from anthropogenic threats in the region (Sutherland et al. 2010, Albins and Hixon 2011).

It is widely agreed that lionfish can no longer be eradicated from their new range (Barbour et al. 2011, Akins 2012). To quantify the magnitude of lionfish predation impacts, and the extent to which lionfish populations need to be controlled to mitigate them, we construct an empirical, size-based model of lionfish-prey interactions which draws on metabolic scaling principles (e.g. Brown et al. 2004, Jennings and Brander 2010) to estimate annual rates of biomass production by lionfish prey, and *in situ* observational studies to estimate rates of prey consumption by lionfish (Côté and Maljković 2010, Green et al. 2011). Our method differs from existing ecological modeling frameworks in two important ways. First, we focus solely on lionfish and their prey fish species, rather than creating a full energy-budget model of coral reef ecosystems (e.g. Arias-González et al. 2011). Our narrower approach reduces the information demands on the model, allowing us to use high-resolution field data on lionfish and prey populations from invaded reefs which yield fish assemblage-specific (i.e., site-specific) predictions. Second, ecological risk occurs wherever there is uncertainty. However, uncertainty in parameter estimates is not routinely propagated through size-based models and hence the significance of and confidence in the outputs are usually unknown (e.g. Blanchard et al. 2011, Nuttall et al. 2011). Our size-based, mass-balance model of lionfish-prey interactions explicitly accounts for uncertainty.

In this paper, we parameterize our size-based model of lionfish predation impact with time-series data from nine invaded coral reefs off southwest New Providence Island, Bahamas. Prey fish biomass declined by an average of 48-88% across these nine reefs between 2008 and 2010 as a result of lionfish predation (Green et al. 2012). Guided by the premise that the biomass of prey populations will decline if lionfish consume prey at greater rates than the prey are produced, we address three specific questions:(1) Does our mechanistic model of lionfish-prey interactions accurately predict observed prey biomass depletion?, (2) in the absence of any management, will predation by lionfish predation cause further declines the biomass of their fish prey?, and (3) to what extent must lionfish populations be reduced to prevent further declines? Our ultimate goal is to create a modelling framework to predict the effects of lionfish predation on the diverse assemblages of fish they consume and to identify targets for removal required to mitigate these ecological effects.

Methods

We first derive a model describing the effect of lionfish predation on the biomass of native fish assemblages, using mass-balance and metabolic scaling principles. We then describe the system of nine invaded Bahamian coral reefs to which we apply our modelling framework, and the field data collection methods used to obtain model parameter estimates. Third, we outline the results of a model validation exercise, comparing predicted changes in prey fish biomass at the nine Bahamian sites with observed changes. Finally, we describe three analyses which use our validated model to assess the present and future effects of lionfish predation on fish biomass across the study system, and how uncertainty and errors were propagated into the model outputs.

Modelling lionfish predation impact

Our model focuses on estimates of two annual, assemblage-specific (i.e. site-specific) rates: biomass production by lionfish prey ($\bar{P}$; g ha^{-1} yr^{-1}), and the rate of prey consumption by lionfish ($\bar{C}$; g ha^{-1} yr^{-1}). The difference between the two is the net rate of biomass production by the prey fish assemblage at a site:

$$\bar{N} = \bar{P} - \bar{C} \qquad \text{Equation 5.1}$$

Our model and analyses are based on the hypothesis that the biomass of prey populations will decline if lionfish consume prey at rates that exceed those of prey production (i.e. $\bar{N}$ < 0).

Estimating prey fish production ($\bar{P}$)

We estimated the rate of annual prey fish production ($\bar{P}$) by converting the body mass of fish prey to rates of annual biomass production using known metabolic relationships, which are based on the intrinsic relationship between an organism's size and the rate at which it produces new biomass (Brown et al. 2004).

$$\bar{P} = \frac{1}{z}\sum_{\forall_z}\sum_{\forall_i}\sum_{\forall_v} P_{v,i,z} \qquad \text{Equation 5.2}$$

where *v* is a single individual of fish species *i* observed on visual transect survey *z* per site. For simplicity, we will refer to $P_{v,i,z}$ as P, which is calculated as:

$$P = ZB \qquad \text{Equation 5.3}$$

Z and *B* are the total mortality rate and body mass, respectively, for each individual fish. The mortality rate *Z* scales as an allometric function of body mass (*B*) with constants *j* and *q*, which approximates the ratio of production rate in g ha^{-1} yr^{-1} to standing biomass in g ha-^{1} (i.e., P/B of Polovina [1984]), such that:

$$Z \approx \frac{P}{B} = \frac{jB^q}{e^{E/kT}} \qquad \text{Equation 5.4}$$

The scaling exponent (*q*) of the relationship between P/B and body mass has been theoretically explored, and empirically validated, as -0.25 (Brown et al. 2004). However, *j* varies with taxonomic group and ecosystem-specific species interactions (Brown et al. 2004). Analyses of juvenile and adult marine tropical fish taxa suggest a *j* value of 3.08 (Lorenzen 1996). The equation $e^{E/kT}$ describes the effect of environmental temperature on prey fish production rates, where *E* is the activation energy, *k* Boltzmann's constant and *T* is ambient water temperature, expressed in degrees Kelvin (Table 5.1).

Prey fish body mass B was estimated using the allometric function:

$$B = a_i L^{b_i} \qquad \text{Equation 5.5}$$

where L is the total length of each individual fish, converted to weight using allometric length-weight scaling constants a_i and b_i which are species-specific and derived from the literature (Fish Base; http://www.fishbase.org).

Estimating lionfish prey consumption ($\bar{C}$)

We estimated annual assemblage-specific prey consumption by lionfish at a site ($\bar{C}$) from four key parameters: lionfish population density, size structure, diet composition and predation rates.

$$\bar{C} = \bar{d}\bar{W}\bar{p}(0.006e^{0.16T}\overline{W_l}^{h})y \qquad \text{Equation 5.6}$$

where $\bar{d}$ is the density of lionfish per site, calculated as the average number of lionfish observed on transects at the site (individuals ha^{-1}). $\bar{W}$ is the mean body mass (in g) of lionfish, calculated as:

$$\bar{W} = \frac{1}{m}\sum\nolimits_{\forall m}(a_l {L_m}^{b_l}) \qquad \text{Equation 5.7}$$

where L_m is the total length of each of *m* lionfish (in cm) observed at the site, and a_l and b_l are lionfish-specific allometric length–weight scaling constants.

In Equation 6, $0.006e^{0.16T}$ describes the scaling relationship between lionfish mass-specific prey consumption rate (g prey^{-1} g lionfish^{-1} day^{-1}) and body weight (g) derived by

(Côté and Green 2012) from two field studies of lionfish prey consumption at different water temperatures (Côté and Maljković 2010, Green et al. 2011; Table 5.1). The scaling constant *h* has a value of -0.29 for lionfish (Côté and Green 2012). The parameter $\bar{p}$ estimates the mean proportion of fish in the total diet of lionfish, which can take a value between 0 and 1. Finally, we extrapolated average daily consumption rates by lionfish to annual rates by multiplying by the constant g, which is 365.4 days/year.

Thus our model of net prey fish production ($\bar{N}$) with all terms made explicit is given by:

$$\bar{N} =$$

$$\frac{1}{z}\ \sum_{\forall_z}\sum_{\forall_i}\sum_{\forall_v}\left(\frac{j(a_i {L_{v,i,z}}^{b_i})^q}{e^{\frac{E}{kT}}}\right) a_i {L_{v,i,z}}^{b_i} - \bar{d}\,\frac{1}{m}\sum_{\forall_m}(a_l {L_m}^{b_l})\,\bar{p}\left(0.006e0.16T\,\frac{1}{m}\sum_m(a_l {L_m}^{b_l})^h\right) g$$

Equation 5.8

Reconstructing depleted prey fish biomass ($\bar{B}_p$)

We used our model of net prey production *($\bar{N}$)* to reconstruct the average biomass of prey fish (g ha^{-1}) at each site that was depleted by lionfish in the past year *y* ($\bar{B}_y$) as:

$$\bar{B}_y = \bar{B}_x + \frac{-\bar{N}_{x-y}}{\left(\frac{\bar{P}_x}{\bar{B}_x}\right)} \qquad \text{Equation 5.9}$$

where $\bar{\mathrm{B}}_\mathrm{x}$ is the mean biomass of prey fish at the site (g ha^{-1}), calculated as the sum of the weights of prey (*B* in Equation 5.5) averaged across visual surveys conducted at the site in year x. $-\bar{N}_{x-y}$ is the deficit in the net rate of prey fish production between year c and p. Dividing this deficit by the average ratio of prey production ($\bar{P}_x$) to standing biomass ($\bar{B}_x$) in year x, gives the standing biomass of prey required to produce new biomass at rates equal to the deficit. We estimated the ratio $\frac{\bar{P}_x}{\bar{B}_x}$ by calculating the average mortality of all individual fish *v* at a site as $\frac{1}{v}\sum_{\forall_v}\frac{jB^q}{e^{E/kT}}$ (Equation 5.4).

Study system and field data

Bahamian coral reefs were first invaded by Indo-Pacific lionfish in 2004 (REEF 2012). Our analyses focus on the impact of lionfish predation on the fish communities of nine invaded sites along a continuous coral reef system bordering the Tongue of the Ocean Trench off of southwest New Providence (Figure 5.1). In the summers of 2008 and 2010 we carried out field surveys and specimen collections of lionfish and their prey at the nine study reefs. We used our 2010 data to parameterize the model, and our 2008 data to validate its predictions of site-specific lionfish predation impact and control. We characterized water temperature (*T*) in our model as 26 ºC ± 3 ºC (mean ± SD), the normal range of water temperatures in the Bahamas (NOAA 2012).

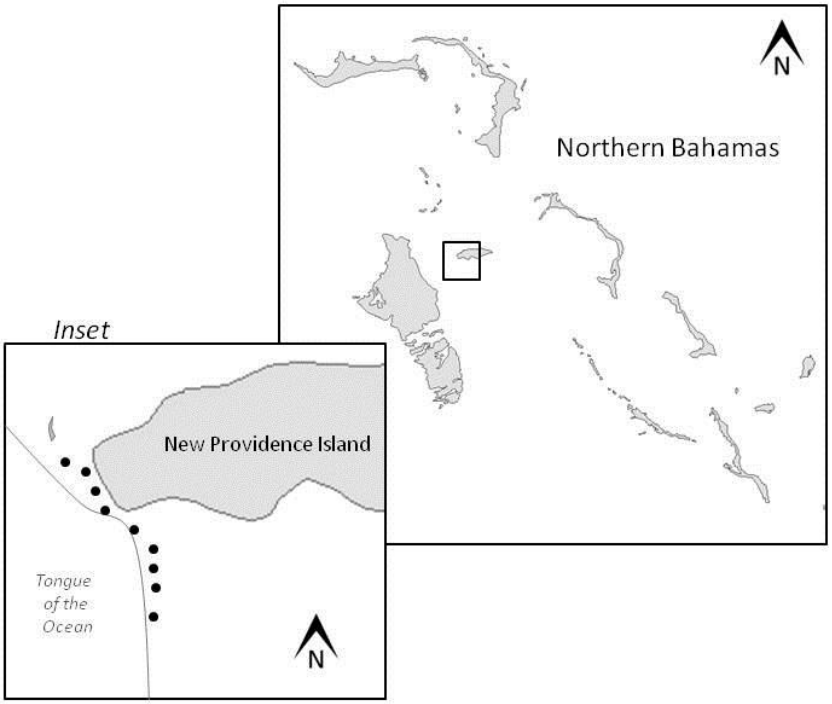

Figure 5.1. Map of study location and sites. Coral reefs in the Bahamas were the first in the region to be invaded by lionfish, with the first specimen reported from reefs off of southern New Providence Island in 2004. *Inset:* Locations of the nine coral reef study sites along the southwest coast of New Providence Island.

Lionfish body size and density

We quantified the number and size (total length to the nearest 1cm) of lionfish on 3 to 6 50 m x 10 m transects per year at each study site. Transects were laid parallel to the reef crest and stratified by depth and zone, with two transects at each of three depths: 20 m (reef wall), 15 m (reef crest) and 10 m (reef flat). We obtained constants for the allometric scaling relationship between length and mass for lionfish ($a_l L_m{}^{b_l}$) from 235 haphazardly selected specimens, ranging in size from 6 mm to 390 mm total length, collected from the sites during the study. For this sample of lionfish, a_l= 0.00497 and b_l=3.291 (R^2=0.99, P=0.001, df = 234).

Prey fish biomass

Lionfish are visual predators that stalk fish prey over reef habitats during crepuscular and daylight hours (Côté and Maljković 2010, Green et al. 2011). To quantify native fishes available to lionfish on our study reefs, we conducted 6 to 12 transects (30 m long x 2 m wide) each year per coral reef site. Transects at each site were laid parallel to the reef crest and stratified by depth and zone, with 2-4 transects at each of three depths: 20 m (reef wall), 15 m (reef crest) and 10 m (reef flat). On each transect, we conducted detailed searchers for all fish species, recording the number, size (total length to the nearest 1 cm) and identity of all reef fishes of less than 15 cm total length (TL). Observation and external tagging of lionfish in the system reveals that individuals residing at each site (i.e. ~1 ha of reef habitat) have access prey in all three zones (S.J. Green, unpublished data), and so we combined prey data across zones to obtain biomass estimates at the site level.

Lionfish diet composition

We determined the species identity and size limits of potential fish prey for lionfish by capturing 440 lionfish across the 9 study reefs in 2008 (N = 5-137 lionfish per site) and 147 lionfish in 2010 (N= 6-40 lionfish per site) and examining their stomach contents. We identified all items ingested to the lowest taxonomic level possible and measured the volume and total length of each identifiable prey item. We identified 42 species of Caribbean reef fish from 16 families in lionfish stomachs (Green et al. 2012). We set the upper limit of potential lionfish prey size by identifying the maximum total length of fish in stomach contents (i.e., 13 cm), and the maximum gape height (i.e., 4.8 cm) of lionfish collected. We therefore excluded as potential prey for lionfish all fish recorded on surveys with body lengths greater than 13 cm and body depths that exceeded 5 cm. We estimated body depths of fish observed using species-specific relationships between fish total length and body depth (Gerstner 1999, FishBase; http://www.fishbase.org). When species-specific information was not available, we used relationships for similarly shaped, closely related species. The proportion of fish in the diet of lionfish ($\bar{p}$) was estimated from lionfish stomach contents. In both years, a large proportion of the diet (by volume) was made up of fish rather than invertebrate prey (across the nine sites: mean ± SD: 0.89 ± 0.08 in 2008 and mean ± SD: 0.70 ± 0.07 in 2010).

Analyses

Model validation

To evaluate the accuracy of our model's predictions, we reconstructed the prey biomass that must have existed at the nine New Providence sites in 2008, based on our estimates of net prey fish production and observed prey fish standing biomass in 2010 ($\bar{B}_y$; Equation 9; p = 2008, c = 2010). We then tested whether the slope of the regression of empirical estimates of prey biomass for 2008 with reconstructed prey biomass for the same year deviated significantly from 1 and the intercept from 0 (Piñeiro et al. 2008).

Predicting future prey biomass decline

To evaluate whether prey fish biomass is continuing to decline across the nine reefs, we estimated the net rate of prey fish biomass production for each site ($\bar{N}$; Equation 5.8) in 2010. We also sought to evaluate how broadening the lionfish's diet, and thus increasing the biomass of fish prey available for consumption, influenced values of $\bar{N}$ across the system. To accomplish this, we increased lionfish diet breadth to include not only the fish species identified in the stomachs of lionfish caught in this study (n = 42 species; Table 5.2) but all prey-sized reef fish species encountered during visual surveys (n = 118 species; Table 5.2). Finally, lionfish predation has the potential to release reef fish prey species from density-dependent regulation of new biomass production, which could lead to underestimation of the net rate of prey fish production at each site. While the carrying capacity of each site is likely to vary greatly in relation to habitat structure, we assumed that the strength of density dependence is constant across all sites. We assumed that the maximum compensatory production caused by increased mortality owing to lionfish predation was three times the estimated production rates of prey at each site, based on field evaluations of density-dependent effects on mortality in reef fishes (Hixon and Carr 1997, Anderson 2001, Carr et al. 2002).

Estimating targets for lionfish control

We calculated the density of lionfish that would result in rates of prey consumption that were equal to prey fish production at each site in 2010, termed the 'sustainable' lionfish density ($\bar{d}_{sustainable}$), by setting $\bar{C}$ equal to $\bar{P}$ at each site (Equation 5.8), and solving for $\bar{\mathrm{d}}$.

Uncertainty and errors

We used Monte Carlo simulation to propagate uncertainty in model parameters into our estimates of $\bar{B}_y, \bar{N}$ and $\bar{\mathrm{d}}_{\mathrm{sustainable}}$ for each site (see Table 5.1 for a summary of parameter sources). For each model, we calculated the median from 1,000 iterations and repeated the simulation 500 times for $\bar{B}_y, \bar{N}$ and $\bar{\mathrm{d}}_{\mathrm{sustainable}}$ at each of the nine study sites. Within each model we specified log-normal distributions for lionfish density and body mass ($\bar{\mathrm{d}}$ and $\bar{W}$) because we failed to reject the assumption of normality for log transformations of these data (Kolmogorov-Smirnov tests, $p > 0.13$ for all tests). We specified normal distributions for water temperature and for proportion of diet composed of fish prey (T and p respectively; Table 5.1). We then constructed empirical 95% confidence intervals of the median by taking the 2.5 and 97.5 percentiles of the resulting distributions as our confidence limits for each metric per site (Vose 2008). We also constructed confidence intervals of the mean log-transformed lionfish densities and prey fish biomass at each site, derived from reef surveys (Figs 5.2 and 5.4).

Table 5.1. Parameters used to model the density at which lionfish begin to over-consume their fish prey on invaded Bahamian coral reefs. Note: v is a single individual of fish species i observed on visual transect survey z per site. *Indicates parameters for which error was propagated through our calculations using Monte Carlo simulation.

Model component	Parameter	Meaning	Value	Source
Prey fish production	$L_{v,i,z}$	*prey fish length	*1 -13cm (individual specific)*	Reef-specific
	j, q	*metabolic biomass-production scaling constants	*q =0.25, j =3.08*	Brown *et al.* 2004, Lorenzen 1996
	a_i, b_i	species-specific length-weight scaling constants	*species-specific*	www.fishbase.org
	E	activation energy	*0.65eV*	Brown *et al.* 2004
	k	Boltzmann's constant	*8.06 x 10^{-5}*	
	T	*water temperature	*299.25 ± 3 K (26 ± 3°C)*	NOAA 2012
Lionfish prey consumption	a_l, b_l	lionfish-specific length-weight scaling constants	$a_l = 0.00497$ $b_l = 3.291$	Reef-specific
	L_m	*lionfish length	*6-390mm (individual specific)*	Reef-specific
	h	*prey consumption scaling constant	*0.29*	Côté and Green 2012
	x	scales daily rate to annual rate	*365.4 days year^{-1}*	
	p	*proportion of diet composed of fish	*0.7± 0.07*	Green et al. 2012
	T	*water temperature	*299.25 ± 3 K (26 ± 3°C)*	NOAA 2012
	r	*radial distance of the area over which lionfish forage	*Radius of reef area + 10m into sand/sea grass* *(Green et al. 2011)*	Reef-specific

Results

Does our model accurately predict observed prey biomass depletion?

We related prey biomass measured in the field in 2008 to model-predicted prey biomass for 2008 at the same nine sites, reconstructed based on the biomass of lionfish and their prey in 2010. The regression slope did not deviate significantly from 1(P =0.61, t =-0.53, df = 8; Coefficient ± SE: 0.97± 0.06), and the intercept did not differ significantly from 0 (P =0.27, t =-1.19, df = 8; Coefficient ± SE: -8.05 ± 6.78) (Figure 5.2), indicating that our model closely predicts the magnitude of lionfish-induced prey declines across the system.

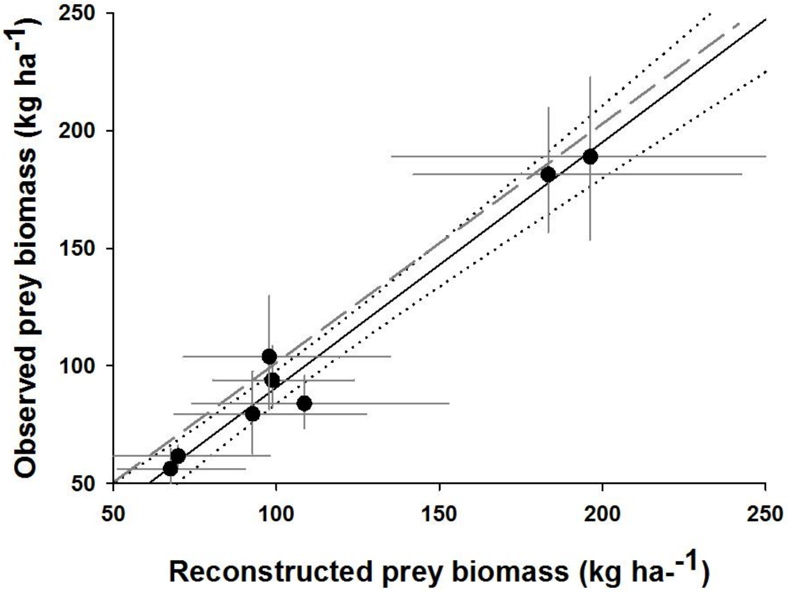

Figure 5.2. Field-observed biomass (kg ha^{-1}) of lionfish fish prey in 2008 and model reconstructions for the same year. Points are bounded by 95% parametric bootstrapped confidence intervals for simulated prey biomass and log-normal confidence intervals for field-observed biomass. Prey fish include 42 reef fish species known to be preyed upon by invasive lionfish. The dashed grey line shows a one-to-one relationship.

Will predation by lionfish predation cause further declines the biomass of their fish prey?

Lionfish populations are likely continuing to remove prey at rates far greater than reef fish populations can replenish through somatic growth and reproduction (Figure 5.3), with lionfish prey consumption outstripping the production of their prey by an order of magnitude at all nine study sites. Our projections for continued prey declines are robust to potential changes in both lionfish diet breadth and density-dependent prey fish production (Figure 5.3). Even when a broad diet (i.e., 118 prey species instead of 42; Table 5.2) is considered, the current (2010) rates of lionfish prey consumption ($\bar{\mathrm{C}}$) still exceed prey production ($\bar{P}$) at all sites (Figure 5.3). Comparing extreme density-dependent compensatory prey fish production with rates of lionfish prey consumption still yielded negative mean net prey production rates at 4 of 9 sites (Figure 5.3).

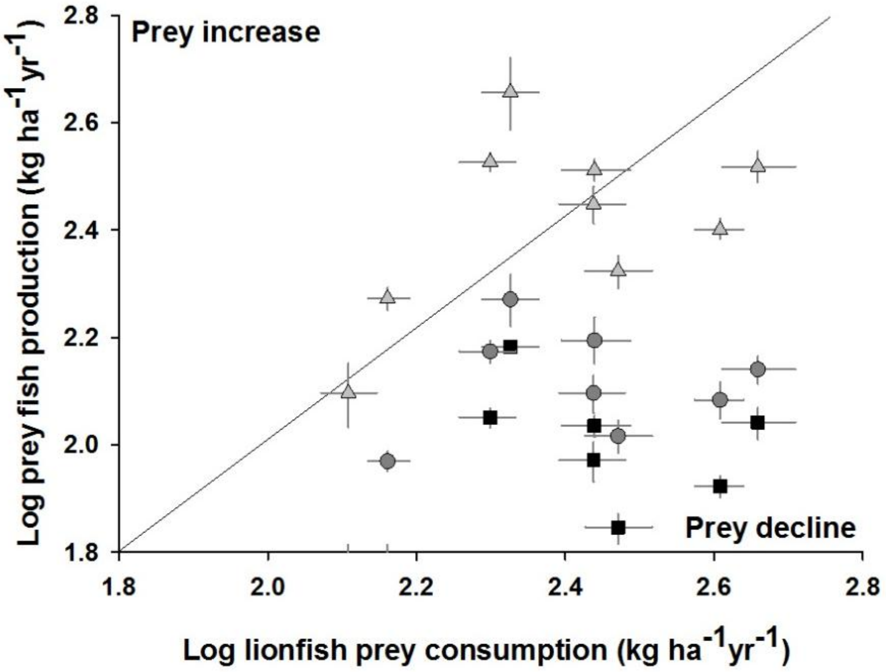

Figure 5.3. Predicted rates of prey consumption by lionfish (kg ha-1 yr-1) in relation to predicted cumulative rates of production by their prey f (kg ha-1 yr-1) on nine invaded reef sites off of New Providence, Bahamas, in 2010. Points represent site means bounded by 95% parametric bootstrapped confidence intervals and presented on a log scale. The bold line represents the trajectory along which prey consumption by lionfish equals prey production. On reefs where consumption is greater than production (i.e., points below the line), prey fish biomass will continue to decline. The black squares represent analysis incorporating only prey observed in lionfish stomachs (n= 42 species). The grey circles show the effect of increasing the diet breadth of lionfish to include all prey-sized fish species (n = 118 species) recorded during fish surveys. The grey triangles show the effect of maximum density-dependent compensation in prey production (i.e., increased three times).

To what extent must lionfish populations be reduced to prevent further declines?

Lionfish removal may be an effective strategy to halt the decline of fish biomass on invaded reefs. To arrest prey fish declines and thus maintain current prey standing biomass, current lionfish densities need to be reduced by, on average, 28-82% across the study reefs (Figure 5.4).

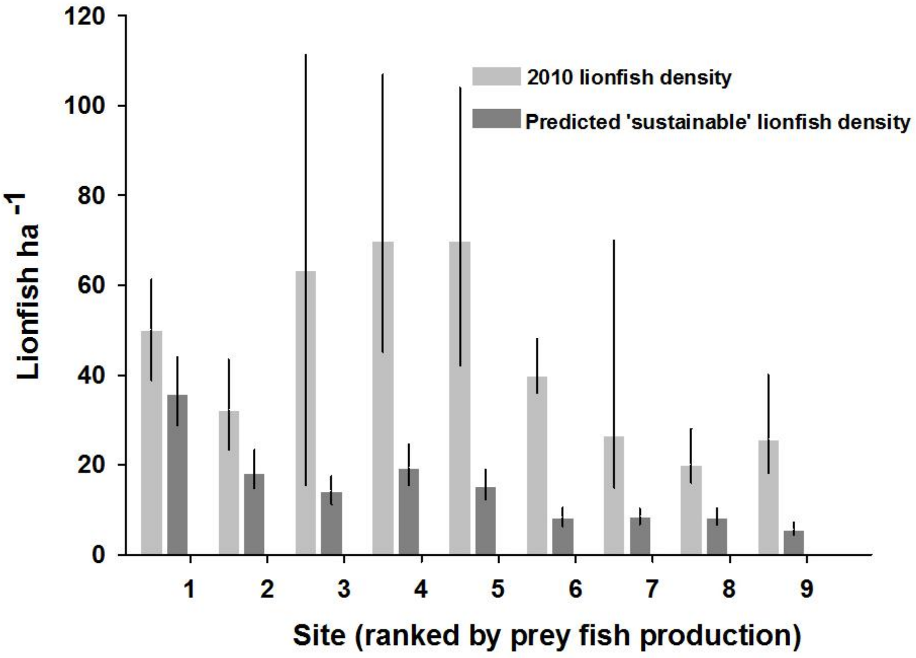

Figure 5.4. Observed (light grey bars) and modeled ‘sustainable’ (dark grey bars) lionfish densities in 2010 at each of nine coral reef sites off of New Providence, Bahamas. We defined ‘sustainable’ densities as those at which the rate of prey consumption by lionfish equals annual prey fish production at each site. Sustainable densities are represented by the median values from model simulations, bounded by 95% parametric confidence intervals. Observed lionfish densities are represented by means from field censuses, bounded by 95% log-normal confidence intervals. Sites are ranked in decreasing order of prey production.

Discussion

Our size-based model of lionfish predation impact accurately predicted the recent and significant declines in the biomass of lionfish prey observed across nine invaded Bahamian reefs (Green et al. 2012). In the absence of rapid management intervention, we forecast that lionfish populations will continue to cause steep declines in the biomass of remaining prey fish populations. Lionfish are now established around the Caribbean and Gulf of Mexico, and are predicted to spread as far south as the central eastern coast of South America (Morris and Whitfield 2009). With rapid increases in lionfish abundance on many invaded habitats following their swift range expansion (e.g. Green and Côté 2009, Albins and Hixon 2011, Green et al. 2012), similar effects are expected across the region, with concomitant impacts on the abundance of large, long-lived species consumed as juveniles at unsustainable rates by lionfish.

In the absence of human intervention, the long-term impacts of lionfish on native reef fishes will depend partly on lionfish responses to changing prey availability. These responses are difficult to predict because there can be substantial time lags between the depletion of prey resources and any behavioural or numerical response of predators (Krebs et al. 1995, Angerbjorn et al. 1999, Fauchald et al. 2000, Bjornstad and Grenfell 2001). However, the ability of lionfish to withstand starvation for protracted periods without significant loss in body condition (Fishelson 1997) and their broad diet (Morris and Akins 2009) suggest that these fish will be able to reduce markedly the populations of many prey before a regulating numerical response is elicited. The lionfish invasion, which is proceeding apace, therefore has serious implications for the persistence of fish diversity and fisheries across the Caribbean region.

Our model yields estimates of the lionfish densities below which the direct effects of predation are likely to be mitigated. Importantly, these predictions assume that prey fish populations could remain stable if lionfish consumption exactly balances prey production. However, prey are undoubtedly subject to stochastic mortality from other sources (Freckleton et al. 2006) and hence a precautionary ‘buffer’ of excess production may generally be necessary to ensure that these mortality events do not further reduce prey standing stock. Our calculations do not include such a buffer; hence our estimates of ‘sustainable’ lionfish densities represent the *maximum* lionfish densities at which further declines in prey fish biomass may be averted.

The ‘target’ lionfish densities that are predicted to arrest prey biomass decline varied greatly across the reefs studied (6-36 lionfish ha^{-1} on average), owing to large variation in the biomass of the prey fish communities and lionfish inhabiting each site. This variability unfortunately precludes the use of a manager-friendly rule of thumb for dealing with lionfish (e.g., reducing lionfish density by half leads to a significant chance of arresting prey decline on most reefs). Instead, it appears that assemblage-specific dynamics between lionfish and native fishes play an important role in determining the severity of predation impacts, and the level of control required to mitigate them. Nevertheless, the field-derived information on native fish and lionfish biomass necessary to obtain site-specific predictions can easily be collected as part of existing marine monitoring programs, through transect surveys of the fish community (Green 2012). Our method can also be used in conjunction with data on lionfish colonization rates to identify areas vulnerable to the effects of lionfish, and set priorities for limited resources. Our model is therefore valuable for managers who are tasked with managing this invasion, as well as a portfolio of other conservation priorities. In particular, the approach is well suited to the scale of marine protected areas, which are currently the top tool for conserving marine ecosystems but may become de-facto reserves for lionfish due to restrictions on extractive uses (Byers 2005). Finally, identifying key habitat for the juveniles of commercially exploited marine fishes (Mumby et al. 2004), which are consumed by lionfish at unsustainable rates, and focusing predictive and control efforts on these areas may be an effective use of limited management resources.

Our approach has great potential value for setting location-specific lionfish removal targets. The generality of our metabolic-scaling approach to estimating fish production means that the model is relevant for fish communities across the various Atlantic habitats occupied by lionfish - including mangroves, temperate hard-bottom systems, estuaries and seagrass beds. Furthermore, we emphasize that predictive modeling can take place before lionfish are present in high densities; so that local action can be taken to prevent predation impacts before they occur. It is clear that complete eradication of lionfish from the western Atlantic is no longer possible (Barbour et al. 2011). However, it would be a mistake to conflate regional and local perspectives. Organizations around the region are enacting local lionfish control programs with success (Akins 2012). While these efforts will need to be sustained over the long term, our model suggests that if control programs maintain lionfish density below target thresholds, they should prevent local fish populations from declining further.

Chapter 6

Suppressing invasive lionfish populations prevents declines in Atlantic coral reef fish prey[4]

Abstract

Invasive species are causing a range of negative impacts to recipient ecosystems. To combat these effects, we propose that targets for invasive species control should be based on an understanding of the ecological mechanism by which an invader affects the recipient ecosystem, and the population levels that elicit unacceptable negative effects. To illustrate this approach, we develop and test targets for the control of predatory Indo-Pacific lionfish (*Pterois volitans* and *P. miles)*, which have recently invaded coral reefs across the Western Atlantic, Caribbean and Gulf of Mexico, with the goal of suppressing lionfish densities below levels which cause declines in the native Atlantic fishes they consume. Our field experiment on 24 natural coral patch reefs in the Bahamas reveals that reducing invasive lionfish below densities at which they are predicted to over-consume prey can protect native fish communities from predation impacts, since the recovery of fish biomass achieved on these reefs was similar that achieved by complete invader removal. Our study suggests that for broadly distributed and highly abundant invaders, expending limited management resources to suppress invaders below densities which cause environmental harm can be as ecologically effective and more cost-effective than striving for local eradication of invaders.

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[4] A version of this chapter is in preparation for publication and co-authored by A. Brooks, J.L. Akins, S. Miller, and I.M Côté.

Introduction

Invasive species are causing a range of impacts to recipient ecosystems, from predation-mediated extinctions of native prey to shifts in the abundance and distribution of native species through competitive exclusion (Baxter et al. 2004, Bando 2006, Molnar et al. 2008, Sax and Gaines 2008). Mitigating these effects is a top priority for conservation, but it remains a major ecological challenge because efforts to suppress invasive populations are rarely guided by targets for control expressed in terms of measurable protection or recovery of the native system (Bax et al. 2001, Perrings 2005, Baxter et al. 2008).

To address this conservation challenge, we suggest that invasive species control should be based on an understanding of the ecological mechanism by which an invader affects the recipient ecosystem, and an identification of the population levels that elicit unacceptable negative effects. By using such population levels as targets for control, invaders can be suppressed below thresholds of ecological impact. This approach is akin to the concept of suppressing a species below thresholds of economic impact, which has been applied to pest invasions (Gren 2008, Gardiner et al. 2009). However, to our knowledge, there are no cases of invasive species control based on suppression below levels predicted to cause ecological effects.

Here we develop and test targets for the control of predatory Indo-Pacific lionfish (*Pterois volitans* and *P. miles)*, which have recently invaded coral reefs across the Western Atlantic, Caribbean and Gulf of Mexico, with the goal of suppressing lionfish densities below levels which cause declines in the native Atlantic fishes they consume. First introduced off the coast of South Florida in the 1980s, lionfish have spread over more than 4,000,000 km^2 in their non-native range in the past six years and are now undergoing exponential increases in abundance, producing a marine predator invasion of unparalleled speed and magnitude (Betancur-R et al. 2011). Lionfish are gape-limited predators that prey on an array of Atlantic fishes (Morris and Akins 2009, Côté et al. in press). There is mounting evidence that lionfish predation is having a significant impact on the biomass of native fishes on heavily invaded reefs (Albins and Hixon 2008, Green et al. 2012). Because few types of fishing gear can successfully capture lionfish, efforts to control their abundance locally currently take the form of removal of individual fish by spear and net in shallow coastal zones (Akins 2012).

In this study, we explicitly test whether suppressing lionfish below densities at which they are predicted to over-consume prey fishes prevents declines in the biomass of native fish communities (Figure 6.1A). To achieve this, we use an ecological model that predicts the effect of invasive lionfish predation on native fish biomass from two rates—prey consumption by invasive lionfish and biomass production by native fish prey (Chapter 5)—to generate reef-specific targets for lionfish control for a series of invaded coral patch reefs in the Bahamas. We then manipulate lionfish densities on these reefs to levels above or below the predicted reef-specific threshold lionfish densities (Figure 6.1B), and monitor the composition and biomass of resident fish community biomass over time. If we have accurately predicted the threshold densities at which lionfish deplete native fishes, we should observe declines in the biomass of fish prey on reefs where lionfish density exceeds the threshold, but not on reefs where lionfish numbers were sufficiently suppressed (Figure 6.1C).

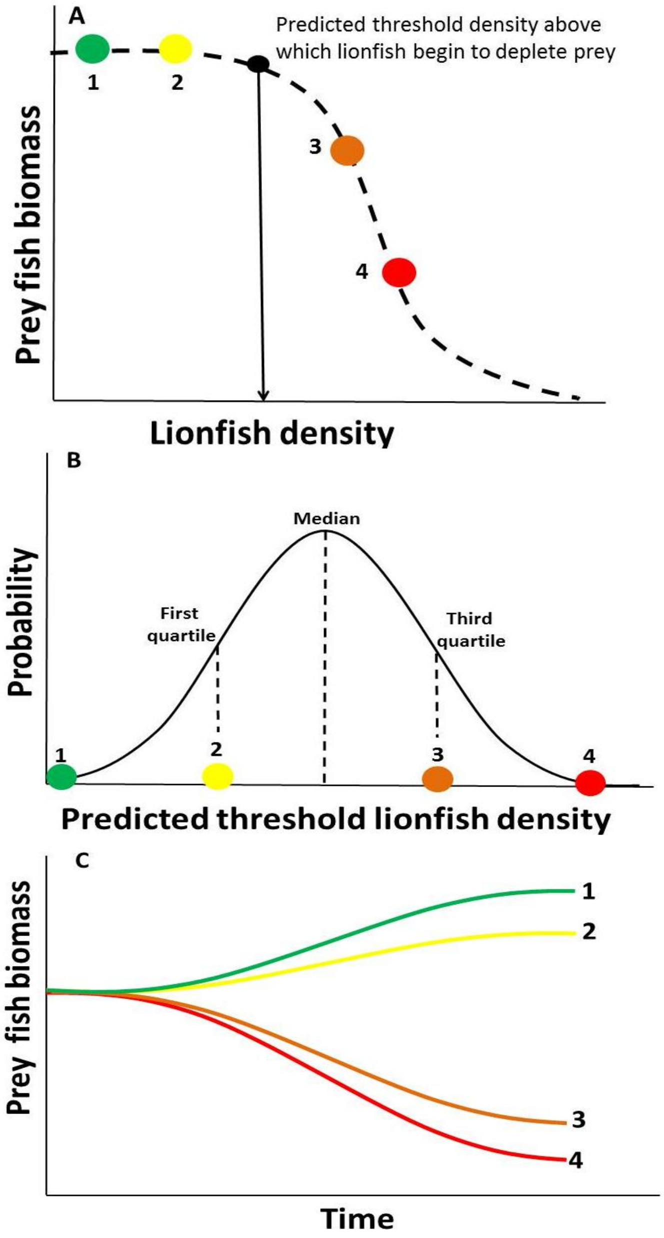

Figure 6.1. A) Predicted relationship between the density of invasive Indo-Pacific lionfish and the biomass of their fish prey on invaded Atlantic coral reefs. We predict that a threshold density of lionfish exists beyond which the rate at which lionfish prey consumption exceeds prey biomass production, and standing prey biomass begins to decline. B) Sample distribution of lionfish threshold densities, generated by a simulation model which incorporates uncertainty in component parameters. To test the accuracy of simulation predictions, we selected four lionfish removal treatments: two below (1 and 2) and two above (3 and 4) the median (i.e., most likely) threshold lionfish density for each reef. C) Over time, we predict that the biomass of prey fishes on reefs where lionfish have been suppressed below threshold densities should be maintained (1 and 2), whereas prey biomass on reefs where lionfish are not sufficiently suppressed should continue to decline (3 and 4).

Methods

Study system

Our study took place on 24 natural coral patch reefs within Rock Sound, off Eleuthera Island, Bahamas (22º22.500 N, 76º49.000 W; Figure 6.2) between December 2009 and June 2011. Reefs in this area were first colonized by lionfish in 2005, with local abundance increasing steadily since then (REEF 2012). Study reefs were 100-150 m^2 in size and separated from all other reefs by at least 500 m of sand and sea grass. Reefs were at similar depths (3-4m), and had similar benthic cover (i.e., dominated by hard corals, contributing 30-40% of cover on average) and structural complexity, with vertical relief of corals averaging 1.5m in height.

Modelling lionfish predation impact

For each reef, we predicted the threshold density above which lionfish deplete resident fish prey, which we modelled as the density at which prey consumption by lionfish ($\bar{C}$) equals the rate of prey fish biomass production ($\bar{P}$) (Chapter 5; Equation 6.1).

$$\bar{d} = \frac{\bar{P}}{\bar{C}} \qquad \text{Equation 6.1}$$

We estimated production rates for potential fish prey ($\bar{P}$) at each reef by converting the standing biomass of prey-sized fishes to annual production rates, using known scaling constants between fish body size, water temperature and net rate of biomass production (Equation 6.2; Table 5.1 in Chapter 5; Lorenzen 1996, Brown et al. 2004). We estimated lionfish prey consumption rates ($\bar{C}$) at each reef from observations of predation behaviour in the invaded range (Côté and Maljković 2010, Green et al. 2011, Côté and Green 2012), and reef-specific data on lionfish body size and water temperatures, such that the reef-specific threshold lionfish density was calculated as:

$$\bar{d} = \frac{\frac{1}{z}\sum_{\forall z}\sum_{\forall i}\sum_{\forall v}\left(\frac{j(a_i {L_{v,i,z}}^{b_i})^q}{e^{\frac{E}{kT}}}\right)a_i {L_{v,i,z}}^{b_i}}{\frac{1}{m}\sum_{\forall m}(a_l {L_m}^{b_l})\bar{p}\left(0.006e0.16T\frac{1}{m}\sum_m (a_l {L_m}^{b_l})^h\right)}\pi r^2 \qquad \text{Equation 6.2}$$

All parameters are defined in Table 5.1 in Chapter 5.

We parameterized the model for each reef site with field data collected at the outset of the experiment in December 2009. We estimated the biomass of prey fish available to lionfish at each site by first conducting 3-5 8 m x 2 m belt transect surveys (depending on reef size) on each reef and in the seagrass within 10 m of the reef, along which we recorded the identity and size (TL to the nearest 1c; $L_{v,i,z}$ in Table 5.1, Chapter 5) of all fish encountered. We took care to look in all crevices for cryptic fishes, using a dive light as needed. While we recorded all individuals on our surveys, we only considered individuals <15 cm TL as potential prey for lionfish (i.e., the maximum prey size for gape-limited lionfish at these sites). We converted prey fish lengths (cm) to weights (g) using species-specific allometric scaling constants (a_i and b_i; Table 5.1, Chapter 5). To estimate the body sizes of lionfish on each reef, we conducted two roving diver surveys of each site, during which we systematically searched the entire reef and recorded the number and total length (TL to the nearest 1cm; L_m; Table 6.1) of all lionfish encountered. We compared the locations and sizes of lionfish recorded by the two surveys to minimise the chance that individuals were missed. We estimated water temperature (T; Table 5.1, Chapter 5) as the distribution of annual sea surface temperatures for the central Bahamas (NOAA 2012). For each of the 24 reefs, we incorporated variation in our parameter estimates through Monte Carlo simulation (Table 5.1; Chapter 5) to generate a distribution of 'threshold' lionfish densities at which over-consumption of prey was predicted to occur. Figure 6.1B shows a schematic of the resulting distribution.

Defining lionfish removal targets

To test whether maintaining lionfish below predicted density thresholds prevents predation-induced declines in prey fish biomass, we divided the 24 study reefs into four lionfish removal treatments (6 reefs per treatment), randomized across the patch reef system (Table 6.1; Figure 6.2). Lionfish on reefs in treatments 1 and 2 were kept below the median density threshold predicted for each reef (Table 6.1), with all lionfish removed from reefs in treatment 1, and lionfish on reefs in treatment 2 maintained at the 25th percentile of their threshold density distributions (Figure 6.1B), hence densities on these reefs were very likely to be below the actual threshold densities. Lionfish on reefs in treatments 3 and 4 were maintained at densities which exceeded the median density threshold predicted for each reef (Table 6.1), with lionfish on reefs in treatment 3 maintained at the 75th percentile of their threshold density distributions, and lionfish maintained at densities which exceeded the 95th percentile on reefs in treatment 4 (Figure 6.1B), hence densities on these reefs were very likely to be above the actual threshold densities. Target density treatments were maintained monthly by SCUBA divers. During each site visit, we conducted two roving diver surveys to assess lionfish abundance and body sizes. We then removed excess lionfish or transplanted additional lionfish from adjacent reefs, to ensure that the lionfish density on each reef matched the target density and average body size. Lionfish removed from the study system were euthanized at the surface in a clove oil and sea water solution following the protocol of (Green et al. 2012).

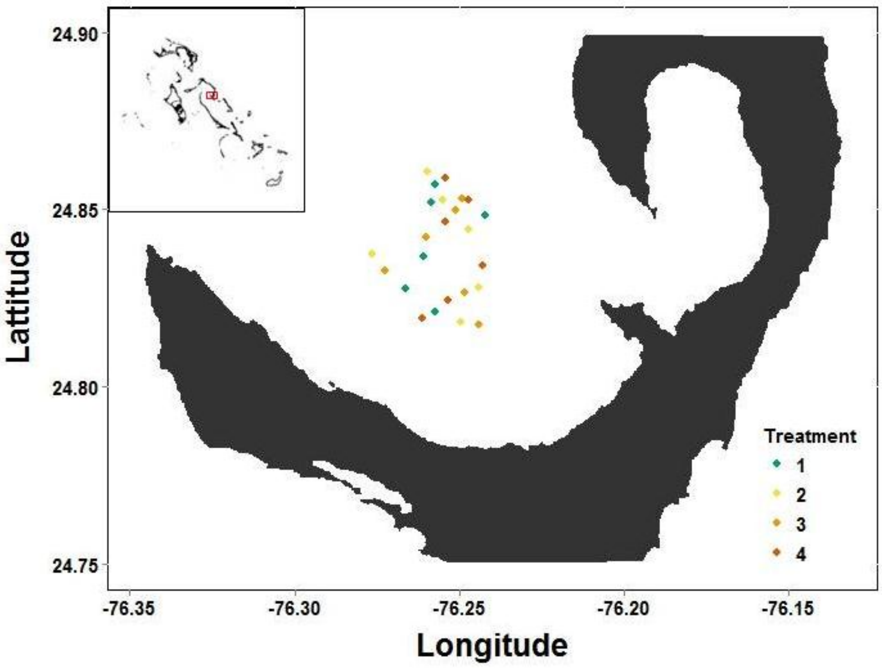

Figure 6.2. Map of the 24 natural patch reefs in Rock Sound off Eleuthera Island, Bahamas, where we conducted our lionfish removal experiment. Lionfish were abundant across the study reefs at the outset of the experiment in December 2009. Colours indicate the lionfish removal treatment for each reef, corresponding to the probability of prey depletion at each site (Table 6.1).

Table 6.1. Predictions of density thresholds at which lionfish begin to over-consume native reef fish prey at 24 invaded coral patch reefs off Eleuthera, Bahamas. The reefs were divided into four treatments, with two treatments below (1 and 2) and two treatments above (3 and 4) the median predicted threshold. Initial density is the number of lionfish observed per reef at the start of the experiment in December 2009, while treatment density is the number of lionfish maintained per reef for the duration of the 18 month study.

Treatment	Percentile	Site	Average lionfish size (cm)	Initial density	Treatment density	Lionfish density associated with probability of prey depletion			
						0.25	0.5	0.75	0.95
1	**0**	74	24	23	0	3	5	8	17
		76	21	31	0	3	4	7	14
		89	24	12	0	1	2	4	9
		93	24	14	0	2	3	5	11
		104	25	15	0	2	3	5	11
		112	24	9	0	2	3	5	11
2	**25th**	79	25	21	1	**1**	2	3	8
		100	23	10	1	**1**	2	4	9
		70	21	48	2	**2**	4	6	14
		72	20	33	2	**2**	4	7	14
		75	20	16	2	**2**	4	7	16
		106	12	8	2	**2**	6	13	41
3	**75th**	108	22	18	3	1	2	**3**	7
		101	19	15	4	1	2	**4**	7
		55	23	18	5	2	3	**5**	10
		77	23	8	5	3	4	**5**	11
		71	16	20	8	2	4	**8**	20
		91	20	30	7	2	3	**7**	18
4	**>95th**	102	20	9	9	1	2	4	**9**
		78	22	11	11	2	3	5	**11**
		94	22	14	9	1	2	4	**9**
		84	24	21	9	2	3	4	**9**
		73	19	26	22	3	5	9	**22**
		90	26	29	9	2	3	5	**9**

Monitoring native fish community response

To evaluate the rate and magnitude of change in fish biomass between the four treatments over time, we repeated belt transect surveys for native fishes on the reefs every six months over an 18-month period (June 2010, December 2010 and June 2011). Again we converted fish lengths (cm) to weights (g) using species-specific allometric scaling constants.

Results and Discussion

At the outset of our experiment, 21 of the 24 study reefs harboured more lionfish than the upper bound of our reef-specific predictions of the threshold densities beyond which reef fish prey should decline (Table 6.1). Thus, lionfish density had to be reduced by 75-95%, depending on the reef, to achieve suppression sufficient to arrest prey depletion (Table 6.1; treatment 2). Over the duration of the experiment, we observed significant seasonal variation in the biomass of the smallest size classes of native fishes (i.e., less than 5 cm total length) on the 24 study reefs, likely as a result of high recruitment across the summer each year (Figure 6.3A; e.g. similar to the trends observed by Albins [2011]). Comparing the biomass of these size classes between post-settlement winter seasons (i.e., December 2009 versus December 2010; Figure 6.3A) reveals that native fish biomass on reefs where lionfish were suppressed below predicted threshold levels (treatment 2) increased as much as on reefs where all lionfish were removed (treatment 1), with biomass increasing by an average of 50% and 70%, respectively (Figure 6.3A). Conversely, the biomass of small fishes declined significantly between post-settlement winter seasons on reefs where lionfish densities far exceeded the predicted thresholds of impact, with average reductions of 15% (treatment 3) and 40% (treatment 4) over the first year of the experiment (Figure 6.3A).

Initially we observed declines in the biomass of larger prey fishes (i.e., 6-15cm TL) on all reefs, save those where lionfish had been completely removed (Figure 6.3B). However, the biomass of larger prey fishes diverged between the four treatments by the end of the experiment (Figure 6.3B), increasing by more than 70% on reefs where all lionfish were removed and, to a lesser extent (20%), on reefs where lionfish densities had been suppressed below the predicted threshold (Figure 6.3B). By the end of the experiment the biomass of larger fish prey had declined significantly on reefs where lionfish exceeded predicted impact thresholds, with average reductions of 40% and 60%, respectively, for treatments 3 and 4 (Figure 6.3B).

Our findings reveal that suppressing invasive lionfish below densities at which they are predicted to over-consume prey on invaded coral reefs can effectively protect native fish communities from predation impacts. The significant margin by which prey fish biomass increased on reefs where lionfish were completely extirpated indicates that these invasive predators had already begun to deplete their fish prey prior to the start of our experiment in 2009. Importantly, over the course of the experiment, suppressing lionfish densities below thresholds predicted to cause impact quickly resulted in the recovery of biomass of the smallest prey fish to levels achieved by complete lionfish removal (Figure 6.3A). However, the rate of biomass recovery for larger-bodied prey fishes (6-15cm TL) was slower on reefs where a few lionfish remained (Figure 6.3B). This finding may be explained by the fact that lionfish preferentially consume small size classes of fish prey (i.e., less than 5 cm TL; Chapter 4). As a result, lionfish predation likely had the largest immediate effect on the smallest native fishes. As surviving juvenile fishes grew, reductions in biomass of small size classes were propagated to the larger size classes. By reducing lionfish densities below those which cause prey depletion, we essentially reversed this effect on the size structure of native fishes over the course of our experiment—resulting in immediate increases in survival of the smallest prey (i.e. < 5 cm TL) and lagged increases in biomass of larger prey (i.e. 6-16cm TL). However, by the end of the experiment, the biomass of larger-bodied prey (i.e. 6-16cm TL) increased by a smaller margin on reefs where lionfish remained at levels below those predicted to over-consume prey (Figure 6.3B; treatment 2), compared with lionfish-free reefs (Figure 6.3B; treatment 1). This difference may be due to continued predation on larger-bodied prey further slowing the recovery of biomass in larger prey size classes on reefs where some lionfish remained, compared with sites where the invader was completely extirpated.

Finally, while there was a clear effect of lionfish removal on the biomass of prey-sized reef fishes during the course of the experiment, the biomass of fish which were too large

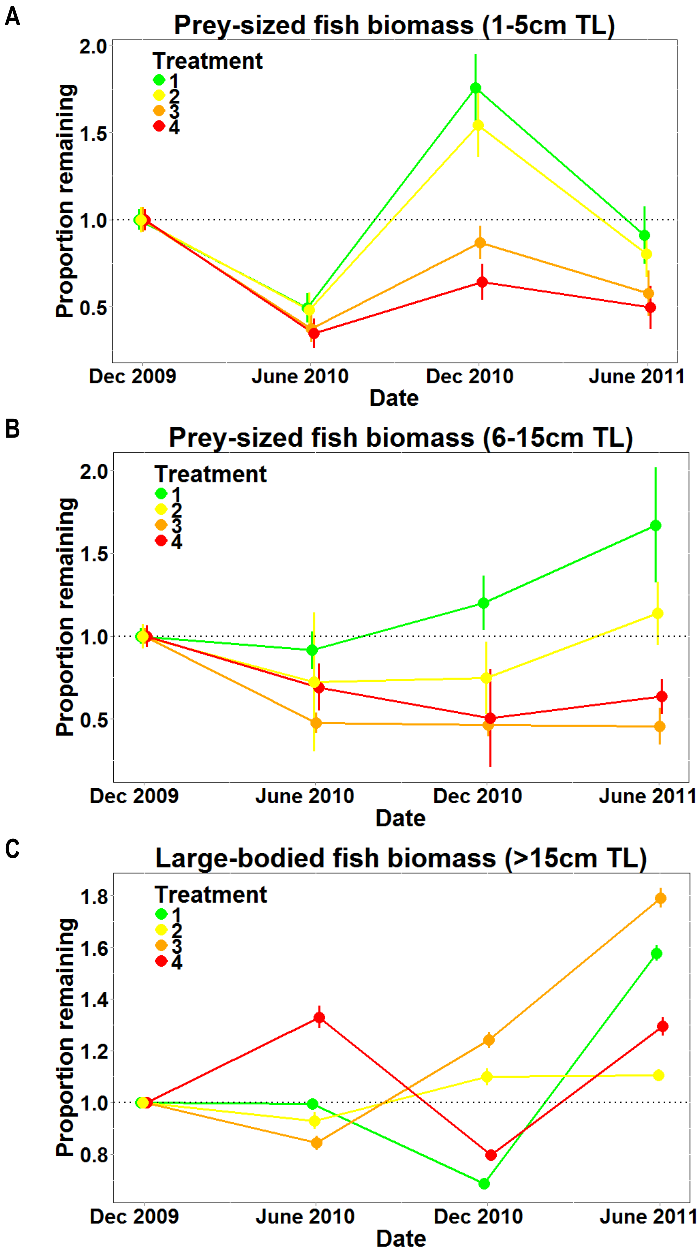

Figure 6.3. The biomass of native reef fishes on the 24 Bahamian study reefs over time. Colours represent lionfish density treatments, varying in the probability that lionfish will deplete their fish prey (Table 6.1). Points represent mean biomass per treatment (n= 6 reefs each), standardized by biomass at the outset of the experiment in December 2009, and bounded by 95% confidence intervals. Thus values above 1 represent prey biomass estimates that exceed initial biomass, while values < 1 indicate declines in biomass. Plots A – C depict temporal patterns for different size classes of native fishes across the duration of the 18-month experiment.

to be preyed upon by lionfish (i.e. >15cm TL) was highly variable across the study reefs over time, and appeared to increase significantly (15-80%, on average) over the final six months of the study across all treatments (Figure 6.3C). Again, this effect may be partially explained by a lag in the time to biomass recovery for larger fish size classes but also by inter-reef movement. The juveniles of most larger-bodied species observed in our study can grow at rates that would have allowed them to reach a size refuge (i.e., >15 cm TL) from lionfish predation in the 18 months of the experiment (Pauly 1980; FishBase http://www.fishbase.org). However, given that fish home range size increases as fishes grow (Kramer and Chapman 1999), the larger (>15 cm TL) fish could easily have moved among reef patches, irrespective of lionfish density, and contributed to the overall increases in biomass for large size classes observed across all reefs by the end of the experiment (Figure 6.3C).

Our experiment validates the utility of setting targets for lionfish population suppression instead of attempting local eradication. This approach was not only ecologically effective, it was also cost effective. To achieve complete extirpation of lionfish reefs (treatment 1), we spent on average 30% longer per site visit than at reefs where a few lionfish were allowed to remain, but at densities below those predicted to cause prey declines (treatment 2). This point is particularly important for managers who must decide how to allocate limited resources efficiently to achieve control. Our approach, which relied on ecological modelling based on a mechanistic understanding of the impact of lionfish, can be used across the invaded region to guide removal activities in high-priority management areas such as MPAs and juvenile fish habitat, which are currently under threat as they are being colonized by lionfish. More broadly, our study is, to our knowledge, the first to predict and test targets for the control of an invasive species, based on suppression below identified levels of ecological impact. Crucially, we suggest that for broadly distributed and highly abundant invaders, such as lionfish on coral reefs across the Caribbean, complete extirpation of the invader is not necessary to mitigate negative ecological changes. Instead, our study supports the notion that expending resources to suppress invaders below densities which cause ecological harm can, over time, result in similar levels of protection and recovery of native ecological communities as maintaining invader-free habitats.

Chapter 7

General Conclusions

My thesis links two long-standing themes in ecological research—the role predators play in structuring biological communities (Paine 1974, Myers et al. 2007) and the biotic effects of species invasions (Elton 1958, Clavero and García-Berthou 2005) — in a way that provides new insights into predator invasions in marine ecosystems. Predation is a key force shaping demographic processes in marine communities (Hixon and Carr 1997, Almany and Webster 2004), and thus predatory invaders are predicted to have particularly severe effects on their structure. My work examines this prediction in relation to the invasion of Indo-Pacific lionfish into Atlantic coral reef fish communities, using a combination of quantitative modelling, manipulative field experiments and observational studies at a range of spatial and temporal scales. Focussing on coral reefs in the Bahamas, my investigation into the patterns, processes and consequences of predation by invasive lionfish on native reef fishes reveals the important role that lionfish now play in structuring invaded fish assemblages, and provides evidence that the invasion poses a very real and immediate threat to the persistence of fish diversity in the region.

Lionfish effects and the state of Atlantic coral reefs

Lionfish are the newest among a suite of stressors, which include over-fishing, coastal development, disease, and climate stress, to affect the structure and function of Atlantic coral reef ecosystems (Pandolfi et al. 2003, Burke and Maidens 2004). The effects of lionfish are likely to influence the magnitude of biological changes induced by these pre-existing stresses, and the ability of management intervention to reverse them. In particular, two key changes to reef communities may be exacerbated by lionfish: 1) the transition from dominance by reef-building corals to macroalgae, a shift largely attributed to reductions in key herbivores, such as parrotfishes, which control algae populations

(Mumby 2006), and 2) the reduction in the diversity, abundance and size of predatory fishes on reefs (Jackson et al. 2001, Paddack et al. 2009). Over-exploitation is thought to be a key driver of declines in herbivorous and predatory fishes (e.g., Stallings 2009), and management intervention, in the form of enhanced fishing regulation and the creation of marine protected areas (MPAs), is now in place to protect adult of these species from fishing mortality. However, my research demonstrates that invasive lionfish consume juveniles of herbivorous and predatory fishes at unsustainable rates (Chapter 3; Chapter 5), and that this reduction in juvenile biomass translates to losses in adult size classes over time (Chapter 6). Thus, in the absence of management intervention to suppress lionfish populations, the invasion is likely to hinder the effectiveness of MPAs and fishing regulation in facilitating the recovering native fish populations, and may ultimately inhibit the recovery of coral communities through continued suppression of algal grazing (Mumby et al. 2006).

Moreover, where over-exploitation is not mitigated through management, the effects of lionfish predation may exacerbate ongoing losses, to the point of irreversible change in ecosystem structure. For example, the combined effect of lionfish predation and fishing mortality may interact to suppress herbivore populations below critical thresholds of grazing, resulting in a phase shift to complete algal dominance (e.g. Hughes et al. 2007). Lionfish-mediated reductions in the juveniles of predatory fishes may also push fished species below minimum viable population levels, resulting in complete extirpation of some species. Future research into the strength of interactions between lionfish and other anthropogenic factors affecting Atlantic coral reefs is needed to quantify the magnitude of these potentially severe effects.

With coral reef tourism and fishing among the most important livelihoods for coastal communities across the tropical Western Atlantic (Cesar et al. 2003, Brander et al. 2007), the ecological effects of invasive lionfish may inevitably result in severe impacts to local economies. Over time, lionfish predation-mediated declines in economically valuable predator species (e.g., groupers and snappers) are likely to result in reduced fisheries catch and thus revenue. In addition, lionfish-mediated change to the biotic composition of reefs could negatively affect tourism if the altered state of these systems reduces their desirability as vacation destinations. For example, a reduction in the diversity and density of fishes on coral reefs or reduced coral cover may negatively affect the experience of divers and snorkelers (e.g., and reduced populations of recreationally fished species may affect catch rates by visiting anglers (e.g., Cook et al. 2006). Although there has been little quantitative investigation into these effects to date, determining the degree to which the ecological effects of lionfish translate to economic impacts is a key step in quantifying the total effect of the invasion, and in building support for management intervention.

Ecological insights into marine predator invasions

Exponential increases in lionfish abundance on newly invaded Atlantic coral reefs, such as those I documented in the Bahamas (Chapter 3), are undoubtedly due to a number of ecological mechanisms contributing to high fecundity and low mortality. While species traits such early maturation, year-round reproduction and anti-predator defenses likely contribute greatly to their success, the predation habits of lionfish, which I show facilitate the exploitation of a range of prey resources at high rates and under varying environmental conditions (Chapters 2-4), may also contribute to rates of population increase near their intrinsic limits. The relationship between prey consumption and reproductive output has not quantified for lionfish, or any other marine predator invasion. Insights from terrestrial plant invasions suggest that greater plasticity in resource acquisition strategies by invaders, compared with their native-range counterparts, results in higher growth rates (Davidson et al. 2011). However, there is a paucity of studies which explicitly explore the link between resource acquisition and reproductive success in the context of species invasions, both on land and in the sea.

Assuming that prey acquisition does affect population growth rates in lionfish, higher predation rates in the invaded range, owing potentially to altered hunting strategies (Cure et al. in press) and naïve prey (Anton et al. in review), may be at least partially responsible for the significantly greater abundance and size of lionfish on invaded Atlantic reefs, as compared with individuals in their native Indo-Pacific range (Darling et al. 2011, Kulbicki et al. 2012). Thus, understanding the degree to which differences in predation habits between invasive and native lionfish results from environmental influence on learned behaviour, or genetically-based divergence between populations in the two ranges, may be a fruitful avenue for future investigation seeking to uncover the drivers of lionfish invasion success. However, the ecological context of lionfish on Caribbean reefs likely also drives differences between native and invasive populations. For example, reduced competition with native Atlantic predators for prey resources, owing to their over-exploitation on Atlantic reefs, may be lead to greater prey availability to lionfish in Atlantic than in Indo-Pacific habitats.

In the long term, the exponential increases in lionfish abundance observed immediately following colonization of invaded Atlantic reefs are unlikely to persist forever. In fact, many invaders exhibit boom and bust cycles, with sharp declines in abundance following initial rapid growth (Simberloff and Gibbons 2004). A possible explanation in many cases is a functional, and ultimately numerical, response by predator populations to prey depletion (Morris et al. 1958, Anderson 2001). However, to date the majority of research on invasive population trajectories focuses on the first few stages of the invasion process (i.e., introduction, spread and the initiation of impacts (Crooks 2005, Catford et al. 2009)) As a result, the cause of invader population decline remains a mystery in the majority cases (Simberloff and Gibbons 2004). Thus, long-term studies which integrate data on lionfish abundance, growth, reproductive status and diet composition, with changes in prey community composition could provide unprecedented insights into the influence of resource use and availability on invasion population dynamics.

Nevertheless, the ability of lionfish to exploit an array of prey types at high rates, as shown in this thesis, perhaps combined with negligible losses to body mass during periods of prey depletion (i.e., as shown experimentally by (Fishelson 1997), is resulting in rapid and severe depletion of prey biomass on Bahamian reefs, so far without the rapid and severe population crashes observed for other invasions. In the absence of management intervention, lionfish populations on newly colonized reefs across the Western Atlantic will continue to increase in similar fashion, likely resulting in severe reductions in native fish populations at a regional scale.

Prospects for managing lionfish and other marine invasions

In addition to coral reefs, lionfish have now become established on virtually all marine habitat types within the Western Atlantic, Caribbean and Gulf of Mexico, and across an extensive depth range (shoreline to 300 m deep; Morris and Whitfield 2009, Albins and Hixon 2011, Green et al. 2012, USGS 2012). Efforts to control lionfish populations are starting across the region and take the form of manual removal of fish by spear and hand nets (Akins 2012). As a result, removals are restricted almost exclusively to shallow coastal areas near human settlements and within MPAs. Complete eradication of the invasion is unlikely with the available management resources (Barbour et al. 2011). However, my research demonstrates that lionfish removal can limit ecological impacts on native fish communities, and offers a method for estimating the level of lionfish density reduction needed to prevent unacceptable effects at local scales (Chapters 5 and 6).

Importantly, my research shows that suppressing lionfish below densities predicted to deplete their prey results in a magnitude of recovery in native fish biomass similar to that achieved by completely extirpation from an invaded reef site, but partial removal takes significantly less effort to maintain (Chapter 6). Thus, my approach to setting targets for lionfish control is of value to managers who must use limited management resources to sustain sufficient invasion control over the long term within priority management areas, such as MPAs and juvenile fish habitats.

Atlantic lionfish are remarkable in that they represent the only opportunity to study an invasion by a marine fish predator as it unfolds. However, the broad distribution achieved by lionfish so far is quite unremarkable among marine invaders (Ruiz et al. 1997), many of which disperse in wind- and water-driven currents as pelagic eggs and larvae (Shanks 2009). Given that humans have limited direct access to the majority of ocean habitats because of depth and pressure restrictions, complete eradication of broadly distributed marine invasions is unlikely on the whole. A shift in focus from eradication to suppression of local populations below densities which elicit unacceptable negative ecological effects, as I have proposed for lionfish, may be the key to aligning the spatial scale at which invasion processes and management intervention occur in marine systems.

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Appendices

Appendix A.

Supporting material for Chapter 3

Table A.1. Species and size classes included in each of the four categories considered in the analysis of biomass change between 2008 and 2010 on nine coral reefs off southwest New Providence, Bahamas. Fishes of < 13 cm were deemed to be potential prey based on the maximum prey size observed in lionfish stomachs at these sites. Functional group was determined from diet composition (Randall 1968) and trophic group (FishBase; http://www.fishbase.org). *Fish species which are commercially exploited in the Bahamas.

Family	**Species**	**Lionfish stomach contents**
Acanthuridae	*Acanthurus bahianus*	
Acanthuridae	*Acanthurus chirurgus*	
Acanthuridae	*Acanthurus coeruleus*	
Apogonidae	*Apogon binotatus*	
Apogonidae	*Apogon planifrons*	x
Apogonidae	*Apogon quadrisquamatus*	
Apogonidae	*Apogon townsendi*	x
Apogonidae	*Phaeoptyx pigmentaria*	x
Atherinidae	*Atherinomorus sp.*	x
Aulostomidae	*Aulostomus maculatus*	x
Blenniidae	*Ophioblennius macclurei*	
Callionymidae	*Callionymus bairdi*	
Carangidae	*Carangoides ruber*	
Carangidae	*Selar crumenophthalmus*	
Chaenopsidae	*Acanthemblemaria aspera*	x
Chaenopsidae	*Acanthemblemaria maria*	
Chaenopsidae	*Acanthemblemaria spinosa*	
Chaenopsidae	*Emblemaria pandionis*	
Chaenopsidae	*Emblemariopsis bahamensis*	
Chaenopsidae	*Lucayablennius zingaro*	x
Chaetodontidae	*Chaetodon capistratus*	
Chaetodontidae	*Chaetodon ocellatus*	
Chaetodontidae	*Chaetodon striatus*	
Chaetodontidae	*Prognathodes aculeatus*	
Cirrhitidae	*Amblycirrhitus pinos*	
Diodontidae	*Diodon holocanthus*	
Gobiidae	*Coryphopterus bol*	x
Gobiidae	*Coryphopterus dicrus*	
Gobiidae	*Coryphopterus eidolon*	x
Gobiidae	*Coryphopterus glaucofraenum*	x

Family	**Species**	**Lionfish stomach contents**
Gobiidae	*Coryphopterus hyalinus*	x
Gobiidae	*Coryphopterus lipernes*	
Gobiidae	*Coryphopterus personatus*	x
Gobiidae	*Ctenogobius saepepallens*	
Gobiidae	*Elacatinus evelynae*	
Gobiidae	*Elacatinus genie*	
Gobiidae	*Elacatinus horsti*	
Gobiidae	*Gnatholepis thompsoni*	x
Gobiidae	*Lythrypnus spilus*	x
Gobiidae	*Oxyurichthys stigmalophius*	
Gobiidae	*Priolepis hipoliti*	x
Grammatidae	*Gramma loreto*	x
Grammatidae	*Gramma melacara*	
Haemulidae	*Haemulon flavolineatum*	
Haemulidae	*Haemulon melanurum*	
Haemulidae	*Haemulon sp.*	
Holocentridae	*Holocentrus adscensionis*	
Holocentridae	*Holocentrus rufus*	
Holocentridae	*Myripristis jacobus*	
Holocentridae	*Neoniphon marianus*	
Holocentridae	*Plectrypops Retrospinis*	
Holocentridae	*Sargocentron coruscum*	x
Holocentridae	*Sargocentron vexillarium*	
Inermiidae	*Inermia vittata*	x
Labridae	*Bodianus rufus*	x
Labridae	*Clepticus parrae*	x
Labridae	*Halichoeres bivittatus*	x
Labridae	*Halichoeres garnoti*	x
Labridae	*Halichoeres maculipinna*	x
Labridae	*Halichoeres pictus*	
Labridae	*Halichoeres radiatus*	
Labridae	*Thalassoma bifasciatum*	x
Labridae	*Xyrichtys novacula*	
Labrisomidae	*Labrisomus haitiensis*	x
Labrisomidae	*Malacoctenus boehlkei*	x
Labrisomidae	*Starksia hassi*	
Malacanthidae	*Malacanthus plumieri*	
Monacanthidae	*Cantherhines pullus*	
Monacanthidae	*Monacanthus tuckeri*	x
Mullidae	*Mulloidichthys martinicus*	
Mullidae	*Pseudupeneus maculatus*	x
Muraenidae	*Gymnothorax miliaris*	
Opistognathidae	*Opistognathus aurifrons*	
Ostraciidae	*Lactophrys triqueter*	
Pomacanthidae	*Centropyge argi*	

Family	**Species**	**Lionfish stomach contents**
Pomacanthidae	*Holacanthus tricolor*	
Pomacentridae	*Abudefduf saxatilis*	
Pomacentridae	*Chromis cyanea*	x
Pomacentridae	*Chromis insolata*	
Pomacentridae	*Chromis multilineata*	x
Pomacentridae	*Microspathodon chrysurus*	
Pomacentridae	*Stegastes diencaeus*	
Pomacentridae	*Stegastes dorsopunicans*	
Pomacentridae	*Stegastes leucostictus*	
Pomacentridae	*Stegastes partitus*	x
Pomacentridae	*Stegastes planifrons*	
Pomacentridae	*Stegastes variabilis*	x
Scaridae	*Cryptotomus roseus*	
Scaridae	*Scarus coeruleus*	
Scaridae	*Scarus iserti*	
Scaridae	*Scarus taeniopterus*	
Scaridae	*Sparisoma atomarium*	
Scaridae	*Sparisoma aurofrenatum*	x
Scaridae	*Sparisoma viride*	
Sciaenidae	*Equetus punctatus*	
Scorpaenidae	*Pterois volitans*	
Serranidae	*Cephalopholis cruentata*	x
Serranidae	*Cephalopholis fulva*	
Serranidae	*Epinephelus adscensionis*	
Serranidae	*Epinephelus guttatus*	
Serranidae	*Epinephelus striatus*	x
Serranidae	*Hypoplectrus gummigutta*	
Serranidae	*Hypoplectrus guttavarius*	
Serranidae	*Hypoplectrus indigo*	
Serranidae	*Hypoplectrus nigricans*	
Serranidae	*Hypoplectrus puella*	
Serranidae	*Hypoplectrus spp.*	x
Serranidae	*Hypoplectrus unicolor*	
Serranidae	*Liopropoma mowbrayi*	
Serranidae	*Liopropoma rubre*	x
Serranidae	*Rypticus subbifrenatus*	
Serranidae	*Serranus tabacarius*	x
Serranidae	*Serranus tigrinus*	x
Synodontidae	*Synodus intermedius*	x
Synodontidae	*Synodus saurus*	x
Synodontidae	*Synodus synodus*	x
Tetraodontidae	*Canthigaster rostrata*	
Tripterygiidae	*Enneanectes altivelis*	

Appendix B.

Supporting material for Chapter 4

Table B.1. List of fish species observed on Bahamian coral reefs and morphological and behavioural characteristics which are hypothesized to effect vulnerability to predation by invasive lionfish. *(F) denotes facultative and (O) denotes obligately cleaning species.

Family	Species name	Cleaner	Nocturnal	Position in water column	Group size	Defense	TL:Body depth ratio
Acanthuridae	*Acanthurus bahianus*	no	0	demersal	solitary	1	2.7
Acanthuridae	*Acanthurus chirurgus*	no	0	demersal	solitary	1	2.3
Acanthuridae	*Acanthurus coeruleus*	no	0	demersal	solitary	1	2
Apogonidae	*Apogon binotatus*	no	1	demersal	solitary	0	5.3
Apogonidae	*Apogon maculatus*	no	1	demersal	solitary	0	4
Apogonidae	*Apogon planifrons*	no	1	demersal	solitary	0	5.1
Apogonidae	*Apogon quadrisquamatus*	no	1	demersal	facultative	0	4.6
Apogonidae	*Apogon townsendi*	no	1	demersal	solitary	0	4.9
Apogonidae	*Phaeoptyx pigmentaria*	no	1	demersal	solitary	0	4.5
Atherinidae	*Atherinomorus sp.*	no	0	demersal	schooling	0	6.4
Aulostomidae	*Aulostomus maculatus*	no	0	demersal	solitary	0	14.4
Blenniidae	*Ophioblennius macclurei*	no	0	benthic	solitary	0	5
Bothidae	*Bothus ocellatus*	no	0	benthic	solitary	0	1.9
Callionymidae	*Callionymus bairdi*	no	0	benthic	solitary	0	9.3
Carangidae	*Carangoides ruber*	yes (F)	0	pelagic	facultative	0	3.7
Carangidae	*Decapterus macarellus*	no	0	pelagic	schooling	0	4.9
Carangidae	*Elagatis bipinnulata*	no	0	pelagic	schooling	0	5.7
Carangidae	*Selar crumenophthalmus*	no	0	pelagic	schooling	0	4.7
Chaenopsidae	*Acanthemblemaria aspera*	no	0	benthic	solitary	0	7.8
Chaenopsidae	*Acanthemblemaria maria*	no	0	benthic	solitary	0	11.7
Chaenopsidae	*Acanthemblemaria spinosa*	no	0	benthic	solitary	0	14
Chaenopsidae	*Emblemaria pandionis*	no	0	benthic	solitary	0	7.2
Chaenopsidae	*Emblemariopsis bahamensis*	no	0	benthic	solitary	0	7
Chaetodontidae	*Chaetodon capistratus*	no	0	demersal	solitary	0	1.9
Chaetodontidae	*Chaetodon ocellatus*	no	0	demersal	solitary	0	2.1

Family	Species name	Cleaner	Nocturnal	Position in water column	Group size	Defense	TL:Body depth ratio
Chaetodontidae	*Chaetodon striatus*	no	0	demersal	solitary	0	1.9
Chaetodontidae	*Prognathodes aculeatus*	no	0	demersal	solitary	0	2.1
Cirrhitidae	*Amblycirrhitus pinos*	no	0	benthic	solitary	0	3.4
Diodontidae	*Diodon holocanthus*	no	1	demersal	solitary	1	5
Gobiidae	*Coryphopterus bol*	no	0	benthic	solitary	0	7.1
Gobiidae	*Coryphopterus dicrus*	no	0	benthic	solitary	0	6
Gobiidae	*Coryphopterus eidolon*	no	0	benthic	solitary	0	6.6
Gobiidae	*Coryphopterus glaucofraenum*	no	0	benthic	solitary	0	5.6
Gobiidae	*Coryphopterus hyalinus*	no	0	demersal	schooling	0	5.8
Gobiidae	*Coryphopterus lipernes*	no	0	benthic	solitary	0	6.7
Gobiidae	*Coryphopterus personatus*	no	0	demersal	schooling	0	6.2
Gobiidae	*Ctenogobius saepepallens*	no	0	benthic	solitary	0	8.7
Gobiidae	*Elacatinus evelynae*	yes (O)	0	benthic	solitary	1	7.1
Gobiidae	*Elacatinus genie*	yes (O)	0	benthic	solitary	1	6.7
Gobiidae	*Elacatinus horsti*	no	0	benthic	solitary	0	5.8
Gobiidae	*Gnatholepis thompsoni*	no	0	benthic	solitary	0	6.4
Gobiidae	*Lythrypnus spilus*	no	0	benthic	solitary	0	5.6
Gobiidae	*Oxyurichthys stigmalophius*	no	0	benthic	solitary	0	7.3
Gobiidae	*Priolepis hipoliti*	no	0	benthic	solitary	0	5.4
Grammatidae	*Gramma loreto*	yes (F)	0	demersal	facultative	0	4.1
Grammatidae	*Gramma melacara*	no	0	demersal	facultative	0	4.7
Haemulidae	*Haemulon aurolineatum*	no	0	demersal	schooling	0	4.2
Haemulidae	*Haemulon flavolineatum*	no	0	demersal	schooling	0	4
Haemulidae	*Haemulon melanurum*	no	0	demersal	schooling	0	4.3
Haemulidae	*Haemulon plumierii*	no	0	demersal	schooling	0	3.6

Family	Species name	Cleaner	Nocturnal	Position in water column	Group size	Defense	TL:Body depth ratio
Mullidae	*Mulloidichthys martinicus*	no	0	demersal	facultative	0	4.9
Mullidae	*Pseudupeneus maculatus*	no	0	demersal	facultative	0	5
Muraenidae	*Gymnothorax miliaris*	no	0	benthic	solitary	1	10.8
Opistognathidae	*Opistognathus aurifrons*	no	0	benthic	solitary	0	4.6
Ostraciidae	*Lactophrys triqueter*	no	0	demersal	solitary	1	2
Pomacanthidae	*Centropyge argi*	no	0	demersal	solitary	1	2.5
Pomacanthidae	*Holacanthus ciliaris*	yes (F)	0	demersal	solitary	1	2
Pomacanthidae	*Holacanthus tricolor*	no	0	demersal	solitary	1	2
Pomacanthidae	*Pomacanthus paru*	yes (F)	0	demersal	solitary	1	1.6
Pomacentridae	*Abudefduf saxatilis*	yes (F)	0	demersal	facultative	0	2.5
Pomacentridae	*Chromis cyanea*	no	0	demersal	facultative	0	3.7
Pomacentridae	*Chromis insolata*	no	0	demersal	facultative	0	3.8
Pomacentridae	*Chromis multilineata*	no	0	demersal	facultative	0	3.9
Pomacentridae	*Microspathodon chrysurus*	yes (F)	0	demersal	solitary	0	2.6
Pomacentridae	*Stegastes diencaeus*	no	0	demersal	solitary	0	3
Pomacentridae	*Stegastes dorsopunicans*	no	0	demersal	solitary	0	2.8
Pomacentridae	*Stegastes leucostictus*	no	0	demersal	solitary	0	3.1
Pomacentridae	*Stegastes partitus*	no	0	demersal	solitary	0	3
Pomacentridae	*Stegastes planifrons*	no	0	demersal	solitary	0	2.6
Pomacentridae	*Stegastes variabilis*	no	0	demersal	solitary	0	2.9
Pterelotridae	*Pterelotris helenae*	no	0	demersal	solitary	0	7.3
Scaridae	*Cryptotomus roseus*	no	0	demersal	facultative	0	5.7
Scaridae	*Scarus coeruleus*	no	0	demersal	solitary	0	4.2
Scaridae	*Scarus iserti*	no	0	demersal	facultative	0	4.6
Scaridae	*Scarus taeniopterus*	no	0	demersal	facultative	0	4.8
Scaridae	*Sparisoma atomarium*	no	0	demersal	facultative	0	3.9

Family	Species name	Cleaner	Nocturnal	Position in water column	Group size	Defense	TL:Body depth ratio
Scaridae	*Sparisoma aurofrenatum*	no	0	demersal	facultative	0	4.7
Scaridae	*Sparisoma viride*	no	0	demersal	facultative	0	4.1
Sciaenidae	*Equetus punctatus*	no	1	demersal	solitary	0	4.7
Scorpaenidae	*Pterois volitans*	no	1	demersal	facultative	0	3.9
Serranidae	*Cephalopholis cruentata*	no	0	demersal	solitary	0	4.6
Serranidae	*Cephalopholis fulva*	no	0	demersal	solitary	0	4.1
Serranidae	*Epinephelus adscensionis*	no	0	demersal	solitary	0	4.5
Serranidae	*Epinephelus guttatus*	no	0	demersal	solitary	0	4
Serranidae	*Epinephelus striatus*	no	0	demersal	solitary	0	3.9
Serranidae	*Hypoplectrus gummigutta*	no	0	demersal	solitary	0	3
Serranidae	*Hypoplectrus guttavarius*	no	0	demersal	solitary	0	3
Serranidae	*Hypoplectrus indigo*	no	0	demersal	solitary	0	2.9
Serranidae	*Hypoplectrus nigricans*	no	0	demersal	solitary	0	3
Serranidae	*Hypoplectrus puella*	no	0	demersal	solitary	0	3.3
Serranidae	*Hypoplectrus unicolor*	no	0	demersal	solitary	0	3.3
Serranidae	*Liopropoma mowbrayi*	no	0	demersal	solitary	0	4.6
Serranidae	*Liopropoma rubre*	no	0	demersal	solitary	0	4.6
Serranidae	*Rypticus subbifrenatus*	no	0	demersal	solitary	0	4
Serranidae	*Serranus tabacarius*	no	0	demersal	solitary	0	4.9
Serranidae	*Serranus tigrinus*	no	0	demersal	solitary	0	5.6
Synodontidae	*Synodus intermedius*	no	0	benthic	solitary	0	13.5
Synodontidae	*Synodus saurus*	no	0	benthic	solitary	0	11.5
Synodontidae	*Synodus synodus*	no	0	benthic	solitary	0	13.5
Tetraodontidae	*Canthigaster rostrata*	no	0	demersal	solitary	0	3.1
Tripterygiidae	*Enneanectes altivelis*	no	0	benthic	solitary	0	6.1