

Research Article

The effectiveness of small-scale lionfish removals as a management strategy: effort, impacts and the response of native prey and piscivores

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Abstract

Lionfishes (*Pterois volitans* and *P. miles*) are now established in all regions of the Caribbean, Gulf of Mexico and the Western Atlantic. As they continue to spread and colonize, reef ecosystems could be undergoing significant changes in species composition. A successful method of control includes targeted removals, but many organized removal efforts occur on large spatial scales, or involve numerous volunteers and personnel. This study addressed the effectiveness of lionfish removal over small spatial scales on a linear coral reef in La Parguera, Puerto Rico and quantified the effort necessary to diminish and maintain low lionfish densities. Three removal events at this reef took place over one month with 11 hunters per day to cull a 14,520 m² area. Timing of recovery of lionfish density varied by area in the removal site, but an overall reduction in lionfish biomass was retained post-removal. Tagging of lionfish in non-removal sites suggested recovery to the culled area was due to re-colonization via recruitment or ontogenetic migration rather than by adult lateral immigration. No detectable effects of the lionfish removal were observed on native prey or piscivore densities. Thus, evidence from this study supports that native fish abundance may not be impacted when lionfish densities are relatively low. Removal efforts should consider lionfish density relative to the densities of the native faunal communities before committing resources to this strategy.

Key words: *Pterois volitans*, invasive species, Caribbean, fish tagging, recolonization

Introduction

Since the mid-1980s, the Indo-Pacific lionfish, *Pterois volitans*, has established a significant presence in the Western Atlantic, including the Caribbean Sea and the Gulf of Mexico. Second only to habitat loss, invasive species are often cited as the largest global threat to biodiversity (Mooney and Cleland 2001), and the presence of lionfish has raised significant concerns regarding their impacts on native fish species. In general, lionfish have been found to significantly affect prey fish populations and associated ecosystem services (Albins and Hixon 2008; Morris and Akins 2009; Green and Côté 2009; Arias-González et al. 2011; Green et al. 2012a; Albins 2013; Albins and Hixon 2013). These negative

impacts of lionfish on marine ecosystems in the Western Atlantic, Gulf of Mexico and the Caribbean emphasize the need for sustained research on their biological and ecological dynamics. Evidence points to targeted population control as the only means of reducing lionfish impact (Barbour et al. 2011; Green et al. 2012a).

Research has identified specific habitats and areas where targeted removals could mitigate potential effects of lionfish and provide the greatest management. These include habitats such as rugose reefs and the edges of drop-offs (Bejarano et al. 2015) as well as sites of high priority management including marine protected areas (Akins 2012). Other studies have assessed the effectiveness of lionfish culling in different regions throughout the Caribbean (Frazer et

al. 2012; de León et al. 2013; Côté et al. 2014; Green et al. 2014). These studies address large scale removal efforts both in terms of effort (e.g., derbies) and spatial scale (e.g., those that span large areas or multiple reef patches). The conclusions are unanimous in showing that culling is effective.

However, many of these studies defined effectiveness solely as the ability to maintain low lionfish densities. In contrast, only one empirical study has directly evaluated the impact of lionfish removal on the potential to restore affected fish communities (Green et al. 2014, but see Valderrama and Fields 2015). Green et al. (2014) produced a model to predict target lionfish densities necessary to allow for native prey biomass to recover in a depressed-density scenario. However, the observed increases in prey biomass and the corresponding target lionfish densities were found to vary greatly across the study's patch reef system due to inter-reef variation in prey biomass. Furthermore, as evidenced in Benkwitt (2015), the effects of lionfish scale non-linearly with increased densities; thus, a universal rule to management cannot be applied to all areas of the invasion simply based on scaling up or down the impacts observed in high density areas. An assessment of lionfish impacts in Venezuela found no detectable effects on the native fish assemblages, even at high lionfish densities (max observed 0.05 fish/m²), indicating that certain reef systems may be able to naturally mitigate impacts without the intervention of removals (Elise et al. 2014). Recently, a five-year study in Belize concluded similar results with no detectable impacts to density, richness or composition of native "prey" fish communities even with variable annual lionfish densities (Hackerott et al. 2017). Effects of lionfish at varying densities and size structure, including low densities, would be beneficial in determining if, where and under what conditions lionfish removal would be effective and efficient. In terms of suggesting practical use to management scenarios, one study used distance sampling to evaluate detection of lionfish at different depths and habitat features wherein the results suggest the use of this strategy in lionfish management (Tilley et al. 2015), while another recent study has developed a model to suggest effort required to reach a certain target density threshold (Usseglio et al. 2017). However, no current studies have dealt with practical issues of small-scale targeted removal, such as the necessary frequency of re-culling and its relation to the mechanisms of lionfish recolonization, or addressed the impacts of lionfish at relatively low densities.

This study assessed the effectiveness of small-scale removals on a linear reef in southwest Puerto Rico to address three goals: (1) To assess the temporal and

spatial effectiveness of localized lionfish removal through an experimental approach, including the quantification of catch/effort relative to population size and density, (2) To assess the effectiveness of a lionfish removal event on the degree and rate of recovery of native reef fish species commonly found in lionfish stomachs and the response of native piscivorous predators, and (3) To assess the time frame and mechanisms of lionfish re-colonization.

Methods

Study site

The study was conducted along the fore reef of Pelotas Reef in La Parguera (17°57'26"N; 67°04'13"W) from May 2013 to June 2014. The study site was approximately 1.2 km in length with a maximum depth of 18 m. This reef was chosen because Pelotas Reef was not a specific target for recreational divers who frequently cull lionfish at popular dive sites in La Parguera and was therefore assumed to have a relatively undisturbed lionfish population. The study site was partitioned into one removal site and two control sites. One control was at the edge of Pelotas Reef while the other control was on the adjacent Conserva Reef, which is separated from Pelotas by a 30 m wide, 10 m deep channel and lacks mangrove habitat (Figure 1). The controls were placed to assess horizontal movement from adjacent reefs into a culled area. The removal site (0.6 km linear area) was separated into three zones (A–C) to equally space both sampling allocation and diving/removal effort. The zones were delineated underwater with a series of semi-permanent rope lines that were laid perpendicular to the reef crest that extended from a depth of 3 m to the base of the fore reef. Additionally, subsurface marker buoys were attached to each rope.

Sampling & experimental design

Underwater visual census (UVC) was used to assess the size class and density of lionfish and density of native piscivores (e.g., snappers, groupers, jacks, etc.). Quadrat sampling was used to determine species richness and abundance of native juvenile and cryptic reef fish species that are typical prey commonly observed in lionfish stomachs (Morris and Akins 2009; Côté et al. 2013; Harms-Tuohy et al. 2016). Sampling was conducted in each of the removal and control sites, and carried out one month before and one, three, six, nine and 12 months after the removal, representing an asymmetrical Before-After-Control-Impact (BACI) design (Table 1). Reef rugosity in each area was calculated using six random 10 m transects following the chain method

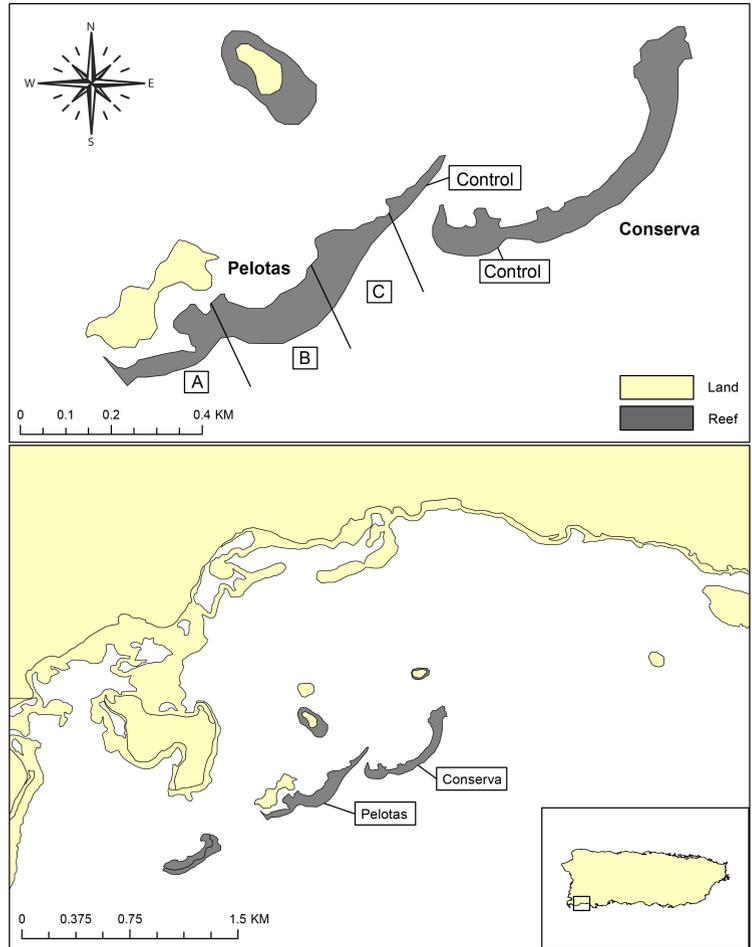


Figure 1. Location of the study site in La Parguera, Puerto Rico. The removal was conducted on Pelotas Reef, the controls were on Pelotas and Conserva Reef. The removal site was separated into three areas (A–C).

Table 1. Timeline denoting tasks for the duration of the project.

Task	May 2013	June 2013	July 2013	Sept 2013	Dec 2013	Mar 2014	June 2014
Lionfish Survey	X	X	X	X	X	X	X
Piscivore Survey	X		X	X	X	X	X
Prey Survey	X		X	X	X	X	X
Lionfish Tagging	X		X				
Removal Events		X					

and calculation in Weil et al. (2005). Slope of the reef was measured from still images using Image J (v. 1.49), while habitat characteristics were noted qualitatively.

Transects of 25 × 3 m were placed parallel to the reef crest stratified by depth (5–18 m), with approximately 3 to 5 m in between each transect moving laterally along the reef. Transects were placed in the same locations each survey. Number and size class of lionfish and number of native piscivores were recorded on each transect. Lionfish size was categorized as Small Juvenile (< 80 mm), Juvenile (81 to 160 mm), Maturing (161 to 215 mm) and Adult

(> 216 mm; TL), where size at maturity is estimated at 189 mm (Gardner et al. 2015). There were 12 transects in each site except one control (Pelotas) where only four transects were suitable (n = 52, per month sampled). Fifteen minutes were spent surveying each transect. The total area surveyed was 14,520 m², including controls on Pelotas and Conserva Reefs. The initial population size was calculated for the total removal site (9,840 m²) by extrapolating the observed lionfish density to the total reef area.

Native fishes representing potential prey species were sampled from five randomly placed 1 × 1 m canvas quadrat tents in the removal and control sites

($n = 25$, per month sampled). A fish anaesthetic (15% quinaldine/seawater solution) was introduced underneath the canvas tent and allowed to soak for 1–2 minutes to anesthetize and retain target fishes (gobies, blennies, cardinalfish, etc.) which were counted and identified to lowest possible taxon (Gibson 1967). This method was preferred over belt transects to more accurately account for nocturnal or cryptic fish that are commonly missed in underwater visual census (Smith-Vaniz et al. 2006) but are known lionfish prey (Morris and Akins 2009; Côté et al. 2013; Harms-Tuohy et al. 2016).

To assess the possible movement of lionfish into the removal site from the two control sites, conventional anchor tags (FD-68B FF, $\frac{3}{4}$ inch; Floy Tag & Mfg., Inc., Seattle, WA, U.S.A.) were inserted into 18 lionfish of various sizes using a Floy[®] pistol grip corrosion resistant tagging gun. Fifteen lionfish were tagged on Conserva Reef, and three fish were tagged on the non-removal, control site of Pelotas Reef. The tagging procedure involved a simplified version of the method used by Akins et al. (2014) and similar to Tamburello and Côté (2015). The anchor tag was chosen for its high visibility underwater and reduced handling time with insertion. One diver would capture the lionfish between a clear vinyl hand net and a black mesh hand net. The black mesh net was used as a distracting device to back the lionfish into the clear net, after which it was secured between the nets until the diver could safely remove it with a gloved hand. The diver would carefully restrain the lionfish by the head and insert the tag into the dorsal musculature with the other hand. The tag was inserted at an anterior angle behind and 3 mm below the 5th dorsal spine. The procedure required less than two minutes, and the fish was immediately released in the exact location in which it was tagged. No trauma was ever detected, and fish were inspected before release by lightly tugging the tag to ensure it was secure. After the release, tagged fish were observed for up to 2 minutes for any unusual behavior. The tagging occurred prior to the baseline visual censuses and the experimental removal, but also continued for one month post-removal. All re-sightings of tagged individuals were documented during post-removal sampling and included location or habitat changes at re-sighting.

Removal design

The experimental lionfish removal spanned a one-month period (June 2013), with three removal events occurring at two-week intervals on Saturday mornings (08:00–10:00). Removal employed only experienced lionfish spearfishermen to both maximize and

standardize effort and to limit any possible damage to the reef or injury to native species. A total of 20 scuba divers participated, with a daily average of 11 divers per removal event. As an incentive, and again to standardize effort, each diver received a spearfishing kit that included a 1.2-m pole spear, collection bag, spine-resistant gloves, underwater flashlight and spine clippers. All divers used the same pole spear throughout the removals. One or two paired-diver teams were dropped into each of the three zones of the removal site and were followed at the surface via surface marker buoys. Divers hunted for approximately 60–90 minutes, roving within their boundaries and from depths of 3–18 m, covering approximately 15,840 m². Upon surfacing, lionfish were placed on ice immediately to preserve them for gut content analysis. Samples were returned to the lab where they were measured for standard and total length (mm), weight (g), sex and maturation state (juvenile/mature) based on macro-examination of the gonad (Green et al. 2012b). After each removal day, a transect survey ($n = 12$ per area) assessing lionfish in only the removal site was employed to estimate the reduction in lionfish density from the day's fishing effort and the remaining population abundance.

Statistical analyses & interpretation

The decline in the rate of population removal (changes in catch per standardized unit of effort = CPUE) was used to estimate initial population size (DeLury 1947) as a cross check of the baseline estimate from visual census. The DeLury method assumes that the proportion removed from a given unit of effort is constant across the study. The method provides a calculation for expanding upon this small-scale design for application to any removal scenario. A unit of effort was defined as a diver in the water for 1–1.5 man hours. Because sea conditions and bottom turbidity can affect the ability to detect lionfish, a correction factor was used to account for poor conditions on the first removal day. This was done by surveying ($n = 12$ transects) a reef with similar lionfish densities under conditions characteristic of both the first and second/third removal events. The proportional reduction in observed lionfish density under the poor conditions (24%) was multiplied to the total effort during the first removal to obtain relative effective effort.

For all statistical comparisons concerning fish densities, the control site on Pelotas Reef was not included to remove the effects of an uneven assessment as this control was not surveyed prior to the removals. However, the Pelotas control site was included when addressing lionfish movement into the

Table 2. Catch per unit effort (CPUE) for each of the removal events. One unit of effort is a diver in the water for 1.5 hours. Cumme is the cumulative effort.

	Catch	Effort(diver)	Catch/Effort	ln(C/E)	Cumme
1-Jun	10	2.82	3.54	1.264597	2.823529
15-Jun	10	10	1	0	12.82353
29-Jun	2	10	0.2	-1.60944	22.82353

removal site. To test the effectiveness of lionfish removal, the densities of lionfish were compared before and after the event for all sampled months, and inside and outside the removal site using a nested permutational multivariate analysis of variance (PERMANOVA, Primer 6). The response variable was counts of lionfish in each transect, and there were four factors (time [2] = before/after removal events, month [6], treatment [2] = removal or control, and area [4] = 3 removal, 1 control). In the design, month was nested in time and area was nested in treatment. Area represented the sampling divisions in the study site and was included as a factor to account for variability in the observed differences of lionfish densities and the expected differential response to removal, associated with inter-reef habitat differences and variations in initial lionfish densities. To test if lionfish re-colonization occurred via recruitment or immigration, the length-frequency distribution of lionfish within each size category was compared before and after removal and separately comparing all months after the removal using Chi Square analysis (SPSS v.19). The biomass of lionfish removed and recovered (median of the bin size) in each treatment (removal and control) was calculated using a length-weight equation with constants supplied from previous literature (Green et al. 2012a, 2014) to further evaluate reductions based on size. The same PERMANOVA design was used to address the response of native prey and piscivores. Prey evenness (H'/H_{\max}) using Shannon Wiener Diversity (H') was calculated for each month of sampling within the removal site (Pielou 1966). The densities of specific piscivores in this study were compared with those obtained in pre-lionfish years on Pelotas Reef (Nemeth 2013).

Results

Lionfish densities & initial population estimates

Thirteen lionfish were observed over all transects in the removal site in May 2013 with an average density of $0.004/m^2 \pm 0.005$ (mean \pm SD) and an estimated population size of 39 ± 17 (95% CI). Twelve lionfish were observed in the control on

Conserva, for an average density of $0.0013/m^2 \pm 0.023$ and an estimated population size of 64 ± 24 . Twenty-two lionfish were removed from Pelotas Reef during the removals of June 2013, while in the control on Conserva Reef lionfish densities did not significantly decline. Across the three removal events, CPUE showed a consistent decline ($y = -0.1437x + 1.7278$, $R^2 = 0.9952$, $p = 0.04$, Table 2) and the DeLury method estimated an initial population size of 39 lionfish within the removal site. Thus, both the survey method and the DeLury method estimated the same initial population size of lionfish for Pelotas Reef. Twenty-three days after the last removal event, only five lionfish were observed in the removal site, for an average density of $0.002/m^2 \pm 0.001$ and a population size of 19 ± 3.4 . One year post-removal, only 10 lionfish were observed, for an average density of $0.003/m^2 \pm 0.001$ with an estimated population of 29 ± 3.34 .

Approximately nine months were required before lionfish densities peaked near their initial density within the total removal site. However, initial lionfish densities in all areas of the removal site were dissimilar, and the response to removal was not the same (Figures 2–4). Lionfish density in the control on Conserva was initially higher than in all the removal zones, and while density also decreased over time, the pattern was fundamentally different from that observed within the removal site. The decline did not start until after July (i.e., after the adjacent removal event), with minimum density not observed until six months later (Figure 5).

Despite the variability observed in Figures 2–5, the PERMANOVA showed no significant differences in lionfish abundance when comparing before and after the removal events, across time and between treatments (Table 3). However, there were significant differences in the densities of lionfish in each area, which differed before and after the removal ($p < 0.05$, Figures 2–4). A post-hoc pairwise comparison indicated that Area C differed in densities before the removal and immediately after (May vs. July; Monte Carlo $p = 0.003$, Anderson et al. 2008) further illustrated by the decrease in lionfish density at this time (Figure 4) which was not detected in other areas. Overall, lionfish densities were reduced in both

Figure 2. Estimated lionfish, other predators and prey densities within removal Area A before (May) and after the removal events (July–June). Error bars represent standard error of the mean. Predator densities were divided by 10 and prey densities by 1000 to plot trends on the same scale.

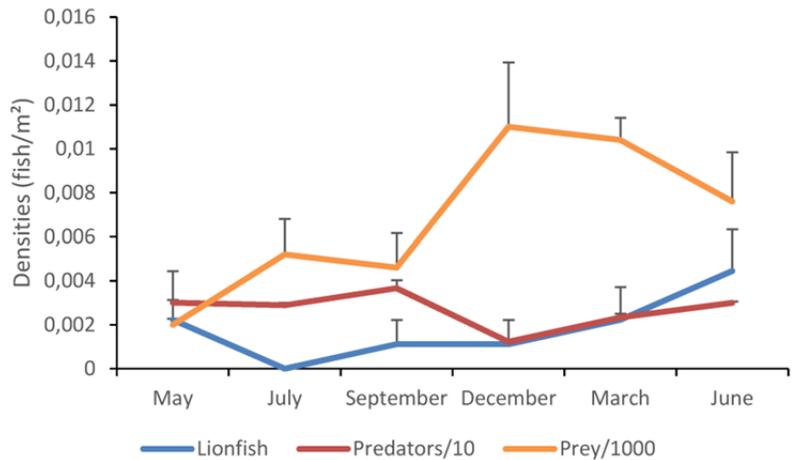


Figure 3. Estimated lionfish, other predators and prey densities within removal Area B before (May) and after the removal events (July–June). Error bars represent standard error of the mean. Predator densities were divided by 10 and prey densities by 1000 to plot trends on the same scale.

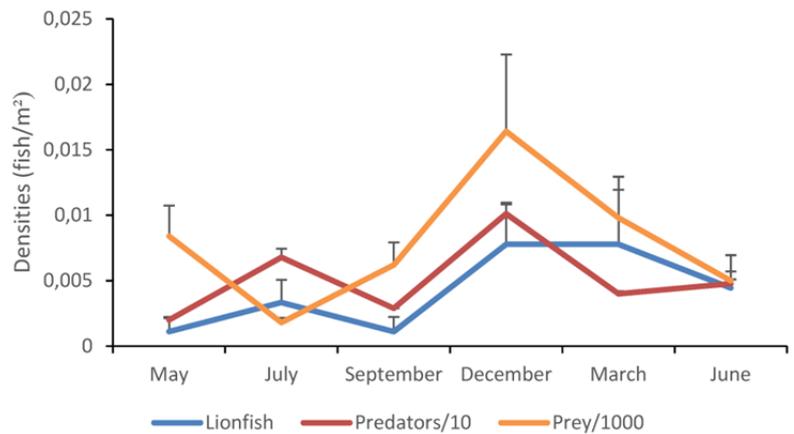
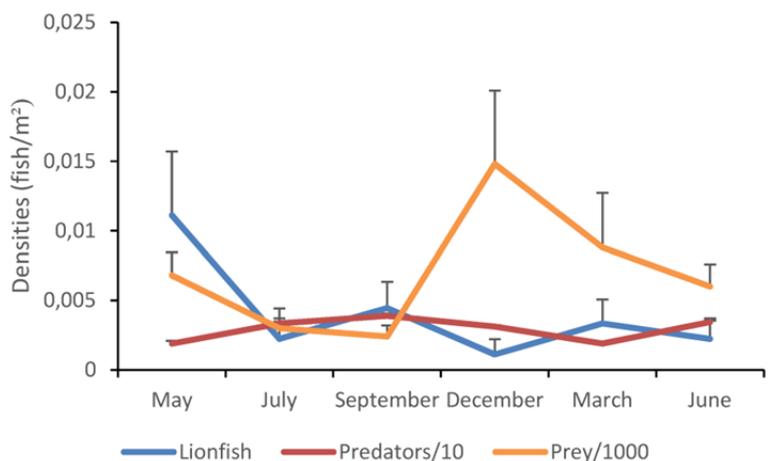


Figure 4. Estimated lionfish, other predators and prey densities within removal Area C before (May) and after the removal events (July–June). Error bars represent standard error of the mean. Predator densities were divided by 10 and prey densities by 1000 to plot trends on the same scale.



treatments, where 62% of the population was extracted from the removal site and 63% observed to decline in the control. However, the temporal decline is drastically different, where the reduction in Pelotas Reef occurred in one month (0.004 to 0.001 fish/m²) versus the six-month decline on Conserva Reef

(0.013 to 0.005 fish/m²). The lowest density observed in the control was effectively equivalent to the starting density in the removal site. Rugosity was similar among areas, except Area C, as well as habitat characteristics on both Pelotas and Conserva Reefs, however slope did marginally vary by area (Table 4).

Figure 5. Estimated lionfish, other predators and prey densities within the control site (Conserva Reef) before (May) and after the removal events (July–June). Error bars represent standard error of the mean. Predator densities were divided by 10 and prey densities by 1000 to plot trends on the same scale.

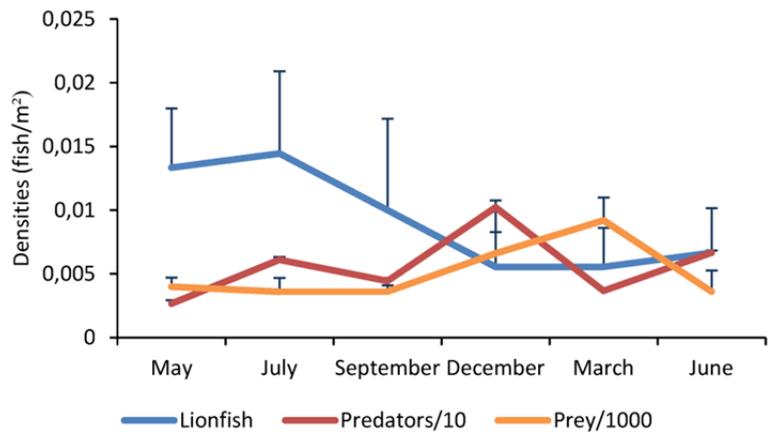


Table 3. PERMANOVA results for the comparison of lionfish abundances before and after the removal and inside and outside the removal site, for all months. Month and Area are nested within Time and Treatment, respectively.

Factor	df	SS	MS	PseudoF	P
Time	1	5.5007	5.5007	0.8288	0.5452
Treatment	1	24.284	24.284	3.1594	0.1311
Month (Time)	4	5.1417	1.2854	1.3472	0.3386
Area (Treatment)	2	9.0056	4.5028	4.7191	0.0608
Time*Treatment	1	1.284	1.284	0.22408	0.9504
Time*Area (Treatment)	2	13.006	6.5028	6.8151	0.0326
Month (Time)*Treatment	4	13.942	3.4854	3.6528	0.0602
Month (Time)*Area (Treatment)	8	7.6333	0.95417	0.40954	0.9132

Lionfish size patterns

During the removal events, lionfish of maturing and adult sizes initially dominated the catch but mean size gradually declined with subsequent removals. The final removal day resulted in two small juvenile lionfish. Visual surveys documented the same trend. Before removal, most individuals surveyed were in the maturing size class followed by the adult size class, while after removal (July) the distribution was significantly different ($\chi^2 = 9.58$, $df = 3$, $p = 0.02$), with abundance dominated by the small juvenile size class with some maturing fish also present (Figure 6). In the controls, no patterns were observed in size structure. Over time (July–September), the size class distribution inside the removal site was observed to gradually shift after removal ($\chi^2 = 14.18$, $df = 3$, $p = 0.003$) from primarily small juvenile to juvenile individuals to primarily maturing-sized individuals in the last census, when the distribution was similar to that observed before removal ($\chi^2 = 0.910$, $df = 3$, $p = 0.823$) except that it lacked the small proportion of small juveniles. Both treatments showed the highest proportion of small juveniles from July to September with none in December. In the control, size structure before and after the removal event was also different ($\chi^2 = 7.924$, $df = 3$, $p = 0.045$), but the

Table 4. The average rugosity (Weil et al. 2005) for each area where 0 is least rugose and 1 is most rugose. A–C indicate removal areas on Pelotas Reef. The slope is measured as the angle created from the interaction of the reef slope and a horizontal line parallel to the bottom.

Factor	Conserva	A	B	C
Rugosity	0.3516	0.3733	0.3633	0.4416
Slope (angle)	59.7	62.2	50.5	45.7

pattern was dissimilar from what was observed in the removal site in that there was no trend towards increasing size classes over time. Similarly, July differed compared to the rest of the study ($\chi^2 = 8.026$, $df = 3$, $p = 0.045$), but again the pattern (mix of size classes) differed from that observed in the removal site where only juveniles were detected. Additionally, no significant differences in sizes were detected when comparing before the removal and the end of the study ($\chi^2 = 4.251$, $df = 3$, $p = 0.236$). Converting abundances to biomass (Figure 7) shows even greater proportional declines from the removal event, while the control site illustrated the same gradual decline.

No tagged lionfish were ever observed in the removal site. In total, 83% were tagged on Conserva Reef ($n = 15$) and 17% tagged on Pelotas Reef ($n = 3$). Only five fish were re-sighted (27% recapture), each

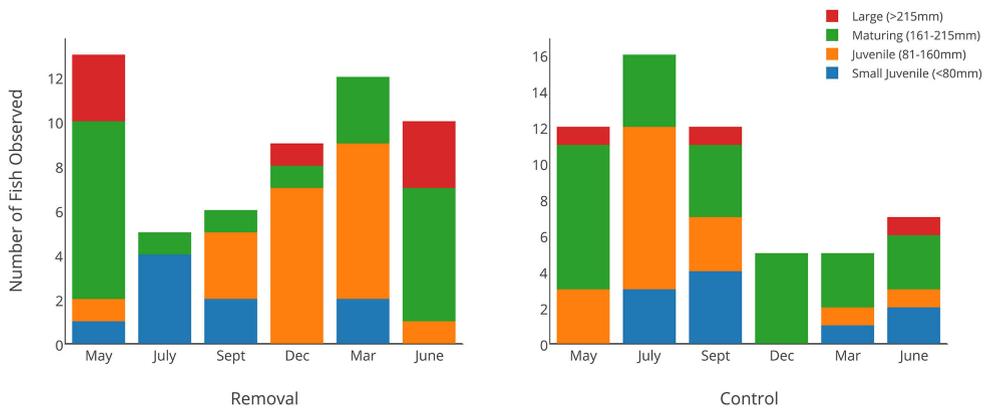


Figure 6. Size class distributions of lionfish within the removal and control area before (May) and after the removal events (July–June).

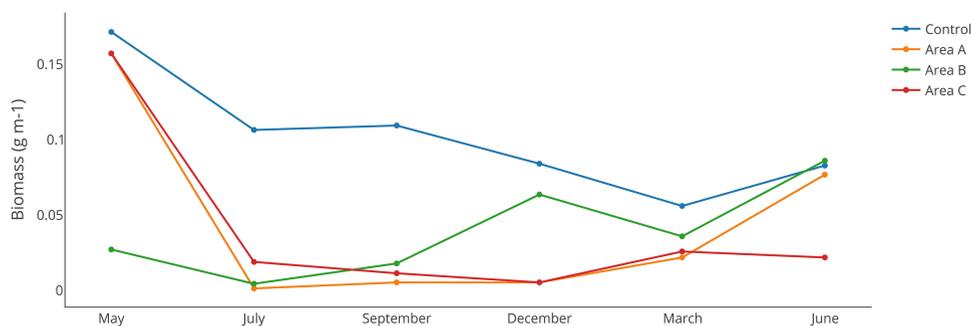


Figure 7. The biomass (g m^{-2}) of lionfish in the three areas of the removal and the control over the study period.

only once. Of those re-sighted, three individuals were detected up to 67 days at liberty in non-removal Pelotas and two individuals were observed up to 53 days in Conserva. Re-sighting of only two individuals on Conserva in July pre-dates the initial decline in lionfish densities in the control. Furthermore, all re-sighted lionfish (juveniles and adults) were observed in the same location they were tagged within the control sites (± 0.5 m). Tags were visually inspected at re-sighting, and none appeared to be dislodged or inadequately anchored to the fish however biofouling prevented the numbered tag from being read from a 0.5 m distance.

Responses of native prey & piscivores

Native prey abundances exhibited temporal variation by month, and differed in abundances before and after the removal events, however these differences were not the same for all areas ($p < 0.05$, Table 5). An increase in prey abundance was observed for all areas, around the same time in December and March (maximum 16 fish/ m^2), and prey abundances were three orders of magnitude greater than lionfish

densities (Figures 2–4). There was also a difference in prey assemblage composition before and after the removal (Supplementary material, Table S1), but species evenness remained relatively constant throughout the study. By December and March, most areas were represented by a different prey species assemblage than what was present before the removal. Newly recruited individuals were observed in the collections, as illustrated by variations in the length-structure of two of the most abundant prey species *Lythrypnus nesiotes* and *Coryphopterus glaucofraenum* (Figure 8).

Prey species abundance in the control site illustrated a similar signal of recruitment, albeit to a lesser degree (maximum 9 fish/ m^2), in December and March as within the removal site. Prey species were represented by six species in pre-removal surveys (May) compared to six to 12 species in post-removal months within the control site (Table S2). Although there was a change in prey assemblage composition within the control site, total prey densities did not appear to differ between treatments or times, but did, however, across months (Table 5).

Table 5. PERMANOVA results for the comparison of native prey abundances before and after the removal and inside and outside the removal site, for all months.

Factor	df	SS	MS	PseudoF	P
Time	1	7730.4	7730.4	1.0246	0.4597
Treatment	1	1419.4	1419.4	0.6698	0.7423
Month (Time)	4	19379	4844.6	3.7873	0.0028
Area (Treatment)	2	5035.2	2517.6	1.9681	0.1174
Time*Treatment	1	1337.8	1337.8	0.47929	0.8989
Time*Area (Treatment)	2	7897.7	3948.8	3.087	0.039
Month (Time)*Treatment	4	6045.6	1511.4	1.1815	0.3435
Month (Time)*Area (Treatment)	8	10233	1279.2	0.8779	0.7057

Table 6. PERMANOVA results for the comparison of native piscivore abundances before and after the removal and inside and outside the removal site, for all months.

Factor	df	SS	MS	PseudoF	P
Time	1	8715.4	8715.4	2.4068	0.0973
Treatment	1	949.35	949.35	0.48163	0.8804
Month (Time)	4	10566	2641.6	3.7461	0.0038
Area (Treatment)	2	4545.6	2272.8	3.2232	0.0362
Time*Treatment	1	1021.6	1021.6	0.70912	0.6982
Time*Area (Treatment)	2	2545.2	1272.6	1.8047	0.149
Month (Time)*Treatment	4	4649.7	1162.4	1.6485	0.109
Month (Time)*Area (Treatment)	8	5641.2	705.15	0.50574	0.9937

Native predator abundances differed among sampling months and sampling areas independent of each other ($p < 0.05$, Table 6). However, there were no clear trends in piscivore abundances between treatments. Piscivore densities were one order of magnitude greater than lionfish densities for all months sampled and in all areas in the removal site (Figures 2–4). Overall species assemblage differed in the pre-removal month (May) compared to the subsequent post-removal months (Table S3). Pre-removal species richness was six and was dominated by groupers (Epinephelidae), snappers (Lutjanidae) and the carangid *Caranx ruber*. In the post-removal surveys, 13 piscivorous species were observed immediately following the removal (July) and species richness ranged from seven to 12 species thereafter. The predator assemblage in the control was not the same as in the removal site indicated by the dominance of *Caranx latus* and *Lutjanus griseus*, which did not significantly contribute to the predator assemblages in the removal site (Table S4).

Discussion

Effectiveness of the small-scale removal

The three days of removal effort over one month dramatically diminished the initial lionfish densities on Pelotas Reef, as indicated by the significant decrease in catch/effort following each of these events and the 56% reduction in the population directly

attributed to the removal (22 fish). Additionally, the reduction of adult and maturing lionfish, with a subsequent increase in small juvenile and juveniles, was indicative of a removal effect on the size structure of the population.

Spatial variability in lionfish density across removal areas was significant, with the greatest density change (and most lionfish removed) coming from Area C. These differences in initial density could be related to rugosity, slope and complexity of the reef (Luckhurst and Luckhurst 1978; Gratwicke and Speight 2005) and may have overshadowed the overall treatment effect. Lionfish have been observed to prefer rugose structure (Dahl and Patterson 2014). Specifically, lionfish prefer continuous coral reefs versus patch reefs, micro-habitat preferences of hard coral and overhangs (Biggs and Olden 2011) and macro-habitat preference to reef edges and drop offs (Bejarano et al. 2015). The overall rugosity, slope and habitat characteristics of the areas surveyed on Pelotas Reef were marginally different and the entire reef is patchily distributed with holes, crevices, overhangs and changes in slope, offering a suite of habitat characteristics preferred by lionfish. Area C was also the most rugose area. However, as lionfish re-colonized, they populated the two other areas of the reef where initial densities were not as high as Area C. Thus, results suggest that differences in micro-habitat complexity (i.e., rugosity and slope) or proximity to back-reef settlement habitat, in these

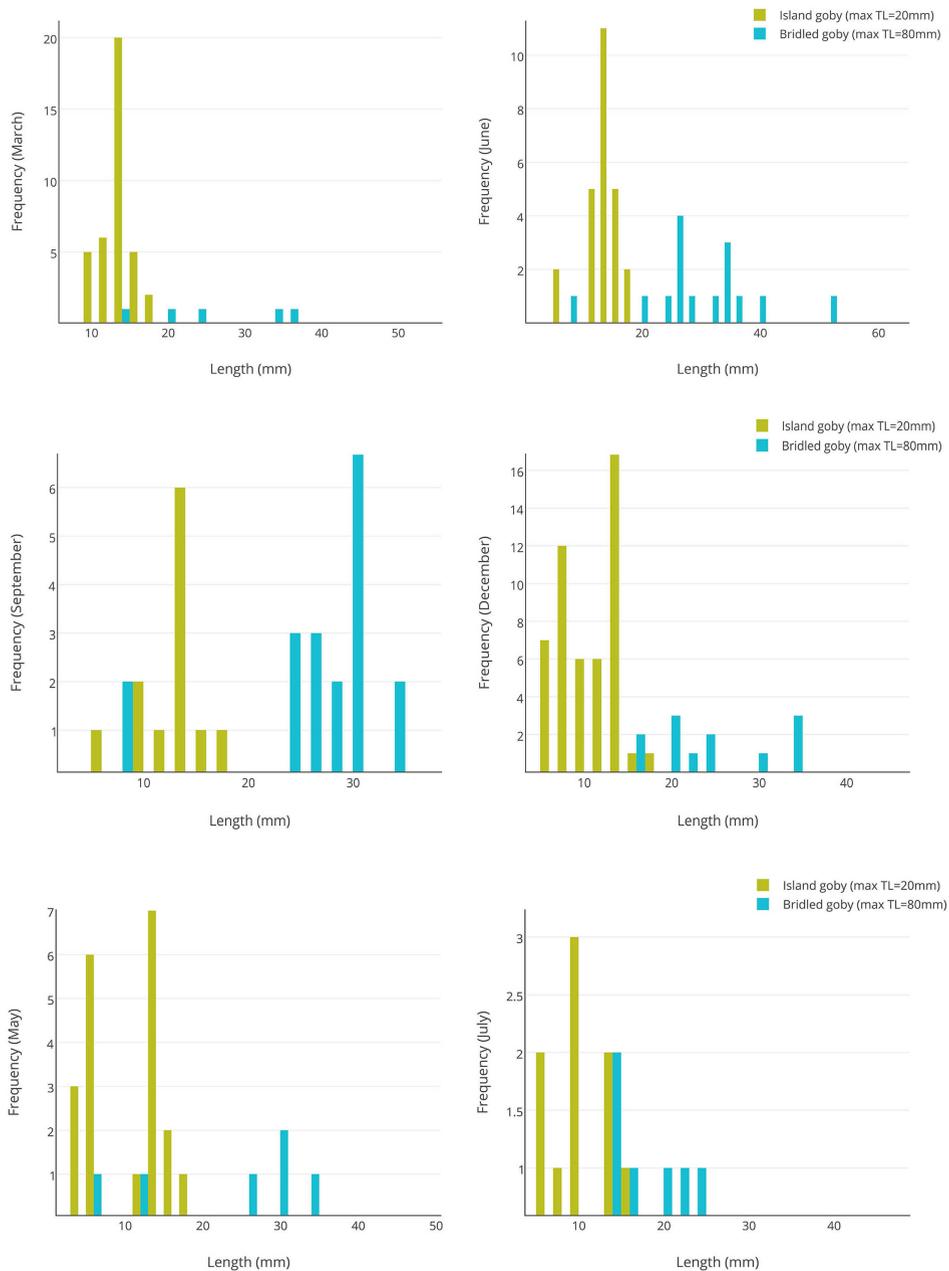


Figure 8. Length frequency distribution of the island goby, *Lythrypnus nesiotes*, and the bridled goby, *Coryphopterus glaucofraenum*, for each sampling month within the removal treatment. Max total length (TL) retrieved from Fishbase.org. Month of sampling is indicated in parenthesis on the vertical axis.

areas were driving the differences in densities observed at the within habitat scale of linear fore reef with hard coral and complex structure.

After the removal, lionfish densities remained low within removal Area C but increased after the removal in the other two removal areas, although total biomass remained reduced. Subsequently, reductions in lion-

fish densities were observed to follow a gradually decreasing trend in the control site. This decline provides a natural replication to the removal in that similar trends were observed despite the lack of any experimental manipulation. It is likely that fishing was occurring on Conserva Reef, which is a steeply sloped linear reef with similar habitat characteristics

as Pelotas and occupied by many commercially important species (i.e., snapper and grouper). However, we received no reports of tagged lionfish caught by local fishermen. A second explanation for the low tag re-sighting rate could be the migration of lionfish to deeper/offshore reefs (Claydon et al. 2012). A recent tagging study reported lionfish to move, albeit infrequently, up to 800 m among discontinuous coral reef patches, and to vacate areas during natural perturbations (i.e., hurricanes) (Tamburello and Côté 2015). Similar movement patterns have been observed in grunts, where some individuals remain inshore, but most ontogenetically migrate offshore or to deeper inshore reefs (Appeldoorn et al. 1997, 2003, 2009).

Re-colonization of the removal site

Trends in the size distribution of lionfish at Pelotas Reef coupled with the results of tagging indicate that re-colonization following removal events occurred due to recruitment of juvenile individuals rather than from lateral migration of adults. Despite the low re-sighting rate, tagged lionfish from both control sites were never observed in the removal site and all re-sightings (up to 67 days post-tagging) were within 0.5 m of tagging sites. This pattern is consistent with previous tagging studies that show high site fidelity in lionfish (Jud and Layman 2012; Bacheiler et al. 2015). In contrast, a greater number of small juvenile and juvenile lionfish were observed post-removal, even up to one year later. This suggests that post-settlement individuals may have been missed during the removal, or that juveniles and smaller individuals moved into the removal site from the reef flat (Harms-Tuohy, pers. obs), which is the preferred habitat of early settlement lionfish (Barbour et al. 2011; Biggs and Olden 2011).

Within both treatments, no small juveniles were recorded in December, which may be indicative of the observed seasonal recruitment of lionfish. As lionfish have been found to grow in increments of up to 0.6 mm/day in lionfish smaller than 200 mm TL (Akins et al. 2014), the observed size distributions indicate that juveniles seen during our study would have required a minimum of 7 months to reach the larger sizes observed, which was well within our study duration. It is possible that some juveniles grew to occupy the other size classes during the study, but the presence of small juveniles in September and March on Pelotas Reef would support movement into the area. In the control, the temporal pattern in changes of size distribution of lionfish was not the same as in the removal site. A greater proportion of juvenile and maturing lionfish were observed imme-

diately following the removal, which transitioned into predominantly maturing fish for the remainder of the study. In the control, these observed differences in size structure were not an effect of removing a size class or observing re-colonization through ontogenetic migration.

Response of native prey

The timing and density of peaks in prey abundance observed in the sampling areas demonstrated that recruitment was evident despite the presence of lionfish. In all areas and across treatments, prey abundance was greatest in December and March, irrespective of lionfish density or biomass. The similarity in the temporal pattern of density indicates a strong recruitment event and is evidence that lionfish were having no detectable effect on the prey communities. Single lionfish have been observed to reduce abundance of prey by up to 80% on small (1–4 m²) artificial and translocated coral patch-reefs in the Bahamas (Albins and Hixon 2008) and predicted to reduce biomass of prey fish on natural reefs in high densities (0.039 fish/m², Green and Côté 2009). While these studies may present valid scenarios for their respective sites and design, predictive modeling to estimate lionfish densities that allow for the recovery of native prey has been contentious (Green et al. 2014; Valderrama and Fields 2015; Green et al. 2015). A recent study of the impacts of lionfish showed that effects on prey abundances do not scale linearly with increased lionfish densities (Benkwitt 2015). Thus, the impacts of lionfish on native communities could be severely overestimated in scenarios that scale up impacts of small artificial patch reef/high lionfish density case studies. Artificial reefs provide valid comparisons to natural reefs in cases where biotic and abiotic factors influencing species richness and abundance are similar (Carr and Hixon 1997), but addressing impacts of novel predators on native communities based on results obtained from manipulative studies on artificial reefs must be carefully interpreted. For instance, prey abundance has been observed to decrease when artificial reefs do not provide the appropriate shelter from predators (Hixon and Beets 1989). Thus, the predation rate of lionfish on prey communities that may be more exposed on artificial reefs cannot be scaled to natural reef systems where this is less of an issue. Furthermore, manipulated high lionfish densities at artificial reef sites could encourage intra-specific competition resulting in overinflated estimates of consumption. In our study, removal of lionfish had no detectable impact on the native prey assemblage.

These results concur with a study in Venezuela that found no impacts of lionfish on the fish communities of Archipelago Los Roques National Park, where average densities were similar to those in our study ($0.003/\text{m}^2$ versus $0.006/\text{m}^2$, respectively; Elise et al. 2014). These densities are relatively low in comparison to other regions (on natural habitat), such as Eleuthera Island, Bahamas ($0.052/\text{m}^2$, Hackerott et al. 2013), New Providence, Bahamas ($0.039/\text{m}^2$, Green and Côté 2009) and Little Cayman Island ($0.065/\text{m}^2$, Frazer et al. 2012). This would indicate that small-scale removals aiming to increase prey faunal density on reefs of similar structure and community assemblages as Pelotas Reef are not worthwhile unless lionfish densities are much greater. For this reason, Hackerott (2014) suggested halting lionfish removal in Belize, as current densities elicit no impacts on native fish over a five-year period.

Response of native piscivores

There is a well-established concern that competition among adult native predators and lionfish could have negative impacts on native predatory species (Albins and Hixon 2008; Morris and Akins 2009; Raymond et al. 2015). Recent studies, however, have demonstrated that some native predators with ecologically similar roles may not competitively interact with lionfish to a detectable degree (Hackerott et al. 2013; Elise et al. 2014; Valdivia et al. 2014; Bejarano et al. 2015). Our study reveals that native piscivore abundance is not affected by lionfish in this level of density. Piscivore abundances were observed to be an order of magnitude greater than lionfish and no increases in abundance were detected relative to lionfish removal. Therefore, the temporal changes in abundance observed at each area are likely a response of migration, prey availability, recruitment, and seasonality factors (Cocheret De La Morinière et al. 2003; Appeldoorn et al. 2009). Piscivore densities common to this study and those sampled in the same months in 2006 (pre-lionfish colonization) on Pelotas Reef resulted in similar estimates (July: 0.13 and 0.14 fish/ m^2 , September: 0.10 and 0.13 fish/ m^2 , respectively; Nemeth and Appeldoorn, unpublished).

Application of the small-scale removal design

Removal events or derbies have been shown to be effective at reducing lionfish densities (Frazer et al. 2012; de León et al. 2013) and control of lionfish has been promoted for several years. These derbies or events attract media attention, engage stakeholders from multiple backgrounds, and improve awareness of both lionfish impacts and market potential. Yet,

these derbies are primarily attended by participants in higher economic tiers with expendable income (Trotta 2014 reported average cost per participant of \$823, but this ran as high as \$2,500), and not all countries or areas affected by the invasion have the same resources or community awareness of the benefits of lionfish removal. This could give smaller island nations or countries with less tourist-driven economies the option to seek less formal, but more targeted public-oriented removal efforts. Our standardized design proved effective at engaging local volunteer divers and required limited funds and incentives (\$2,700 total), while the timeframe of removal (three days in one month) was adequate to reduce lionfish densities in our already low-density scenario. Volunteers were invited to participate based on their experience in culling lionfish, which allowed us to maximize our catch while engaging non-scientists (i.e., recreational divers, local fishermen) in the joint effort of control. Our design can be modified to apply to specific lionfish populations, and to enhance cost effectiveness. For example, our design of three removals over one month was specific to our scientific objectives, but from a management perspective the total of 4.5 hours of culling per person could be collapsed into a single day (conditions permitting), thus reducing overall costs, especially to the participants (e.g., in our study from \$120/person for gas and lunch over three days, to only \$40/person). To address repeated culling and monitoring, our catchability coefficient ($q = 0.1437$) represents the minimum proportion of the population removed from our $9,840\text{-m}^2$ area by each additional unit of effort (1.5 man-hours), which can be used by managers to estimate effort required to reduce lionfish density in their region using the following equation: % Population Remaining = $100 - e^{(0.1437 * E)}$ where E is the cumulative effort.

For high-priority conservation areas, such as marine protected areas (MPA), management can adopt this method to employ a limited number of personnel, with a few dedicated days of removal, and scheduled but intermittent surveying to assess effectiveness. Furthermore, implementing culling in buffer zones could significantly reduce the number of lionfish migrating into a culled MPA. These buffer zones could include nursery habitats for juvenile lionfish undergoing ontogenetic migration from seagrass, mangrove or shallow back reef habitats onto the fore reef of the MPA (Barbour et al. 2011; Biggs and Olden 2011), which the present study suggests as the likely critical connection for re-colonization on Pelotas. However, if the goal of the removal or control program is to allow recovery of native fish, then initial densities of lionfish should

be evaluated before investing in the effort. Predictive modeling has been suggested as a logical approach to determining the lionfish density threshold needed to observe recovery of prey biomass (Green et al. 2014), but in this context management would benefit more from actual density estimates, which using our catchability estimate would allow for the calculation of catch and effort necessary to achieve estimated lionfish densities. While the present study responded to past density-based studies, we emphasize that size structure is also important. In our study, size structure allowed for the examination of life history stages and how they changed during removal and recolonization. Size structure is also critical for the estimation of biomass. Lionfish biomass and how its partitioned among life stages might be expected to be more directly related to predation impacts on prey, especially on a species-specific basis. Additionally, site-specific variation in prey biomass may reduce the usefulness of a predictive model in application to all areas. Thus, the need for site-specific monitoring becomes more evident.

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Supplementary material

The following supplementary material is available for this article:

Table S1. Density (fish/m²) of all native prey species observed in each sampling month within the removal site on Pelotas Reef.

Table S2. Density (fish/m²) of all prey species observed in each sampling month within the control site on Conserva Reef.

Table S3. Density (fish/m²) of all native piscivores observed in the sampling months in the removal site on Pelotas Reef.

Table S4. Density (fish/m²) of all native piscivores observed in the control site on Conserva Reef.

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