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Linking removal targets to the ecological effects of invaders: a predictive model and field test

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Abstract.

Species invasions have a range of negative effects on recipient ecosystems, and many occur at a scale and magnitude that preclude complete eradication. When complete extirpation is unlikely with available management resources, an effective strategy may be to suppress invasive populations below levels predicted to cause undesirable ecological change. We illustrate this approach by developing and testing targets for the control of invasive Indo-Pacific lionfish (*Pterois volitans* and *P. miles*) on Western Atlantic coral reefs. We first developed a size-structured simulation model of predation by lionfish on native fish communities, which we used to predict threshold densities of lionfish beyond which native fish biomass should decline. We then tested our predictions by experimentally manipulating lionfish densities above or below reef-specific thresholds, and monitoring the consequences for native fish populations on 24 Bahamian patch reefs over 18 months. We found that reducing lionfish below predicted threshold densities effectively protected native fish community biomass from predation-induced declines. Reductions in density of 75- 95%, depending on the reef, were required to suppress lionfish below levels predicted to over-consume prey. On reefs where lionfish were kept below threshold densities, native prey fish biomass increased by 50-70%. Gains in small (<6cm) size classes of native fishes translated into lagged increases in larger size classes over time. The biomass of larger individuals (>15cm total length), including ecologically important grazers and economically important fisheries species, had increased by 10-65% by the end of the experiment. Crucially, similar gains in prey fish biomass were realized on reefs subjected to partial and full removal of lionfish, but partial removals took 30% less time to implement. By contrast, the biomass of small native fishes declined by more than 50% on all reefs with lionfish densities exceeding reef-specific thresholds. Large inter-reef variation in the biomass of prey fishes at the

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outset of the study, which influences the threshold density of lionfish, means that we could not identify a single rule-of-thumb for guiding control efforts. However, our model provides a method for setting reef-specific targets for population control using local monitoring data. Our work is the first to demonstrate that for ongoing invasions, suppressing invaders below densities that cause environmental harm can have a similar effect, in terms of protecting the native ecosystem on a local scale, to achieving complete eradication.

Key words: Exotic species; eradication; population control; ecological model; size-based analysis; predation; marine management; metabolic scaling theory; productivity

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INTRODUCTION

Invasive species are causing a range of ecological effects on recipient ecosystems, from shifts in the abundance and distribution of native species through competitive exclusion to predation-mediated extinctions of native prey (Baxter et al. 2004, Bando 2006, Molnar et al. 2008, Sax and Gaines 2008). A growing body of research is devoted to estimating targets for invasive species removal, which is the main approach used to mitigate the often-severe effects of invaders on recipient ecosystems (Perrings 2005). These studies typically use characteristics of the invader in single-species population models to estimate the rate of mortality required to achieve population decline, with the intent of extirpating the invader from its non-native range (i.e., Buckley et al. 2003, Taylor and Hastings 2004, Govindarajulu et al. 2005). However, the scale and magnitude of many invasions outstrip the resources available to combat them, precluding complete eradication, and instead setting up a long-term battle for control (Van Driesche et al. 2008). For such invasions, targets for population controls could instead be expressed in terms of measurable ecosystem protection or recovery in priority habitats (Bax et al. 2001, Perrings 2005, Baxter et al. 2008). The idea of suppressing invaders below levels that eclict ecological change is akin to the concept of suppressing a species below thresholds of economic impact, which has been applied to agricultural pest invasions (Gren 2008, Gardiner et al. 2009). Yet to our knowledge, there are no cases of invasive species control based on suppression below levels predicted to cause undesirable ecological change.

Indo-Pacific lionfish (*Pterois volitans* and *P. miles)* are broadly distributed and highly abundant marine invaders which have begun to cause severe negative ecological effects, and for which eradication is unlikely (Côté et al. *in press*). First introduced off the coast of South Florida in the 1980s, lionfish have spread over more than 4,000,000 km^2 in the Western Atlantic,

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Caribbean and Gulf of Mexico over the past eight years and have undergone exponential increases in abundance at many sites (Betancur-R et al. 2011). Lionfish are gape-limited predators that consume an array of Atlantic fishes and crustaceans (Morris and Akins 2009, Côté et al. 2013), and 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).

Traditional marine conservation tools, such as marine reserves, appear to be ineffective at preventing lionfish colonization, despite abundant populations of large fish that could act as competitors or predators of lionfish (Hackerott et al. *in press*, but see Mumby et al 2010). The efforts currently underway to control lionfish abundance are primarily taking the form of removal of individual fish by spear and net (Akins 2012). Although the depth range of lionfish extends from shoreline to more than 150 m, the limited number of gear types that can successfully catch them means that culling takes place almost exclusively in shallow coastal areas close to human settlements and in priority areas, such as marine protected areas (MPAs). So far, the only guidance available for managing the invasion stems from traditional matrix modeling to identify region-wide mortality targets aimed at achieving complete eradication (Barbour et al. 2011, Morris et al. 2011). However, the mismatch between these large-scale population estimates and the small-scale nature of removals highlights the need to develop targets for lionfish control that aim to minimize the impacts of the invasion at local scales.

The main direct effect of lionfish on invaded marine communities is predation on native fish species, resulting in rapid declines in native fish biomass (Green et al. 2012; Albins and Hixon 2008). Therefore, suppressing lionfish below densities at which they over-consume prey fishes (i.e. consume them faster than they can replenish themselves) should prevent declines in

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native fish biomass (Fig. 1a). To explicitly test this hypothesis, we construct an ecological model that predicts the density of lionfish that causes predation-induced declines in fish prey from two rates: prey consumption by invasive lionfish and biomass production by native fish prey. We then use our model to generate reef-specific targets for lionfish control for invaded coral patch reefs in the Bahamas. Next, we manipulate lionfish densities on these reefs to levels above or below the predicted reef-specific target lionfish densities (Fig. 1b), and monitor native fish biomass over time. If we have accurately predicted the densities at which lionfish deplete native fishes, we should observe declines in the biomass of fish prey on reefs where lionfish density exceeds the target, but not on reefs where lionfish numbers were sufficiently suppressed (Fig. 1c). By creating a general modelling framework to accurately predict the effects of lionfish on the diverse assemblage of native prey they consume, our ultimate goal was to illstrate that harnassing information on the ecological effects of invasive species on native communities yields targets for removal at a scale relevant for local management action.

METHODS

Modelling targets for invasive lionfish control

Our model of lionfish predation 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}) per site. The difference between the two is the net rate of biomass production ($\overline{N_p}$) by the prey fish assemblage at a site:

$$\overline{N_p} = \bar{P} - \bar{C} \quad (1)$$

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Our model and analyses are based on the hypothesis that the biomass of prey fishes residing on a reef will decline if lionfish consume prey at a rate that exceeds the rate of prey production (i.e., $\overline{N_p} < 0$; Fig. 1a).

Rates of 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 (Brown et al. 2004). This approach considers the intrinsic relationship between a fish's size and the rate at which it produces new biomass (Allen 1971; Banse and Mosher 1980; Jennings 2005). This simple approach assumes that variation in the rate of natural mortality from native predators is not a substantial influence on prey production at each reef site. However, there is evidence that lionfish can exert mortality on their prey that far exceeds that from native predators, resulting in local extirpation of reef fishes (Pusack et al. 2013; Albins 2012), supporting our approach of singling out lionfish predation as a main driver of prey biomass dynamics. In addition, variation in reef fish biomass, owing to recruitment variation, could affect our estimates of fish standing biomass, and thus productivity. However, the magnitude of variation in fish biomass is often far greater between reefs than within-reefs over time (Cassele and Warner 1996; Hamilton et al. 2006; Hixon et al. 2012) and, for broadcast spawning fishes, recruitment and mortality in the first year of life has been shown to contribute little to overall population growth rate (Heppell et al. 1999) . Our method captures spatial variation in fish biomass by generating reef-specific models, and we approximated within-reef variation in fish biomass by conducting multiple spatially-segregated surveys of fish biomass time, and incorporating variance among surveys into estimates of site-specific production.

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151 $\bar{P}$ was calculated as:

$$\bar{P} = \frac{1}{z}\sum_{\forall z}\sum_{\forall i}\sum_{\forall v} P_{v,i,z}$$

152 (2)

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

$$P = ZB$$

155 (3)

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

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

160 (4)

161 The scaling exponent (q) of the relationship between *P/B* and body mass has been theoretically
162 explored, and empirically validated (Brown et al. 2004), as -0.25. However, j varies with
163 taxonomic group and ecosystem-specific species interactions (Brown et al. 2004). Analyses of
164 juvenile and adult marine tropical fish taxa suggest a j value of 3.08 (Lorenzen 1996). The
165 equation $e^{E/kT}$ describes the effect of environmental temperature on prey fish production rates,
166 where E is the activation energy, k Boltzmann's constant and T is ambient water temperature,
167 expressed in degrees Kelvin (Table 1).

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

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$$B = a_i L^{b_i} \quad (5)$$

where L is the total length of 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).

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

$$\bar{C} = \bar{d}\bar{W}\bar{p}(0.006e^{0.16T}\overline{W_l}^{h})y \quad (6)$$

where $\bar{d}$ is the density of lionfish per hectare of habitat, 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:

$$\bar{W} = \frac{1}{m}\sum_{\forall_m}(a_l {L_m}^{b_l}) \quad (7)$$

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, 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. The function $0.006e^{0.16T}$ describes the scaling

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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 1). The scaling constant *h* has a value of -0.29 for lionfish (Côté and Green 2012). Finally, we extrapolated average daily consumption rates by lionfish to annual rates by multiplying by the constant *y,* which is 365.4 days/year. Our approach to estimating consumption assumes that prey density has little effect on lionfish consumption rates because. Field and experimental observations of invasive lionfish reveal that they achieve high rates of prey capture (Green et al. 2011) and cause prey mortality rates near 1 (Pusack 2013) across prey densities.

Our model of net prey fish production ($\overline{N_p}$), with all terms made explicit, is given by:

$$\overline{N_p} = \frac{1}{z}\sum_{\forall_z}\sum_{\forall_i}\sum_{\forall_v}\left(\frac{j(a_i {L_{v,i,z}}^{b_i})^q}{e^{\frac{E}{kT}}}\right) a_i {L_{v,i,z}}^{b_i} - \bar{d}\frac{1}{m}\sum_{\forall_m}(a_l {L_m}^{b_l})\,\bar{p}\left(0.006e0.16T\frac{1}{m}\sum_{m}(a_l {L_m}^{b_l})^{h}\right)y \quad (8)$$

Target lionfish density ($\bar{d}$). The density 'threshold' at which lionfish begin to deplete resident fish prey on an invaded reef is modelled as the density at which prey consumption by lionfish ($\bar{C}$) equals the rate of prey fish biomass production ($\bar{P}$) ($\overline{N_p}$ = 0 in Equation 1). Thus, by setting $\overline{N_p} = 0$ and solving for $\bar{d}$ in Equation 8, this target density is given as:

$$\bar{d} = \frac{\frac{1}{z}\sum_{\forall_z}\sum_{\forall_i}\sum_{\forall_v}\left(\frac{j(a_i {L_{v,i,z}}^{b_i})^q}{e^{\frac{E}{kT}}}\right) a_i {L_{v,i,z}}^{b_i}}{\frac{1}{m}\sum_{\forall_m}(a_l {L_m}^{b_l})\bar{p}\left(0.006e0.16T\frac{1}{m}\sum_{m}(a_l {L_m}^{b_l})^{h}\right)}\pi r^2 \quad (9)$$

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In equation 9, we scale $\bar{d}$ by the area over which lionfish forage, which for patch reefs was estimated as πr^2; a circular area where the radius r is half the diameter of the patch reef (in m), plus a 10m buffer which accounts for observations of lionfish foraging in seagrass patches adjacent to reefs on which they are resident (Green et al. 2010; Table 1).

Importantly, our model of $\bar{d}$ assumes that prey fish populations at a reef could remain stable if lionfish consumption exactly balances prey production. However, prey are undoubtedly subject to stochastic mortality and recruitment 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 this buffer; hence our estimates of 'sustainable' lionfish densities represent the *maximum* lionfish densities at which further declines in prey fish biomass may be averted.

Study system

Our study took place on 24 natural coral patch reefs in Rock Sound, off Eleuthera Island, Bahamas (22º22.500 N, 76º49.000 W; Fig. 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 2013). Study reefs were 100-150 m^2 in size and separated from all other reefs by at least 500 m of sand and seagrass. All 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.

Parameter estimates

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We parameterized the model for each reef site with field data collected at the outset of the experiment in December 2009 (Figure 2). Estimates of water temperature (T; Table 1) were drawn from the distribution of annual sea surface temperatures for the Bahamas (NOAA 2013).

Lionfish body sizes and initial density. To estimate the abundance and 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 1) of all lionfish encountered. We compared the locations and sizes of lionfish recorded during the two surveys to minimise the chance that individuals were missed or double-counted. We converted total length (cm) to weight (g) using the allometric scaling equation $a_l L^{b_l}$ where a_l= 0.00497, b_l=3.291 (Green et al. 2012).

Prey fish biomass. 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 1) 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 1).

Lionfish diet composition. More than 100 species of native fish have been identified from the diets of lionfish on invaded sites (Côté et al. 2013; Green et al. 2012; Morris and Akins 2009), indicating that gape-limited lionfish appear to be restricted in what they consume largely by prey

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size. We therefore set the upper limit of potential lionfish prey size by identifying the maximum total length of prey fish in stomach contents (i.e. 13 cm), and the maximum gape height (i.e. 4.8 cm; used to approximate maximum body depth of potential prey) of lionfish collected from reefs in the Bahamas (Green et al. 2012). 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 ($\bar{p}$) in the Bahamas (by volume) has been estimated from stomach contents to be 0.89 ± 0.08 (Green et al. 2012).

Model simulations

We created a model of $\bar{d}$ for each of the 24 study reefs, and incorporated variation in our parameter estimates through Monte Carlo simulation to generate a distribution of reef-specific 'threshold' lionfish densities at which lionfish prey consumption matches prey production rates (Equation 9; see Table 1 for a summary of parameter sources). We show a hypothetical distribution of $\bar{d}$ for a generic site (Figure 1b). Specifically, we calculated the median from 1,000 iterations of each model and repeated the simulation 500 times, generation a distribution for the median of $\bar{d}$. We did this procedure for each of the 24 sites. For each model we specified log-normal distributions for lionfish body mass ($\overline{W}$) 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 the proportion of diet composed of fish prey (T and p respectively; Table 1). We then constructed empirical 95% confidence intervals of the median by taking the 2.5 and 97.5 percentiles of the resulting

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distributions as our confidence limits for $\bar{d}$ for each site (Table 2; Vose 2008). All simulations were done in the statistical software R (R Core Development team 2008).

Testing the model: Experimental lionfish removals

To test whether maintaining lionfish below predicted threshold densities ($\bar{d}$) would prevent predation-induced declines in prey fish biomass, we divided the 24 study reefs into four removal treatments (6 reefs per treatment), randomized across the patch reef system (Table 2; Fig. 2). Lionfish on reefs in treatments 1 and 2 were kept below the median (probability = 0.5) density threshold predicted for each reef (Table 2). In particular, all lionfish were removed from reefs in treatment 1, and lionfish on reefs in treatment 2 were maintained at the 25th percentile of the probability distribution for their reef-specific threshold density (probability =0.25; Fig. 1b). Hence, densities on the reefs in treatments 1 and 2 were very likely to be below the actual threshold densities and net production of prey should be positive. Lionfish on reefs in treatments 3 and 4 were maintained at densities that exceeded the median density threshold predicted for each reef (Table 2). Lionfish on reefs in treatment 3 were maintained at the 75th percentile of their threshold density distributions (probability =0.75), and lionfish were maintained at densities that exceeded the 95th percentile on reefs in treatment 4 (Fig. 1b). Hence, densities on these reefs were very likely to be above the actual threshold densities and net production of prey should be negative. 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.

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298 Lionfish removed from the study system were euthanized humanely at the surface in a clove oil
299 and seawater solution, following the protocol of Green et al. (2012).
300
301 *Monitoring prey fish response*
302 To evaluate the relative rate and magnitude of change in fish biomass between the four
303 treatments over time, we repeated belt transect surveys for native fishes (see *Parameter*
304 *estimates*) on the reefs every six months over an 18-month period (June 2010, December 2010
305 and June 2011). Again we converted fish lengths (cm) to weights (g) using species-specific
306 allometric scaling constants. We assessed trends in the biomass of native fishes across the four
307 lionfish removal treatments by first expressing native fish biomass at each reef in each time
308 period as a proportion of biomass on the reef at the start of the experiment (i.e. baseline), and
309 then calculating mean and 95% confidence intervals for proportion biomass remaining for each
310 treatment.
311 To assess the timing of changes to the size structure of resident fish communities as
312 lionfish predation is reduced, we divided our analyses of the fish community into three size
313 groups: small-sized (i.e. 0-5cm TL), medium-sized (6-15cm TL), both of which could be
314 consumed by lionfish, and large-sized individuals beyond the size limits consumed by lionfish
315 (i.e. >15cm). To determine whether reducing predation on prey-sized juveniles of large-bodied
316 species results in greater biomass of large size classes over time, we included in our analysis of
317 large-bodied fishes (i.e. >15m TL) only those species that were also observed on the reefs at
318 sizes <15cm TL, and thus were vulnerable to lionfish predation at the start of the experiment
319 (Table A1).
320

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RESULTS

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 densities above which lionfish should deplete their reef fish prey (Table 2; at probability = 0.95). Thus, lionfish density had to be reduced by 25-95%, depending on the reef, to achieve suppression sufficient to arrest prey decline (Table 2; at probability = 0.5).

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 during the summer each year (Fig 3a; e.g. (Caselle and Warner 1996). Comparing the biomass of these size classes between post-settlement winter seasons (i.e., December 2009 versus December 2010; Fig. 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 (Fig. 3a). By contrast, the biomass of small fishes declined significantly from one winter to the next on reefs where lionfish densities far exceeded the predicted thresholds of impact, with average reductions of 15% (treatment 3) and 40% (treatment 4) in one year (Fig. 3a). Comparing changes between pre-recruitment summer sampling periods reveals that more prey-sized fishes persisted on sites where all lionfish were removed and where they were suppressed below predicted thresholds (treatment 2), with biomass higher in June 2011 than June 2010 by 40% and 30%, respectively. However, the biomass of prey fishes remained depressed on reefs where lionfish densities remained above levels predicted to over-consume them (treatment 3 and 4; Figure 3a).

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Initially we observed declines in the biomass of larger size classes of prey fishes (i.e., 6-15cm TL) on all reefs, save those where lionfish had been completely removed (Fig. 3b). However, the biomass of larger prey fishes diverged between the four treatments by the end of the experiment (Fig. 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 (Fig. 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 (Fig. 3b).

Finally, the biomass of individuals that were too large to be preyed upon by lionfish (i.e.,>15cm TL) was highly variable across the study reefs over the first 12 months, but increased significantly (15-80%, on average) over the final six months of the study across all treatments (Fig. 3c).

DISCUSSION

Our study reveals that suppressing invasive lionfish below densities at which they are predicted to over-consume prey can effectively prevent predation-induced declines in prey fish biomass. The significant margin by which prey fish biomass increased on reefs where lionfish were completely extirpated indicates that these invasive predators were already depleting native fish prior to the start of our experiment in 2009. Importantly, over the course of the experiment, suppressing lionfish densities below thresholds predicted to cause predation-induced declines quickly resulted in the recovery of biomass of the smallest prey fish to levels achieved by complete lionfish removal (Fig. 3a). Rates of biomass recovery for larger size classes of lionfish

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prey (6-15cm TL) were slower than for the smallest size classes of prey fishes on reefs where lionfish were suppressed below levels predicted to over-consume them (Fig. 3a & b). This pattern may be explained by the fact that lionfish preferentially consume small size classes of fish prey (i.e., <5 cm TL; Green 2012). 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 over time. 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. 6-15cm TL).

By the end of the experiment, the biomass of larger-bodied prey (i.e. 6-15cm TL) had increased by a smaller margin on reefs where lionfish remained at levels below those predicted to over-consume prey, compared with lionfish-free reefs (Fig. 3b; treatment 2 vs. treatment 1). This slower rate of recovery is in line with our prediction that net prey production rates, while positive, would be lower on reefs where some lionfish remained, owing to higher predation mortality, compared with reefs where all lionfish had been removed (Fig 1a-c). Significant increases in the largest size classes (> 15cm TL) of reef fishes that had been vulnerable to lionfish predation as juveniles on our study reefs over the final six months of the study may be partially explained by a lag in the time to biomass recovery for larger fish size classes, and 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 (www.fishbase.org). However, given that fish home range size increases as fishes grow (Kramer and Chapman 1999), the larger (>15 cm TL)

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388 fish could easily have moved among reef patches (e.g. Frederick 1997), irrespective of lionfish
389 density, and contributed to the overall increases in biomass for large size classes observed across
390 all reefs by the end of the experiment (Fig. 3c).

391 Increases in the biomass of juvenile size classes (<15 cm TL) translated into greater
392 biomass of large size classes of the same species over time. Hence, local control could be
393 effective in minimizing the contribution of lionfish to at least two ongoing changes to Caribbean
394 coral reefs. The first change is the transition from dominance by reef-building corals to
395 macroalgae, a shift largely attributed to reductions in key herbivores, such as parrotfishes, which
396 control algae populations (Mumby 2006). The second change is the reduction in the diversity,
397 abundance and size of predatory fishes on reefs (Paddack et al. 2009). Four species of large-
398 bodied parrotfish in the genera *Scarus* and *Sparisoma*, important grazer of macroalgae on
399 Caribbean reefs, and commercially important fishes, such as the Nassau grouper (*Epinephelus*
400 *striatus*) and yellowtail snapper (*Ocyurus chrysurus*), increased in biomass across all sizes
401 classes over the course of our experiment (Figure 3C; Table A1). However, time series data
402 measuring the magnitude of ecological (e.g. grazing) and economic (e.g. to fisheries) damage
403 prevented or reversed that can be attributed to lionfish removal are needed to fully estimate the
404 benefits of this management action.

405 Our large-scale field test of reef-specific model predictions, in which the relative
406 magnitude and direction of changes in prey fish biomass were well-predicted by the simple size-
407 based scaling relationship between fish size and production rate and lionfish predation mortality,
408 suggests that variation in natural mortality from native predators and recruitment are less
409 important influences on prey biomass dynamics than effects of lionfish predation, at least at the
410 spatial and temporal scale at which suppressed lionfish on invaded reefs. In fact, compensatory

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411 recruitment would have served to mask the effects of lionfish predation on fish biomass,
412 particularly at intermediate lionfish densities. However, declines in biomass of recruit-sized fish
413 were in line with the predictions for our model, which did not include a compensatory production
414 component. This suggests that compensation, if present, is minor compared with the effect of
415 lionfish predation mortality. The simplicity of our metabolic-scaling approach to estimating fish
416 production, which relies primarily on fish community standing biomass and size structure, means
417 that the model could be applied fish communities across the various Atlantic habitats occupied
418 by lionfish - including mangroves, temperate hard-bottom systems, estuaries and seagrass beds
419 (Barbour et al. 2010; Jud et al. 2011; Lesser and Slattery 2011). Importantly, the 'target' lionfish
420 densities predicted to arrest prey biomass decline varied greatly across the 24 patch reefs, owing
421 to large inter-reef variation in the biomass of the prey fish communities. Variability in target
422 densities unfortunately precludes the use of a single rule of thumb for dealing with lionfish (e.g.,
423 reducing lionfish density by half leads to a significant chance of arresting prey decline on most
424 reefs). Instead, it appears that assemblage-specific values of biomass for prey and lionfish
425 determine the severity of predation-induced prey declines, and the level of control required to
426 mitigate them. However, the information on native fish and lionfish biomass needed to obtain
427 site-specific predictions is currently collected by many existing marine field monitoring
428 programs, when those include transect surveys of fish communities (i.e., Green 2012).

429 Our method can also be used in conjunction with data on lionfish colonization rates to
430 identify areas vulnerable to the effects of lionfish, and set spatial priorities given limited
431 resources. We emphasize that predictive modeling can take place before lionfish are present in
432 high densities, so that local action can be taken to prevent predation effects before they occur.
433 Our approach is therefore valuable for managers who are tasked with managing this invasion, as

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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 (e.g., Byers 2005). Identifying key habitat for the juveniles of commercially exploited marine fishes (i.e., Mumby et al. 2004), many of which are consumed by lionfish at unsustainable rates (Green et al. 2012), and focusing predictive and control efforts on these areas may also be an effective use of limited management resources.

Importantly, lionfish reduced the biomass of prey-sized reef fishes by at least 50% on all reefs where their densities exceeded reef-specific thresholds, and the magnitude decline was similar on sites where no lionfish were removed and those where removals occurred, but not to the degree needed to suppress populations below levels that over-consumed prey. The fact that lionfish can withstand starvation for protracted periods without significant loss in body condition (Fishelson 1997), consume a broad diet that can include crustaceans (Côté et al. 2013), and exert high rates of density-independent mortality leading to extirpation of prey species (Pusack 2013), suggests they will be able to reduce markedly the populations of many prey before a regulating numerical or functional response is elicited. The probability of extirpation is greatest for rare species if they are selectively consumed by lionfish (e.g. Almany et al. 2007). Thus, in the absence of effective human intervention, the lionfish invasion, which is proceeding apace, therefore has serious implications for the persistence of native fishes. With rapid increases in lionfish abundance on many invaded habitats across the western Atlantic (Côté et al. *in press*), 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.

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Eradication of lionfish from the western Atlantic is not possible with the available management resources (Barbour et al. 2011). However, our experiment validates the utility of setting targets for lionfish population suppression instead of attempting local eradication. This approach was not only ecologically effective (in terms of preventing declines in native prey fish biomass), it was also cost effective. To achieve complete extirpation of lionfish reefs (treatment 1), we spent on average 30% longer per site (i.e. 60 versus 78 minutes of dive time, on average) than at reefs where a few lionfish were allowed to remain 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. Organizations around the region are enacting local lionfish control programs (Akins 2012). If guided by relevant target threshold densities for lionfish, can make most efficient use of removal resources to prevent local fish populations from declining. Future research quantifying the relationship between cost of control and ecological protection, and the factors affecting cost, would greatly aid this effort.

While eradication can and has been achieved for some invasions (Myers et al. 2000, Simberloff 2001), many invasions, such as lionfish on Caribbean coral reefs, are occurring at a speed and magnitude that outstrips the resources available to contain and eliminate them. Our study is the first to demonstrate that for such invasions, complete extirpation is not necessary to minimize negative ecological changes within priority habitats. Instead, we provide evidence that suppressing invaders below densities which cause ecological harm can protect and recover native ecological communities. Our general approach is characterized by three steps that can be applied across invasions: (1) quantifying the mechanisms by which an invader affects native communities, (2) identifying population thresholds of the invader that elicit community effects, and (3) setting these thresholds as targets for control. Using these step to link removal targets

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with the ecological effects of ongoing invaders will ultimately result in a more efficient allocation of limited resources to management, because the invaders need only be controlled below levels which cause unacceptable ecological change—an important benefit for conservation practitioners seeking to allocate resources in a way that sustains sufficient invasive species control over the long term in priority habitats.

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639 Appendix A contains a work flow diagram for estimating lionfish density targets from our
640 simulation model (Fig. A1), and information on the species and size classes of native reef
641 fishes found on our study reefs in the Bahamas (Table A1).

642 - Figure A1: Simulation model work flow diagram

643 - Table A1: Species size class information

644

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Table 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 the calculations using Monte Carlo simulation.

Model component	Parameter	Meaning	Value	Source
Prey fish production ($\bar{P}$)	$L_{v,i,z}$	*prey fish length	1 -13cm (individual-specific)	Assemblage-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 ^{o}K (26 ± 3°C)	NOAA 2013
Lionfish prey consumption ($\bar{C}$)	a_l, b_l	lionfish-specific length-weight scaling constants	a_l = 0.00497;b_l = 3.291	Green et al. 2012
	L_m	*lionfish length	6-390mm (individual-specific)	Assemblage-specific
	h	*prey consumption scaling constant	0.29	Côté and Green 2012

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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 ^{o}K (26 ± 3°C)	NOAA 2013
r	*radial distance of the area over which lionfish forage	Radius of reef area + 10m into sand/seagrass (Green et al. 2011)	Assemblage-specific
y	constant scaling daily to annual consumption	365.4 days/year	

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650 Table 2. Predictions of density thresholds at which lionfish begin to over-consume native reef fish prey on 24 invaded coral patch
651 reefs off Eleuthera, Bahamas. Percentile refers to the probability distribution of predicted density thresholds (e.g., Fig. 1B). The reefs
652 were divided into four treatments, with two treatments below (1 and 2) and two treatments above (3 and 4) the median predicted
653 threshold (probability = 0.5). Initial density is the number of lionfish observed per reef at the start of the experiment in December
654 2009, while treatment density is the number of lionfish maintained per reef for the duration of the 18-month experiment. Bolded
655 numbers are targets used in removal experiment for reefs in each treatment. Numbers in brackets represent the % reduction in lionfish
656 numbers required to achieve the corresponding probability of prey depletion.

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 (87)	5 (78)	8 (65)	17 (26)
		76	21	31	0	3 (90)	4 (87)	7 (77)	14 (55)
		89	24	12	0	1 (92)	2 (83)	4 (67)	9 (25)
		93	24	14	0	2 (86)	3 (79)	5 (64)	11 (21)
		104	25	15	0	2 (87)	3 (80)	5 (67)	11 (27)

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		112	24	9	0	2 (78)	3 (67)	5 (44)	11 (0)
2	25th	79	25	21	1	**1 (95)**	2 (90)	3 (86)	8 (62)
		100	23	10	1	**1 (90)**	2 (80)	4 (60)	9 (10)
		70	21	48	2	**2 (96)**	4 (92)	6 (88)	14 (71)
		72	20	33	2	**2 (94)**	4 (88)	7 (79)	14 (58)
		75	20	16	2	**2 (88)**	4 (75)	7 (56)	16 (0)
		106	12	8	2	**2 (75)**	6 (25)	13 (0)	41 (0)
3	75th	108	22	18	3	1 (94)	2 (89)	**3 (83)**	7 (61)
		101	19	15	4	1 (93)	2 (87)	**4 (73)**	7 (53)
		55	23	18	5	2 (89)	3 (83)	**5 (72)**	10 (44)
		77	23	8	5	3 (63)	4 (50)	**5 (38)**	11 (0)
		71	16	20	8	2 (90)	4 (80)	**8 (60)**	20 (0)
		91	20	30	7	2 (93)	3 (90)	**7 (77)**	18 (40)
4	>95th	102	20	9	9	1 (89)	2 (78)	4 (56)	**9 (0)**
		78	22	11	11	2 (82)	3 (73)	5 (55)	**11 (0)**
		94	22	14	9	1 (93)	2 (86)	4 (71)	**9 (36)**

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	84	24	21	9	2 (90)	3 (86)	4 (81)	**9 (57)**
	73	19	26	22	3 (88)	5 (81)	9 (65)	**22 (15)**
	90	26	29	9	2 (93)	3 (90)	5 (83)	**9 (69)**

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658 FIG. LEGENDS

659 Fig. 1. A) Hypothesized association between prey consumption by Indo-Pacific lionfish (g ha^{-1}
660 yr^{-1}) and the production of fish prey (g ha^{-1} yr^{-1}) on invaded Atlantic coral reefs. The dashed line
661 indicates the 1:1 line where prey production equals consumption by their lionfish predators. We
662 predict that on reefs where consumption outstrips production, the standing biomass of reef fishes
663 will decline. Shading indicates the direction and magnitude of 'net' production rates, which we
664 define as the difference between rates of prey production and lionfish consumption, varying
665 continuously from high rates of positive production (green; prey increase) to high rates of
666 negative production (red; prey decline). (B) Hypothetical probability distribution of predicted
667 lionfish densities, generated by a simulation model that incorporates uncertainty in component
668 parameters, beyond which lionfish consume prey at a rate that exceeds prey biomass production
669 and standing prey biomass begins to decline (i.e. net production rate is negative). To test the
670 accuracy of simulation predictions, we selected four lionfish removal treatments: two below (1
671 and 2) and two above (3 and 4) the median (i.e., most likely) threshold lionfish density for each
672 reef. C) Predicted trajectories of prey fish biomass if our simulation model is accurate. The
673 biomass of prey fishes on reefs where lionfish have been suppressed below the predicted
674 threshold densities should be maintained over time (1 and 2), whereas prey biomass on reefs
675 where lionfish are not sufficiently suppressed should continue to decline (3 and 4).

676
677 Fig. 2. Study site and map of the 24 natural patch reefs in Rock Sound, off Eleuthera Island,
678 Bahamas, where we conducted our lionfish removal experiment. Lionfish were abundant across
679 the study reefs at the outset of the experiment in December 2009. Colours indicate the lionfish

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680 removal treatment for each reef, corresponding to the probability of prey depletion at each site
681 (Table 2).

682 Fig. 3.The proportional change in biomass of native reef fishes on 24 Bahamian patch reefs over
683 time in response to lionfish density manipulations. Colours represent lionfish density treatments,
684 which varied in the probability that lionfish will deplete their fish prey based on whether they
685 were above or below the predicted threshold density at which lionfish over-consume prey (Table
686 2). Points represent mean biomass per treatment (n= 6 reefs each), standardized by biomass at
687 the outset of the experiment in December 2009, and bounded by 95% confidence intervals.
688 Values above 1 represent prey biomass estimates that exceed initial biomass, while values < 1
689 indicate declines in biomass. Plots A – C depict temporal patterns for different size classes of
690 native fishes across the 18-month experiment.

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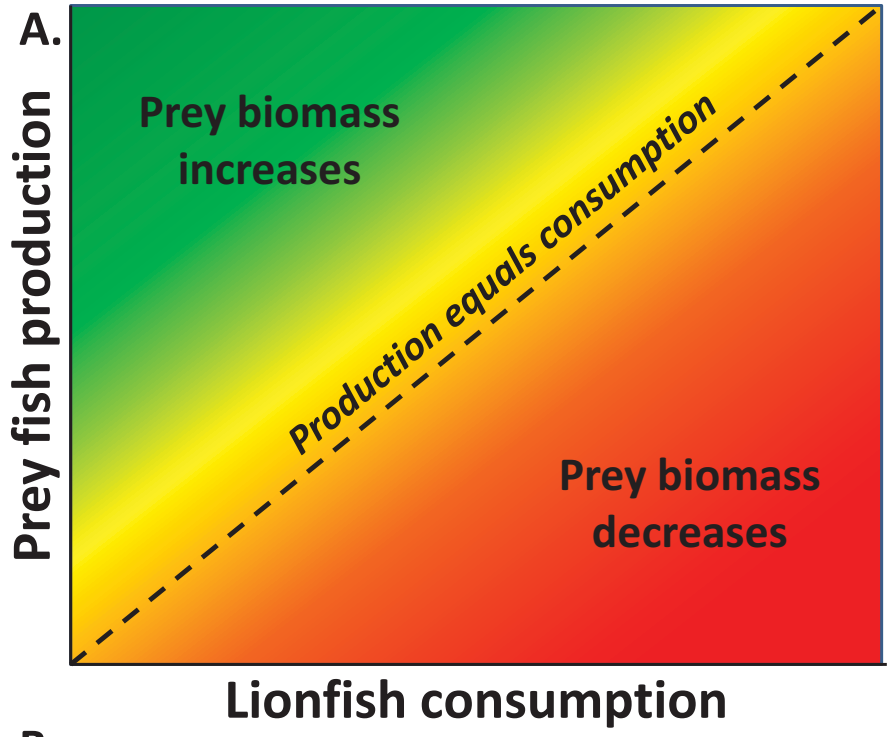
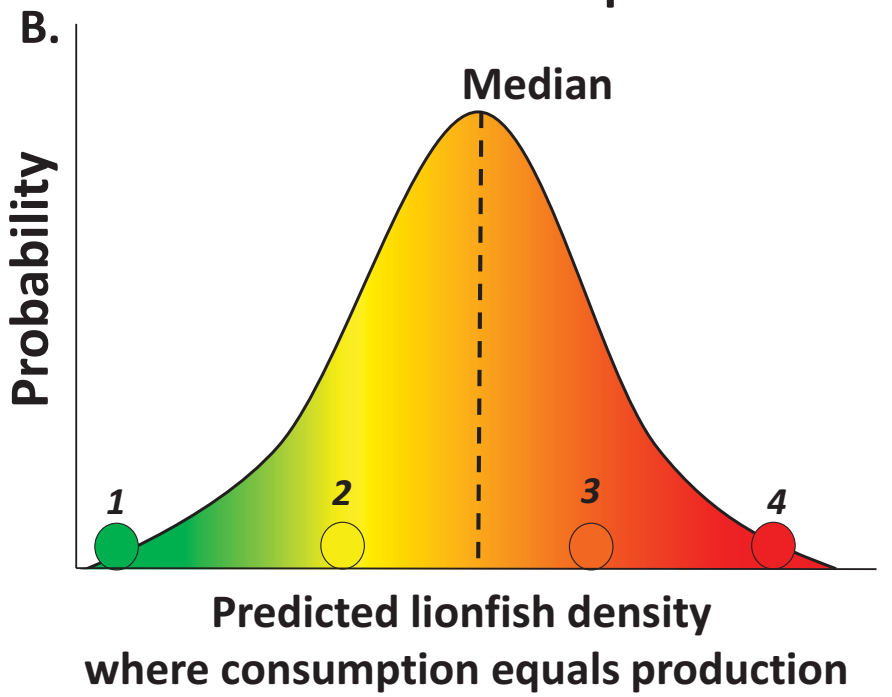
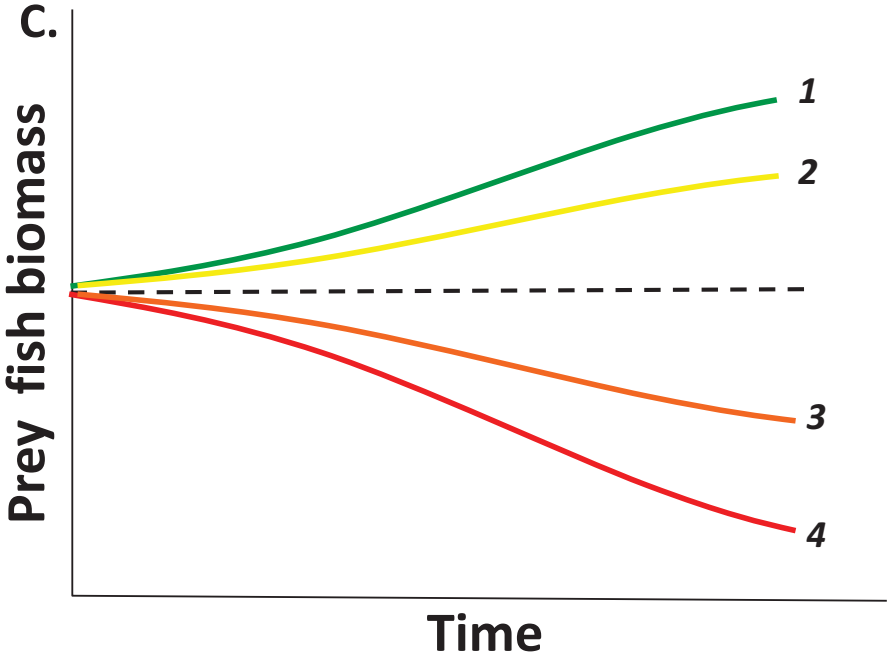
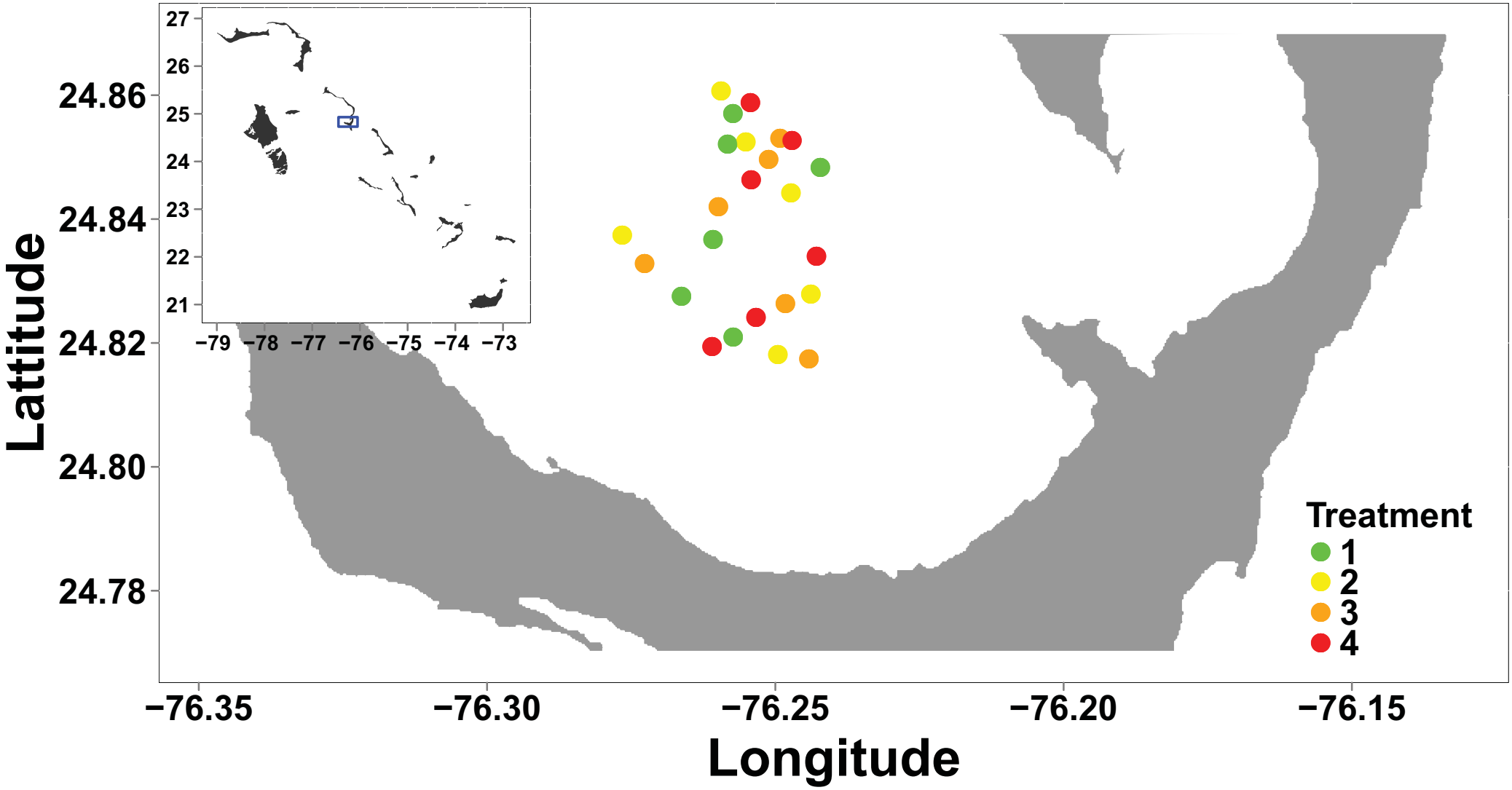
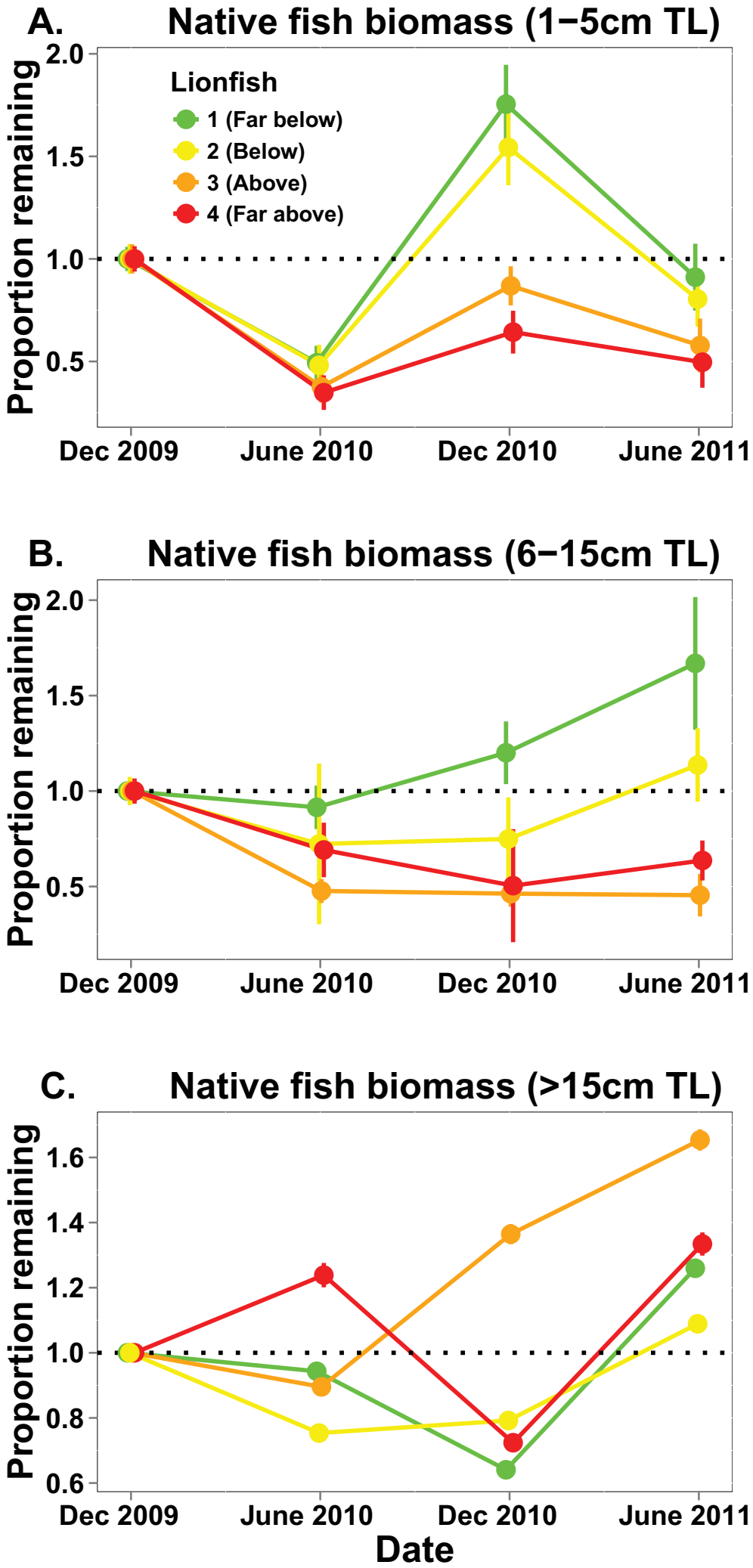

A.
Prey fish production
Prey biomass increases
Production equals consumption
Prey biomass decreases
Lionfish consumption


B.
Probability
Median
1
2
3
4
Predicted lionfish density
where consumption equals production


C.
Prey fish biomass
1
2
3
4
Time

ECOLOGICAL SOCIETY OF AMERICA




A.
Native fish biomass (1−5cm TL)
Lionfish
1 (Far below)
2 (Below)
3 (Above)
4 (Far above)
Proportion remaining
2.0
1.5
1.0
0.5
Dec 2009
June 2010
Dec 2010
June 2011
B.
Native fish biomass (6−15cm TL)
Proportion remaining
2.0
1.5
1.0
0.5
Dec 2009
June 2010
Dec 2010
June 2011
C.
Native fish biomass (>15cm TL)
Proportion remaining
1.6
1.4
1.2
1.0
0.8
0.6
Dec 2009
June 2010
Dec 2010
June 2011
Date