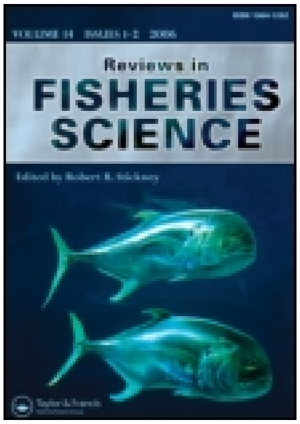

Reviews in Fisheries Science
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/brfs20

Coping with the Lionfish Invasion: Can Targeted Removals Yield Beneficial Effects?

Thomas K. Frazer [a] , Charles A. Jacoby [b] , Morgan A. Edwards [a] , Savanna C. Barry [a] & Carrie M. Manfrino [c d]

[a] Fisheries and Aquatic Sciences Program, School of Forest Resources and Conservation, University of Florida, Gainesville, Florida, USA

[b] Soil and Water Science Department, University of Florida, Gainesville, Florida, USA

[c] Department of Geology & Meteorology, Kean University, Union, New Jersey, USA

[d] Central Caribbean Marine Institute, Princeton, New Jersey, USA

Version of record first published: 12 Jul 2012.

To cite this article: Thomas K. Frazer, Charles A. Jacoby, Morgan A. Edwards, Savanna C. Barry & Carrie M. Manfrino (2012): Coping with the Lionfish Invasion: Can Targeted Removals Yield Beneficial Effects?, Reviews in Fisheries Science, 20:4, 185-191

To link to this article: http://dx.doi.org/10.1080/10641262.2012.700655

Reviews in Fisheries Science, 20(4):185–191, 2012

ISSN: 1064-1262 print / 1547-6553 online
DOI: 10.1080/10641262.2012.700655

Coping with the Lionfish Invasion: Can Targeted Removals Yield Beneficial Effects?

THOMAS K. FRAZER,[1] CHARLES A. JACOBY,[2] MORGAN A. EDWARDS,[1] SAVANNA C. BARRY,[1] and CARRIE M. MANFRINO[3,4]

[1]Fisheries and Aquatic Sciences Program, School of Forest Resources and Conservation, University of Florida, Gainesville, Florida, USA
[2]Soil and Water Science Department, University of Florida, Gainesville, Florida, USA
[3]Department of Geology & Meteorology, Kean University, Union, New Jersey, USA
[4]Central Caribbean Marine Institute, Princeton, New Jersey, USA

*Invasive species generate significant environmental and economic costs, with maintenance management constituting a major expenditure. Such costs are generated by invasive Indo-Pacific lionfish (*Pterois *spp.) that further threaten already stressed coral reefs in the western Atlantic Ocean and Caribbean Sea. This brief review documents rapid range expansion and potential impacts of lionfish. In addition, preliminary experimental data from targeted removals contribute to debates about maintenance management. Removals at sites off Little Cayman Island shifted the size frequency distribution of remaining lionfish toward smaller individuals whose stomachs contained less prey and fewer fish. Fewer lionfish and decreased predation on threatened grouper, herbivores and other economically and ecologically important fishes represent key steps toward protecting reefs. However, complete evaluation of success requires long-term data detailing immigration and recruitment by lionfish, compensatory growth and reproduction of lionfish, reduced direct effects on prey assemblages, and reduced indirect effects mediated by competition for food. Preventing introductions is the best way to avoid impacts from invasive species, and early detection linked to rapid response ranks second. Nevertheless, results from this case study suggest that targeted removals represent a viable option for shifting direct impacts of invasive lionfish away from highly vulnerable components of ecosystems.*

Keywords invasive species, maintenance management, Caribbean, coral reefs, *Pterois* spp.

INTRODUCTION

In broad terms, invasive species have generated global environmental and economic costs estimated to exceed US$1.4 trillion annually (Pimental et al., 2001). Once they have evaded prevention, early detection, and rapid responses to become established, invasive species create direct, detrimental impacts via predation and competition for resources; indirect impacts by altering habitats and interactions among species; and disruptions of ecosystem structure and function by decreasing or homogenizing biodiversity (Carlton and Geller, 1993; Vitousek et al., 1997; Pimental et al., 2001; Knowlton and Jackson, 2008). In many cases, negative outcomes from invasions impinge heavily on threatened and endangered species or exacerbate problems caused by climate change, pollution, overfishing, and other anthropogenic stresses (Knowlton and Jackson, 2008; Schofield, 2010).

The resilience displayed by many invasive species has begun to polarize views on the value of maintenance management. Arguments proposing acceptance of less harmful species as a way of freeing resources to address more harmful species (Davis et al., 2011) have been met with spirited replies (Alyokhin, 2011; Lerdau and Wickham, 2011; Lockwood et al., 2011; Simberloff et al., 2011). The replies highlighted the broader-scale and longer-term loss of biodiversity

Address correspondence to Dr. Thomas K. Frazer, Fisheries and Aquatic Sciences Program, School of Forest Resources and Conservation, University of Florida, P.O. Box 110600, Gainesville, Florida 32611, USA. E-mail: frazer@ufl.edu

associated with invasives, the benefits of remaining vigilant and responding rapidly to eliminate undesirable species before they spread, and the success of some efforts to eradicate or constrain abundances of some invasive species. All of these issues apply to predatory, Indo-Pacific lionfish (*Pterois* spp.).

THE LIONFISH INVASION: RANGE EXPANSION, IMPACTS, AND MANAGEMENT RESPONSES

Establishment and Range Expansion

Genetic analyses suggest that the lionfish invasion resulted from one introduction sited in Florida, rather than multiple, independent introductions at different locations (Betancur-R et al., 2011). Regardless of the source, lionfish are now firmly established throughout the western Atlantic Ocean, Caribbean Sea, and Gulf of Mexico (Schofield, 2009, 2010; Schofield et al., 2011). From 1985 to 2001, they spread up the Atlantic seaboard from Dania Beach, Florida (Semmens et al., 2004; Whitfield et al., 2007; Morris and Akins, 2009). A rapid expansion through the Caribbean followed, with reports from Bermuda in 2000 (Whitfield et al., 2002), the Bahamas in 2004 (Snyder and Burgess, 2006), Cuba in 2005, and the Turks and Caicos Islands in 2006 (Schofield, 2009). By 2009, lionfish had reached the Cayman Islands, Jamaica, Dominican Republic, Puerto Rico, Mexico, Honduras, Costa Rica, Haiti, U.S. Virgin Islands, Belize, Panama, and Columbia (González et al., 2009; Schofield, 2009; Aguilar-Perera and Tuz-Sulub, 2010). As predicted (Morris and Whitfield, 2009), recent data indicate lionfish have colonized the northern Gulf of Mexico, with sightings off Florida, Alabama, Louisiana, and Texas (Schofield et al., 2011). Overall, rapid range expansion by invasive lionfish generates legitimate ecological and economic concerns.

Impacts

Ecological concerns stem primarily from direct and indirect effects of predation exerted by large numbers of lionfish. In some locations, *Pterois volitans* densities approach 400 fish per hectare, which is approximately 5–15 times the densities recorded in their native range (Morris and Whitfield, 2009; Green and Côté, 2009; Darling et al., 2011; Kulbicki et al., 2012). Such high densities suggest minimal mortality from disease, parasites, or predators, which may include grouper (Maljković et al., 2008; Morris and Whitfield, 2009; Albins and Hixon, 2011; Mumby et al., 2011). In addition to occurring in higher numbers, lionfish are larger in the invaded range, which suggests decreased competition and reduced constraints on growth (Darling et al., 2011). In the absence of natural control mechanisms, high numbers of large lionfish pose a threat to the ecology and human use of coral reefs, because lionfish are effective, generalist predators that consume up to 4% of their body weight per day in fish and invertebrates, potentially leading to reduced abundances of native species and increased competition for food (Morris and Akins, 2009; Côté and Maljković, 2010; Barbour et al., 2010; Albins and Hixon, 2011; Muñoz et al., 2011; Layman and Allgeier, 2012). In the Bahamas, for example, lionfish on experimental patch reefs reduced recruitment of native reef fishes that serve as forage for important fishery species by an average of 79% (Albins and Hixon, 2008), and lionfish reduced the total biomass of 42 prey species by 65% on 9 natural reefs (Green et al., 2012). Further concerns arise from observations that lionfish can occupy and feed in alternative habitats, including mangroves (Barbour et al., 2010; Claydon et al., 2012) and seagrass beds (Chevalier et al., 2008; Biggs and Olden, 2011; Claydon et al., 2012), which serve as important nurseries for juvenile reef fish (Beck et al., 2001). In addition to these direct effects, lionfish predation on parrotfishes, surgeonfishes, and damselfishes reduces grazing on algae, potentially leading to overgrowth of reefs and subsequent loss of corals (Albins and Hixon, 2011). For example, lionfish on a mesophotic reef in the Bahamas reduced the diversity of fishes, including herbivores, which preceded a shift to algal dominance (Lesser and Slattery, 2011). In many places, deleterious effects of lionfish can be expected to exacerbate detrimental changes from other stressors, including anthropogenic nutrient loads, overfishing, pollution, coral bleaching, coral disease, and climate change (Morris and Whitfield, 2009; Schofield, 2010; Albins and Hixon, 2011).

The socioeconomic impacts of the lionfish invasion have yet to be evaluated fully, but they are potentially substantial. Predation on and competition with the early life-history stages of commercial fisheries species can reduce recruitment success and further lower fishery yields that already are predicted to decrease 30–45% by 2015 due to degradation of Caribbean reefs (Burke and Maidens, 2004). In addition, reduced biodiversity, enhanced algal overgrowth of corals, and the possibility of envenomation from lionfish spines can compromise the attractiveness of popular dive destinations, which presently generate US$2.1 billion per year (Morris and Whitfield, 2009; Burke and Maidens, 2004).

Management Responses

Given their current geographic range, rapid population growth, and tools presently available to natural resource managers, eradication of lionfish in the western Atlantic, Caribbean Sea, and Gulf of Mexico is unlikely (Morris and Whitfield, 2009; Schofield, 2010; Albins and Hixon, 2011). Moreover, recent modeling indicates that lionfish populations probably are highly resilient, with extremely high levels of sustained fishing mortality predicted to be necessary for effective, widespread control (Barbour et al., 2011; Morris et al., 2011a). Nevertheless, spatially restricted harvesting or culling of lionfish could represent efficient removal and control strategies in key locations (Morris and Whitfield, 2009; Barbour et al., 2011). In fact, lionfish are taken as bycatch in lobster traps (Martinez, 2011), and the consumption of lionfish is being promoted widely (Ferguson and Akins, 2010; Morris et al., 2011b; Weis, 2011). Efforts to remove lionfish have been initiated in several Caribbean nations (e.g., Biggs and Olden, 2011), but the approach has engendered considerable debate about the resulting costs and benefits.

Thus far, debates about removing lionfish have lacked useful estimates of key metrics that help document the efficacy of such approaches. Such documentation should include, for example, a relationship between effort and reductions in lionfish abundance, estimates of the rate at which lionfish abundances rebound, rates of prey consumption for different abundances and sizes of lionfish, and, ultimately, long-term data that demonstrate beneficial ecological effects from removals. Toward this end, initial results are provided from an ongoing, community-based lionfish removal program at Little Cayman Island. This work yields the first quantitative estimates of catch per unit effort (CPUE) from multiple locations with similar physiographic characteristics, i.e., depth and substrate type, and it also sheds light on the potential effectiveness and benefits associated with a sustained removal effort. Although eradication of lionfish in the western Atlantic and Caribbean appears unlikely, this feasible removal regime did lower densities and remove larger lionfish, which reduced detrimental predation and shifted predation pressure away from particularly vulnerable fish species. These results are both timely for natural resource managers grappling with the lionfish invasion throughout the Caribbean region and a contribution to the broader debate about the potential value of efforts to eradicate or control invaders that are established (Simberloff, 2009; Davis et al., 2011; Alyokhin, 2011; Lerdau and Wickham, 2011; Lockwood et al., 2011; Simberloff et al., 2011).

POTENTIAL EFFICACY OF LIONFISH REMOVALS: A PILOT STUDY AT LITTLE CAYMAN ISLAND

Off Little Cayman Island, lionfish were first observed on coral reefs within Bloody Bay Marine Park in 2008. Little Cayman is a small (17 × 2 km), low-lying island 120 km northeast of Grand Cayman and 145 km south of Cuba. The island is home to less than 200 permanent residents and > 50% of the surrounding waters are designated as protected areas. As a consequence, coral reef habitats and their associated flora and fauna have been minimally impacted by human activities.

Methods

Removals took place off Little Cayman Island in 2011 at 11 sites marked by permanent moorings. Sites comprised 100-m wide sections of reef walls that had similar topographic complexity and spanned depths of 10–27 m. All of the sites selected for lionfish removal represented popular dive destinations known to be inhabited by lionfish.

Lionfish removals were organized and performed by local dive masters and experienced volunteers who allowed access to their fish. CPUE was calculated as the number of lionfish removed by divers divided by the sum of their bottom times in hours. Fish collected during removals had their total lengths measured and their stomachs extracted for analysis of gut contents. Stomachs were dissected, and all material was identified to the lowest possible taxonomic level using keys to Caribbean species before being dried and weighed, although only data aggregated to higher taxonomic levels are presented here (Williams, 1984; Abele and Kim, 1986; Bohlke and Chaplin, 1993; Humann and DeLoach, 2002).

Catch data generated from removals were analyzed to determine if (i) CPUE varied among sites, (ii) CPUE was simply a function of effort, and (iii) CPUE decreased with repeated removals. A one-way analysis of variance tested for significant variation in CPUE among initial removals at ten sites, and a Pearson correlation coefficient assessed the relationship between mean CPUE and mean bottom time for divers. In addition, an exponential curve was fit to mean CPUEs from a series of 7 removals conducted over 205 days at one of the sites, i.e., Blacktip Boulevard.

Strip-transect surveys generated estimates of lionfish densities that were independent of removals. Surveys were conducted 1–2 hr prior to sunset at three sites subject to removals: Bus Stop (one removal), Mixing Bowl (three removals), and Blacktip Boulevard (seven removals), as well as at Rock Bottom (a control site not subject to lionfish removal). Such surveys should yield reliable estimates of relative densities, because lionfish are easy to identify, active during the hours just before dusk, and not prone to being attracted to or repelled by divers (Brock, 1954; Sale and Douglas, 1981; McCormick and Choat, 1987; Green et al., 2011). During surveys, one diver deployed a 50-m line, and two other divers made a single pass to count lionfish in 2-m wide transects on either side of this line. Within each site, transects were separated by approximately 3 m, with divers working up reef walls to yield two to eight transects per site. For comparison across sites and to previously reported data, counts of lionfish were summed across transects within a site and scaled to numbers per hectare.

Data from processing of stomach contents were analyzed to determine if (i) larger lionfish had a greater biomass of prey in their stomachs and (ii) lionfish of different sizes ate different types of prey. A Pearson correlation coefficient (r) measured the strength of the relationship between dry weights of gut contents and total lengths of lionfish. Changes in diet were illustrated by cumulative frequency distributions documenting the occurrence of two key prey types, shrimp and fish, in lionfish of differing total lengths.

Results and Discussion

Groups of divers (one to three individuals) generated CPUEs ranging from 0.0 to 42.2 fish h^{-1}, with an overall mean CPUE ±

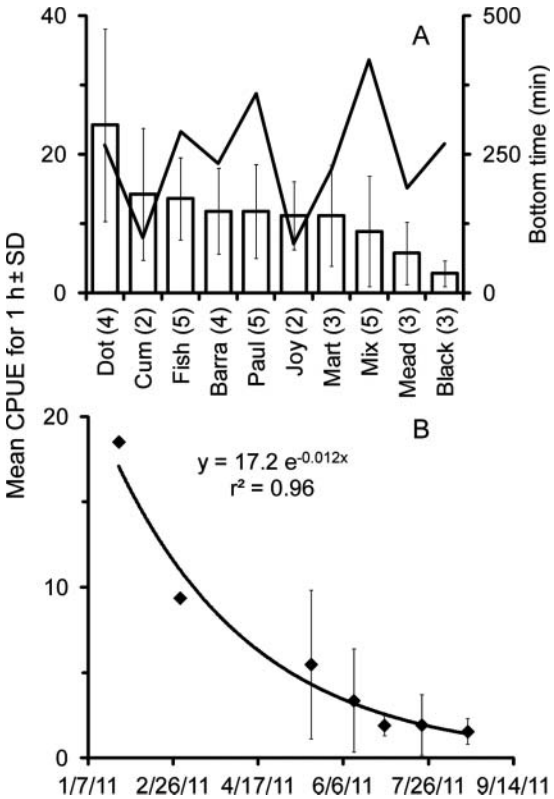

Figure 1 Catch statistics from removals of lionfish: (A) mean CPUE (bars) ± standard deviations (SD) and total bottom time for divers (line) at ten sites and (B) exponential curve fitted to mean CPUE ± SD from seven removals at Blacktip Boulevard (number of groups of divers in parentheses, Dot = Dottie's Hotspot, Cum = Cumber's Caves, Fish = Fisheye Fantasy, Barra = Barracuda Bite, Paul = Paul's Anchors, Joy = Joy's Joy, Mart = Martha's Finyard, Mix = Mixing Bowl, Mead = The Meadows, Black = Black Hole).

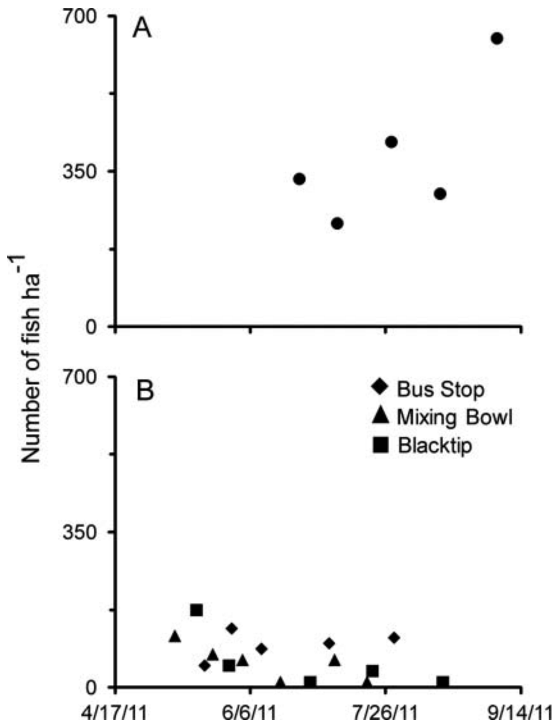

Figure 2 Results from lionfish surveys presented as numbers of lionfish per hectare scaled from the sums of numbers sighted along multiple, 2 × 50 m transects: (A) numbers of lionfish per hectare at Rock Bottom Wall, a control site where fish were not removed, and (B) numbers of lionfish per hectare at sites where fish were removed one to seven times. Lionfish were removed from Bus Stop on 23 February (96 fish); Mixing Bowl on 18 January (32 fish), 17 February (39 fish), and 11 May (44 fish); and Blacktip Boulevard on 1 January (100 fish), 2 March (60 fish), 18 May (44 fish), 12 June (12 fish), 30 June (7 fish), and 18 August (1 fish). Note that surveys began three to four months after initial removals.

standard error of 9.4 ± 0.8 fish h^{-1}. Mean CPUEs generated by initial removals that involved at least two groups of divers were not correlated with total bottom times ($r = -0.555$, $P = 0.879$), nor did they differ significantly among ten sites (Figure 1A; $F_{9,26} = 1.95$, $P = 0.089$). These results indicated that the efficiencies of divers (dive masters and experienced volunteers) were similar at multiple sites and that variation in CPUE reflected variation in the relative abundance of lionfish. Further evidence that variation in CPUE was related to lionfish abundance comes from the observation that CPUE decreased exponentially as repeated removals over a 205-day period successfully reduced the abundance of lionfish at Blacktip Boulevard (Figure 1B).

Standardized surveys, initiated after one or two rounds of removal, confirmed that lionfish densities at Bus Stop, Mixing Bowl, and Blacktip Boulevard were reduced relative to densities at Rock Bottom Wall, a control site where lionfish were not removed (Figures 2A,B). Estimated densities at Rock Bottom Wall ranged from 233 to 650 fish ha^{-1}, with no evidence of a decrease (Figure 2A). In particular, the seven removals at Blacktip Boulevard netted a total of 229 lionfish, and estimated densities fell from 175 fish ha^{-1} to 13 fish ha^{-1} (Figure 2B). In addition, these data indicated that numbers were not replenished during the periods between surveys (12–30 days; Figure 2B). It also is worth noting that removals at Bus Stop and Mixing Bowl were discontinued after only one to three trips (minimum 30-day interval between visits), because lionfish densities (1–8 fish per dive or 12–133 fish ha^{-1}) no longer warranted investment of community resources, and densities remained depressed for ≥ 70 days (Figure 2B).

In addition to reducing the density of lionfish, multiple removals at Blacktip Boulevard also shifted the size frequency distribution of the remaining fish. Across all sites, total lengths of captured lionfish ranged from 65 to 395 mm (Figure 3A), and total lengths of lionfish taken from Blacktip Boulevard on 25 January 2011 ranged from 95 to 375 mm (Figure 3B). The removal on 12 June 2011 yielded a narrower size range of lionfish at Blacktip Boulevard, 140–295 mm total length, with 83% of the fish being smaller than 220 mm total length.

Lionfish that differed in size had different quantities of prey in their guts, and the taxonomic composition of the prey items also differed. The guts of smaller lionfish held less biomass, as shown by a positive correlation between dry weights of gut contents and total lengths of lionfish ($r = 0.314$, $P < 0.001$,

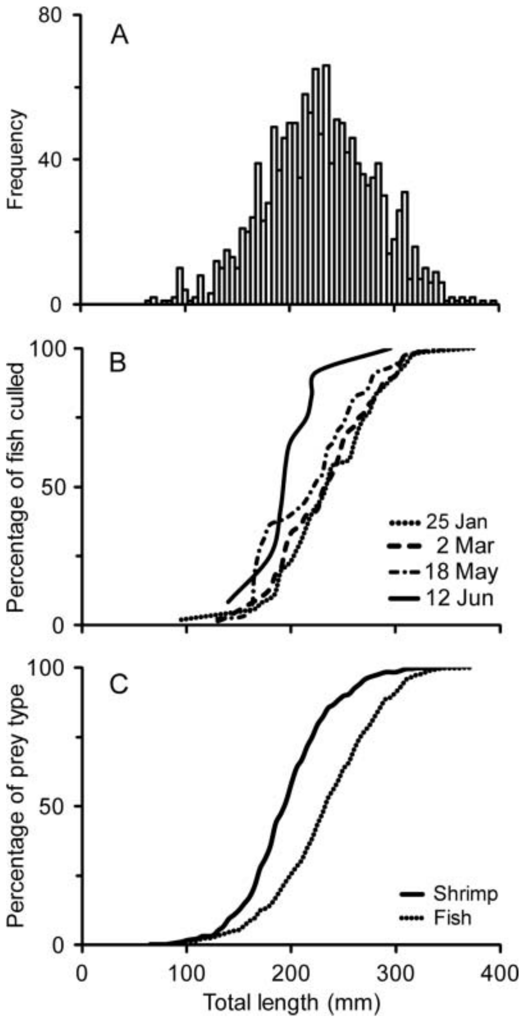

Figure 3 Changes in lionfish sizes and diets due to removals: (A) overall size frequency distribution for 1,407 fish from initial culls at all sites; (B) cumulative size frequency distribution for lionfish captured from Blacktip Boulevard on 25 January ($n = 52$), 2 March ($n = 60$), 18 May ($n = 44$), and 12 June ($n = 12$); and (C) cumulative frequency distribution for occurrences of shrimp and fish in the stomachs of 1,407 lionfish with varying total lengths.

$n = 671$). In addition, smaller lionfish fed primarily on shrimp in the families Gonodactylidae, Palaemonidae, and Rhynchocinetidae rather than fish (Figure 3C).

CONCLUSIONS

Evidence that volunteers can reduce lionfish abundances across multiple sites and evidence that lionfish do not disperse rapidly to fill vacated habitat suggest that targeted removals can be effective as a management strategy to reduce predation by lionfish. Furthermore, a tag and recapture study in Florida indicated that high site fidelity may represent a common behavior for lionfish (Jud and Layman, 2012).

In addition to the benefits arising from reduced abundances, removals shifted predation away from larger prey and reef fishes by reducing numbers of larger lionfish. Here and elsewhere (Morris and Akins, 2009), larger lionfish eat more fish, and smaller lionfish eat more shrimp. Such a shift in predation pressure would likely benefit economically and ecologically important reef fishes, including juveniles of the threatened Nassau grouper and other groupers, along with herbivores such as parrotfishes, surgeonfishes, and damselfishes. The magnitude of indirect effects on economically and ecologically important species through competition for shrimp and other small prey remains to be characterized. In fact, it is suggested that there is an immediate need for long-term studies with adequate replication of treatments (removal sites and controls) to more rigorously assess the ecological outcomes and benefits of sustained lionfish removal efforts.

In contrast to models predicting that lionfish numbers in the region will be controlled only by extremely intensive and sustained fishing mortality (Arias-González et al., 2011; Barbour et al., 2011; Morris et al., 2011a), these initial results strongly suggest that targeted removals represent useful management tools. Focused and repeated removals may be needed to constrain numbers and sizes of lionfish to levels that significantly decrease predation, especially on key species of reef fish, but also on other ecologically important organisms, such as shrimp, that serve as important prey for other predatory species. The required level of effort for consistent control remains to be determined, and it is likely to be affected by medium to long-term movement or recruitment of lionfish, as well as the potential onset of compensatory growth and reproductive effort in response to altered densities and size frequency distributions (Ricker, 1954; Rose et al., 2001; Lorenzen, 2008).

Overall, the story of invasive lionfish highlights a need to change how people deal with exotic organisms (Wittenberg and Cock, 2001). Poorly regulated and managed movement of exotic plants and animals represents an unsustainable approach that generates immediate, undesirable impacts and long-lasting, widespread opportunity costs. Preventing introductions represents the best solution, and it should be based on pervasive education that highlights the dangers of releasing exotic organisms in combination with significantly improved regulation of industries that traffic in such species. As an extremely valuable backup, there is a dire need to improve environmental monitoring so that newly introduced organisms can be detected and eradicated before they become established. Such efforts require well-designed surveillance programs, contingency funds linked to regional pacts that enable rapid responses, and an ability to accept short-term disruption of ecosystems during eradication as a necessary trade-off for long-term benefits. Should such efforts fail, there will be a need for rigorous investigations of costs and benefits associated with maintenance management, such as this study of lionfish removal off Little Cayman Island.

ACKNOWLEDGMENTS

All activities complied with local governmental regulations, and approvals by review boards or ethics committees were not required because removals were organized and performed by local dive masters and volunteers who allowed access to their fish. The authors thank these dedicated volunteers for their efforts. Thanks also go to the Cayman Islands Department of Environment for their support. Comments from M. Hixon and C. Osenberg significantly improved the manuscript.

REFERENCES

Abele, L. G., and W. Kim. *An illustrated guide to the marine decapod crustaceans of Florida.* Tallahassee, Florida: State of Florida (1986).

Aguilar-Perera, A., and A. Tuz-Sulub. Non-native, invasive red lionfish (*Pterois volitans* [Linnaeus 1758]: Scopaenidae), is first recorded in the southern Gulf of Mexico, off the northern Yucatan Peninsula, Mexico. *Aquat. Invasions*, **5 (Suppl. 1):** S9–S12 (2010).

Albins, M. A., and M. A. Hixon. Invasive Indo-Pacific lionfish *Pterois volitans* reduce recruitment of Atlantic coral-reef fishes. *Mar. Ecol. Prog. Ser.*, **367:** 233–238 (2008).

Albins, M. A., and M. A. Hixon. Worst case scenario: Potential long-term effects of invasive predatory lionfish (*Pterois volitans*) on Atlantic and Caribbean coral-reef communities. *Environ. Biol. Fish.*, DOI 10.1007/s10641–011-9795–1 (2011).

Alyokhin, A. Non-natives: put biodiversity at risk. *Nature*, **475:** 36 (2011).

Arias-González, J. E., C. González-Gándara, J. L. Cabrera, and V. Christensen. Predicted impact of the invasive lionfish *Pterois volitans* on the food web of a Caribbean coral reef. *Envir. Res.*, **111:** 917–925 (2011).

Barbour, A. B., M. S. Allen, T. K. Frazer, and K. D. Sherman. Evaluating the potential efficacy of invasive lionfish (*Pterois volitans*) removals. *PLoS One*, **6:** e19666 (2011).

Barbour, A. B., M. L. Montgomery, A. A. Adamson, E. Díaz–Ferguson, and B. R. Silliman. Mangrove use by the invasive lionfish *Pterois volitans*. *Mar. Ecol. Prog. Ser.*, **401:** 291–294 (2010).

Beck, M. W., K. L. Heck Jr., K. W. Able, D. L. Childers, D. B. Eggleston, B. M. Gillanders, B. Halpern, C. G. Hays, K. Hoshino, T. T. Minello, R. J. Orth, P. F. Sheridan, and M. P. Weinstein. The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *BioScience*, **51:** 633–641 (2001).

Betancur-R, R., A. Hines, A. Acero P., G. Ortí, A. E. Wilbur, and D. W. Freshwater. Reconstructing the lionfish invasion: Insights into Greater Caribbean biogeography. *J. Biogeorgr.*, **38:** 1281–1293 (2011).

Biggs, C. R., and J. D. Olden. Multi-scale habitat occupancy of invasive lionfish (*Pterois volitans*) in coral reef environments of Roatan, Honduras. *Aquat. Invasions*, **6:** 347–353 (2011).

Bohlke, J. E., and C. C. G. Chaplin. *Fishes of the Bahamas and adjacent territorial waters.* Austin, Texas**:** University of Texas Press (1993).

Brock, V. E. A preliminary report on a method of estimating reef fish populations. *J. Wildlife Manag.*, **18:** 297–308 (1954).

Burke, L., and J. Maidens. *Reefs at risk in the Caribbean.* Washington, DC**:** World Resources Institute (2004).

Carlton, J. T., and J. B. Geller. Ecological roulette: The global transport of non-indigenous marine organisms. *Science*, **261:** 78–82 (1993).

Chevalier, P. O., E. Gutiérrez, D. Ibarzabal, S. Romero, V. Isla, J. Calderín, and E. Hernández. Primer registro de *Pterois volitans* (Pisces: Scorpaenidae) para aguas cubanas. *Solenodon*, **7:** 37–40 (2008).

Claydon, J. A. B., M. C. Calosso, and S. B. Traiger. Progression of invasive lionfish in seagrass, mangrove and reef habitats. *Mar. Ecol. Prog. Ser.*, **448:** 119–129 (2012).

Côté, I. M., and A. Maljković. Predation rates of Indo-Pacific lionfish on Bahamian coral reefs. *Mar. Ecol. Prog. Ser.*, **404:** 219–225 (2010).

Darling, E. S., S. J. Green, J. K. O'Leary, and I. M. Côté. Indo-Pacific lionfish are larger and more abundant on invaded reefs: A comparison of Kenyan and Bahamian lionfish populations. *Biol. Invasions*, **13:** 2045–2051 (2011).

Davis, M. A., M. K. Chew, J. Hobbs, A. E. Lugo, J. J. Ewel, G. J. Vermeij, J. H. Brown, M. L. Rosenzweig, M. R. Gardener, S. P. Carroll, K. Thompson, S. T. A. Pickett, J. C. Stromberg, P. Del Tredici, K. N. Suding, J. G. Ehrenfeld, J. P. Grime, J. Mascaro, and J. C. Briggs. Don't judge species on their origins. *Nature*, **474:** 153–154 (2011).

Ferguson, T., and L. Akins. *Lionfish cookbook: The Caribbean's new delicacy*. Key Largo, Florida**:** REEF Environmental Education Foundation (2010).

González, J., M. Grijalba-Bendeck, A. Acero P., and R. Betancur-R. The invasive red lionfish, *Pterois volitans* (Linnaeus 1758), in the southwestern Caribbean Sea. *Aquat. Invasions*, **4**: 507–510 (2009).

Green, S. J., J. L. Akins, and I. M. Côté. Foraging behaviour and prey consumption in the Indo-Pacific lionfish on Bahamian coral reefs. *Mar. Ecol. Prog. Ser.*, **433**: 159–167 (2011).

Green, S. J., J. L. Akins, A. Maljković, and I. M. Côté. Invasive lionfish drive Atlantic coral reef fish declines. *PLoS One*, **7**: 332596 (2012).

Green, S. J., and I. M. Côté. Record densities of Indo-Pacific lionfish on Bahamian coral reefs. *Coral Reefs*, **28**: 107 (2009).

Humann, P., and N. DeLoach. *Reef Fish Identification: Florida, Caribbean, Bahamas*. Jacksonville, Florida: New World Publications (2002).

Jud, Z. R., and C. A. Layman. Site fidelity and movement patterns of invasive lionfish, *Pterois* spp., in a Florida estuary. *J. Exp. Mar. Biol. Ecol.*, **414–415**: 69–74 (2012).

Knowlton, N., and J. B. C. Jackson. Shifting baselines, local impacts, and global change on coral reefs. *PLoS One*, **6**: e54 (2008).

Kulbicki, M., J. Beets, P. Chabanet, K. Cure, E. Darling, S. R. Floeter, R. Galzin, A. Green, M. Harmelin-Vivien, M. Hixon, Y. Letourneur, T. Lison de Loma, T. McClanahan, J. McIlwain, G. MouTham, R. Meyers, J. K. O'Leary, S. Planes, L. Vigliola, and L. Wantiez. Distributions of Indo-Pacific lionfishes *Pterois* spp. in their native ranges: Implications for the Atlantic invasion. *Mar. Ecol. Prog. Ser.*, **446**: 189–205 (2012).

Layman, C. A., and J. E. Allgeier. Characterizing trophic ecology of generalist consumers: A case study of the invasive lionfish in The Bahamas. *Mar. Ecol. Prog. Ser.*, **448**: 131–141 (2012).

Lerdau, M., and J. D. Wickham. Non-natives: Four risk factors. *Nature*, **475:** 36–37 (2011).

Lesser, M. P., and M. Slattery. Phase shift to algal dominated communities at mesophotic depths associated with lionfish (*Pterois volitans*) invasion on a Bahamian coral reef. *Biol. Invasions*, **13:** 1855–1868 (2011).

Lockwood, J. L., M. F. Hoopes, and M. P. Marchetti. Non-natives: Plusses of invasion ecology. *Nature*, **475:** 36 (2011).

Lorenzen, K. Fish population regulation beyond "stock and recruitment": The role of density-dependent growth in the recruited stock. *Bull. Mar. Sci.*, **83:** 181–196 (2008).

Maljković, A., T. E. Van Leeuwen, and S. N. Cove. Predation on the invasive red lionfish, *Pterois volitans* (Pisces: Scorpaenidae), by native groupers in the Bahamas. *Coral Reefs*, **27:** 501 (2008).

Martinez, S. FW: Lion fish in lobster traps. In: *GCFINET*. Marathon, Florida: Florida Fish and Wildlife Conservation Commission Marine Research Institute; 8 September 2011, 8 January 2012. Available from http://listserv.gcfi.org/SCRIPTS/WA-GCFI.EXE?A1 = ind1109&L = GCFINET#9 (2011).

McCormick, M. I., and J. H. Choat. Estimating total abundance of a large temperate-reef fish using visual strip-transects. *Mar. Biol.*, **96:** 469–478 (1987).

Morris, J. A. Jr., and J. L. Akins. Feeding ecology of invasive lionfish (*Pterois volitans*) in the Bahamian archipelago. *Environ. Biol. Fish.*, **86:** 389–398 (2009).

Morris, J. A., K. W. Shertzer, and J. A. Rice. A stage-based matrix population model of invasive lionfish with implications for control. *Biol. Invasions*, **13:** 7–12 (2011a).

Morris, J. A. Jr., A. Thomas, A. L. Rhyne, N. Breen, L. Akins, and B. Nash. Nutritional properties of the invasive lionfish: A delicious and nutritious approach for controlling the invasion. *AACL Bioflux*, **4:** 21–26 (2011b).

Morris, J. A. Jr., and P. E. Whitfield. *Biology, ecology, control and management of the invasive Indo-Pacific lionfish: An updated integrated assessment*. NOAA Technical Memorandum NOS NCCOS 99. Washington, DC: United States Department of Commerce (2009).

Mumby, P. J., A. R. Harborne, and D. R. Brumbaugh. Grouper as a natural biocontrol of invasive lionfish. *PLoS One*, **6:** e21510 (2011).

Muñoz, R. C., C. A. Currin, and P. E. Whitfield. Diet of invasive lionfish on hard bottom reefs of the southeast USA: Insights from stomach contents and stable isotopes. *Mar. Ecol. Prog. Ser.*, **432:** 181–193 (2011).

Pimental, D., S. McNair, J. Janecka, J. Wightman, C. Simmonds, C. O'Connell, E. Wong, L. Russel, J. Zern, T. Aquino, and T. Tsomondo. Economic and environmental threats of alien plant, animal, and microbe invasions. *Agr. Ecosyst. Environ.*, **84:** 1–20 (2001).

Ricker, W. E. Stock and recruitment. *J. Fish. Res. Bd. Canada*, **11:** 559–623 (1954).

Rose, K. A., J. H. Cowan, K. O. Winemiller, R. A. Myers, and R. Hilborn. Compensatory density dependence in fish populations: Importance, controversy, understanding and prognosis. *Fish Fish.*, **2:** 293–327 (2001).

Sale, P. F., and W. A. Douglas. Precision and accuracy of visual census techniques for fish assemblages on coral patch reefs. *Environ. Biol. Fish.*, **6:** 333–339 (1981).

Schofield, P. Geographic extent and chronology of the invasion of non-native lionfish (*Pterois volitans* [Linnaeus 1758] and *P. miles* [Bennett 1828]) in the Western North Atlantic and Caribbean Sea. *Aquat. Invasions*, **4:** 473–479 (2009).

Schofield, P. Update on geographic spread of invasive lionfishes (*Pterois volitans* [Linnaeus 1758] and *P. miles* [Bennett 1828]) in the Western North Atlantic Ocean, Caribbean Sea and Gulf of Mexico. *Aquat. Invasions*, **5:** S117–S122 (2010).

Schofield, P. J., J. A. Morris Jr., J. N. Langston, and P. L. Fuller. Pterois volitans/miles. *USGS Nonindigenous Aquatic Species Database, Gainesville, Florida*. Available from http://nas.er.usgs.gov/queries/FactSheet.aspx?SpeciesID = 963 RevisionDate: 9/16/2011 (2011).

Semmens, B. X., E. R. Buhle, A. K. Salomon, and C. V. Pattengill–Semmens. A hotspot of non-native marine fishes: Evidence for the aquarium trade as an invasion pathway. *Mar. Ecol. Prog. Ser.*, **266:** 239–244 (2004).

Simberloff, D. We can eliminate invasions or live with them. Successful management projects. *Biol. Invasions*, **11:** 149–157 (2009).

Simberloff, D., J. Alexander, F. Allendorf, J. Aronson, P. M. Antunes, S. Bacher, R. Bardgett, S. Bertolino, M. Bishop, T. M. Blackburn, A. Blakeslee, D. Blumenthal, A. Bortolus, R. Buckley, Y. Buckley, J. Byers, R. M. Callaway, F. Campbell, K. Campbell, M. Campbell, J. T. Carlton, P. Cassey, J. Catford, L. Celesti-Grapow, J. Chapman, P. Clark, A. Clewell, J. Canning Clode, A. Chang, M. Chytrý, M. Clout, A. Cohen, P. Cowan, R. H. Cowie, A. W. Crall, J. Crooks, M. Deveney, K. Dixon, F. C. Dobbs, D. Cameron Duffy, R. Duncan, P. R. Ehrlich, L. Eldredge, N. Evenhuis, K. D. Fausch, H. Feldhaar, J. Firn, A. Fowler, B. Galil, E. Garcia-Berthou, J. Geller, P. Genovesi, E. Gerber, F. Gherardi, S. Gollasch, D. Gordon, J. Graham, P. Gribben, B. Griffen, E. D. Grosholz, C. Hewitt, J. L. Hierro, P. Hulme, P. Hutchings, V. Jarošík, C. Johnson, L. Johnson, E. L. Johnston, C. G. Jones, R. Keller, C. M. King, B. G. J. Knols, J. Kollmann, T. Kompas, P. M. Kotanen, I. Kowarik, I. Kuhn, S. Kumschick, B. Leung, A. Liebhold, H. MacIsaac, R. Mack, D. G. McCullough, R. McDonald, D. M. Merritt, L. Meyerson, D. Minchin, H. A. Mooney, J. T. Morisette, P. Moyle, H. Müller-Schärer, B. R. Murray, S. Nehring, W. Nelson, W. Nentwig, S. J. Novak, A. Occhipinti, H. Ojaveer, B. Osborne, R. S. Ostfeld, J. Parker, J. Pederson, J. Pergl, M. L. Phillips, P. Pyšek, M. Rejmánek, A. Ricciardi, C. Ricotta, D. Richardson, G. Rilov, E. Ritchie, P. A. Robertson, J. Roman, G. Ruiz, H. Schaefer, B. Schaffelke, K. A. Schierenbeck, D. C. Schmitz, E. Schwindt, J. Seeb, L. D. Smith, G. F. Smith, T. Stohlgren, D. L. Strayer, D. Strong, W. J. Sutherland, T. Therriault, W. Thuiller, M. Torchin, W. van der Putten, M. Vilà, B. Von Holle, I. Wallentinus, D. Wardle, M. Williamson, J. Wilson, M. Winter, L. M. Wolfe, J. Wright, M. Wonham, and C. Zabin. Non-natives: 141 scientists object. *Nature*, **475:** 36 (2011).

Snyder, D. B., and G. H. Burgess. The Indo-Pacific red lionfish, *Pterois volitans* (Pisces: Scorpaenidae), new to Bahamian ichthyofauna. *Coral Reefs*, **26:** 175 (2006).

Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Milello. Human domination of the Earth's ecosystems. *Science*, **277:** 494–499 (1997).

Weis, J. S. Invasion and predation in aquatic ecosystems. *Curr. Zool.*, **57:** 613–624 (2011).

Whitfield, P. E., T. Gardner, S. P. Vives, M. R. Gilligan, W. R. Courtenay Jr., G. C. Ray, and J. A. Hare. Biological invasion of the Indo-Pacific lionfish *Pterois volitans* along the Atlantic coast of North America. *Mar. Ecol. Prog. Ser.*, **235:** 289–297 (2002).

Whitfield, P. E., J. A. Hare, A. W. David, S. L. Harter, R. C. Muñoz, and C. M. Addison. Abundance estimates of the Indo-Pacific lionfish *Pterois volitans/miles* complex in the Western North Atlantic. *Biol. Invasions*, **9:** 53–64 (2007).

Williams, A. B. *Shrimps, lobsters, and crabs of the Atlantic Coast of the eastern United States, Maine to Florida*. Washington, DC: Smithsonian Institution Press (1984).

Wittenberg, R., and M. J. W. Cock. *Invasive alien species: A toolkit of best prevention and management practices*. Wallingford, United Kingdom: CAB International (2001).