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LETTER

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Mobilizing volunteers to sustain local suppression of a global marine invasion

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Abstract

Species invasions often occur at geographic scales that preclude complete eradication, setting up long-term battles for population control. To understand the extent to which exotic species removal by volunteers can contribute to local invasion suppression and alleviate invasion effects, we studied the activities of volunteers culling invasive lion-fish during annual "derby" events in the Atlantic. From 2012 to 2014, single-day derbies reduced lionfish densities by 52% over 192 km² on average each year. Differences in recolonization and productivity between regions meant that annual events were sufficient to suppress the invasion below levels predicted to cause declines in native species in one region, but not the other. Population reduction was not related to catch per unit effort, confirming the importance of in situ monitoring to gauge control effectiveness. Culling by volunteers may be a useful tool in areas where exotic species are easily identified and safely captured, and culling can be promoted as an ongoing recreational activity. Strategically guiding volunteer effort toward sensitive or underserved habitats could aid practitioners in optimizing their use of limited resources for invasion management.

KEYWORDS

citizen science, eradication, exotic species removal, fishing tournament, hunting, lionfish, non-native species, population suppression, *Pterois volitans/miles*, public engagement, volunteer effort

1 | INTRODUCTION

Invasive species continue to drive major changes in biodiversity and ecosystem function globally (Grosholz, 2002; Mooney & Cleland, 2001). The scale of many established invasions precludes complete eradication with available management resources (Parkes & Panetta, 2009; Pluess et al., 2012). This is particularly true for marine invasions that can rapidly achieve broad distributions by dispersal via a pelagic larval phase and reside in geographically isolated/deep habitats that are refuges from removal activity (Drolet, Locke, Lewis, & Davidson, 2014). In these cases, management intervention could focus on alleviating effects to native species in pockets of invaded habitat through intense and ongoing removal activity, with success measured in terms of suppressing the invader below ecologically and economically damaging levels in target areas (Green, Dulvy, & Brooks, 2014; Hulme, 2006). This approach is analogous to providing spatial refuge from fishing mortality for a portion of target species' populations (e.g., marine-protected areas; Mosquera, Côté, Jennings, & Reynolds, 2000), or continuously suppressing pests and weeds on farms below densities that cause unacceptable levels of damage (e.g., Cardinale, Harvey, Gross, & Ives, 2003). Fishing continues at regional scales outside

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protected areas and weedy/pest species persist within agricultural landscapes as a whole. However, in both cases, the intensity of effects is managed locally to produce ecological and economic benefits at these same scales.

A key challenge for implementing this strategy for invasive species is harnessing sufficient human and capital resources to achieve and maintain suppression when complete eradication is not feasible (e.g., Gardener, Atkinson, & Renteria, 2010). Programs that involve volunteers in exotic species removal are increasingly used to foster awareness about the threats invasive species pose, and increase public engagement to address the problem (Crall et al., 2010, 2011; FWCC, 2016; Wenning, 2015). For example, establishing tournaments or derbies in which volunteers earn prizes and notoriety by competing to remove invaders. Such events can engage large numbers of participants in removing exotic organisms (e.g., FWCC, 2016; Malpica-Cruz, Chaves, & Côté, 2016; Rivera-Posada & Pratchett, 2012; Taylor & Edwards, 2005). However, the extent to which such actions can suppress invasive populations and alleviate their negative ecological effects is rarely quantified. Tracking the response of invasive populations-including potential effects of size-selective harvest on population structure (Fenberg & Kaustuv, 2008)and native biodiversity in relation to suppression activities is essential for evaluating and adapting activities to ensure they meet management objectives in the long term.

The invasion of Indo-Pacific lionfish (Pterois volitans/ miles) into Atlantic ecosystems is one that now occurs at a scale precluding complete eradication. First reported off the coast of South Florida in the 1980s, lionfish have rapidly established dense populations across the Caribbean, Gulf of Mexico, and Western Atlantic (Côté, Green, & Hixon, 2013). Lionfish predation is responsible for rapid reductions in native fish populations in several parts of the region, with the magnitude of effect linked to population densities of lionfish and the standing biomass of the native reef fish community (Albins & Hixon, 2008; Benkwitt, 2014; Green, Akins, Maljković, & Côté, 2012). Currently, removal of lionfish by divers and snorkelers, using hand nets or spears, is the main approach used to reduce lionfish numbers. While targeted control can protect and recover the integrity of invaded native communities at local scales (Albins, 2008; Green et al., 2014), the resources for control are substantially exceeded by the scale of the invasion. The broad distribution and depth range of lionfish (USGS, 2015), dispersal via a long pelagic larval phase (Ahrenholz & Morris, 2010), and high fecundity (Morris, Shertzer, & Rice, 2011) means that removal must be sustained over the long term in order to continue suppressing the invasion and its effects.

Lionfish derbies and tournaments were first implemented in 2009 with the intent of increasing public awareness about the invasion, gathering specimens for research, and training volunteers to identify and safely handle the venomous species (Akins, 2012). The increasing number of derbies held across the region presents an excellent opportunity to investigate the extent to which volunteer removal activities during such events can be an effective means of population suppression. Using lionfish derbies as a test case, we address six key questions: (1) What is the total area over which removal can be affected during a derby event? (2) Is capture during derbies size-selective? (3) To what extent are local invader populations suppressed by derby activities? (4) At what rate do lionfish recolonize following derby events? (5) Is removal sufficient to reduce and sustain densities below those predicted to cause predation-mediated declines in native species? (6) Is the magnitude of invader removal related to catch per unit effort (CPUE)?

To answer these questions, we collected landings and participant effort data for lionfish removal derbies held over three years in two regions of the tropical Western Atlantic. Over this same time period, we conducted before-after-controlimpact (BACI) field surveys for lionfish. We then compared the level of population suppression achieved to management targets generated by an ecological model that estimates the densities at which lionfish predation is forecast to cause declines in the standing biomass of their native reef fish prey.

2 | METHODS

2.1 | The derbies

Our study focused on derbies that engaged volunteers in culling invasive lionfish in Green Turtle Cay, Bahamas, and Key Largo, Florida, over a period of three years (2012-2014; Table 1). Lionfish were first reported from the Bahamas in 2004, and densities in the Northern Bahamas began to increase rapidly in 2007 (REEF, 2015; USGS, 2015). In contrast, the invasion was first reported from the Florida Keys in 2009 (USGS, 2015). By the time of our study, lionfish had been sighted in all habitat types found in both study regions (USGS, 2015). Each event consisted of a single day of culling, with volunteer teams (of up to four participants each) locating and removing lionfish from the local marine environment from sunrise until 5 pm on derby day (Table 1; REEF, 2017a). Teams returned to a central derby scoring station where the number and individual sizes (total length [TL] to the nearest 1 mm) of all lionfish collected were recorded. Cash prizes were awarded to the teams that collected the most, biggest, and smallest lionfish with the aim of promoting capture across size classes and increasing the number of winners (REEF, 2017b). All participants used hand nets and/or pole spears, and no other species were permitted to be captured while participating in the derby.

						Average lionfish	Total area	% density (fish/ha)	reduction	% biomass (kg/ha)	reduction
Region	Year	# volunteers	Total catch	CPUE ₁	$CPUE_2$	size (mm g)	fished (km ²)	Target ^a	Achieved ^b	Target ^a	Achieved ^b
Green Turtle Cay, Bahamas	2012	44	771	17.5	0.12	200/95	139	70	67	66	70
	2013	38	1,206	31.7	0.13	194/86	235	57	67	24	72
	2014	49	908	18.5	0.11	163/48	156	35	24	0	55
Key Largo, Florida	2012	33	461	14.1	0.06	194/86	218	41	59	40	60
	2013	83	707	8.5	0.04	219/128	207	22	74	38	76
	2014	59	573	9.7	0.05	263/233	194	7	23	47	11
$CPUE_1 = Catch per unit eff$ $CPUE_2 = fish participant^{-1}$	fort, measured day ⁻¹ km ⁻² .	l as fish participant ⁻¹	day ⁻¹ .								

^bMean change from pre- to postderby levels

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2.2 | Assessing invader populations pre- and post-derby

To determine the margin by which culling reduced lionfish populations during each derby, we surveyed nearshore marine habitats for lionfish before and after each event. We hypothesized that culling effort would decline with increasing distance from the derby scoring station, due to the constraints placed on returning to a central location at the end of the day. We therefore randomly selected 60 survey sites ranging from <1 to >50 km from the central scoring station in each region in order to capture changes in areas that were likely to be culled versus those that were unlikely to be culled during each event ($N_{\text{total}} = 120$; Figure 1; see "Estimating derby fishing effort and area" below). Sites in each region included the range of habitat types including patch coral reefs, artificial structures, shoreline ledges, and seagrass beds at depths of 5–15 ft. Habitat types were homogenous within each region, but differed between the two regions, with Florida sites dominated by patch reefs across the system, and the Bahamas dominated by shoreline ledges (see "Supporting Information A" for a detailed description of our visual survey protocol). We calculated the mean and 95% confidence limits for normally distributed lionfish density and biomass at each survey site prior to and after each derby by summing the abundance and weights, respectively, of lionfish observed at each and dividing by the survey area. We also constructed linear models to examine differences in lionfish body size before and after culling events in each year, body size over time, and recolonization rates between years and treatments for each region using the software R (Zuur, Ieno, Walker, Saveliev, & Smith, 2009).

2.3 | Estimating targets for invader suppression

To evaluate how population density reduction compares to the densities at which lionfish may begin to cause declines in native prey, we parameterized an ecological model that links lionfish densities to the magnitude of their predation effect on reef fishes (Green et al., 2014). This relatively simple approach considers the intrinsic relationship between a fish's size and the rate at which it produces new biomass under a range of environmental temperatures (Banse & Mosher, 1981; Brown et al., 2004) and assumes that variation in the rate of natural mortality from native predators is not a substantial influence on prey production at each reef site compared with added mortality from invasive lionfish (Albins, 2012; Benkwitt, 2014; Supporting Information B). Fish communities in which lionfish are limited at or below modeled density ranges have been shown to resist predation-induced declines (Green et al., 2014, 2015), and the approach is now being tested as a method to generally evaluate

25.4

Latitude (°N)

25.0

24.8

-80.8

-80.6



-75

FIGURE 1 Two regions in the tropical Western Atlantic where we studied invasive lionfish derbies (center panel), with detail on study sites in: KL = Key Largo, Florida (left panel) and GTC = Green Turtle Cay, Bahamas (right panel). Yellow stars represent the landing stations where volunteer fishers returned their catch at the end of each derby event. Dots indicate sites where we censused invasive lionfish before and after each derby from 2012 to 2014. Dot shading indicates the number of derbies (maximum = 3) where at least a portion of participants indicated they had fished in the area

-80

Longitude (°W)

management interventions in several invaded locations (ANSTF, 2015; Chapman, Anderson, Gough, & Harris, 2016; Johnston, Gittings, & Morris, 2015; McCreedy, Toline, & McDonough, 2012).

-80.4

Longitude (°W)

-80.2

-80.0

-85

Inputs into the model include field data gathered at the start of the study in both regions, and rates of temperatureand size-dependent biomass consumption and production for fishes (see "Supporting Information B" for full parameter descriptions). The model incorporates variation in prey fish species composition and density, lionfish body size, and temperature into estimates of consumption and production rates through Monte Carlo simulation (see "Supporting Information B" for model structure and simulation procedures). Model output takes the form of a probabilistic distribution of the density of lionfish at which rates of prey consumption by lionfish exceed rates of biomass production by the reef fishes they consume. To parameterize the model, we gathered field estimates of (1) the size and density of all reef fish under 13 cm TL (the maximum size that is considered feasible for the average-sized gape-limited lionfish to consume [Green et al., 2012]), including juvenile size classes of large bodied fish species, along belt transect surveys at 20 sites randomly selected from the 60 in each study region (see "Supporting Information A" for a detailed description of our visual survey protocol), (2) size distribution of invasive lionfish within the study area (gathered from our lionfish population surveys, described above), and (3) water temperature.

We used the parameterized model to simulate the range of density and biomass values at which lionfish are predicted to deplete the standing biomass of prey in each region. We then compared the distribution of our model output (specifically, values between the first and third quartiles of the distribution) with the mean density and biomass of lionfish observed at the study sites before and after derby events, both within the areas fished during derbies, and in the adjacent reference areas that were not fished (see below for designation of sites as "fished" or "unfished").

-77.6

-77.5

Longitude (°W)

-77.4

-77.3

729

2.4 | Estimating derby fishing effort and area

Each team reported their number of members and the areas over which they searched for lionfish during the event, which were recorded on a local area map. We calculated total area fished during each derby as the area over which one or more teams fished during each tournament, compiled from the maps of fished area completed by each team. We then coded each of our survey sites as either "fished" or "unfished," based on whether they overlapped with the areas identified as lionfish fishing zones by one or more of the teams in each year. We then tabulated the number of derbies in which each site was fished across the three years (Figure 1). Sites that were never visited during a derby acted as a scientific control, against which we could compare changes in lionfish density and biomass at sites that were culled in at least one derby event over the study period. Thus, our estimates of the effect of derbies are likely to be conservative, because some sites included in our "fished" group were not culled in all years.

We also recorded the number and sizes of lionfish collected by each team at the derby landing station. Total catch and CPUE are standard fisheries-dependent metrics for evaluating fishing pressure, and thus, impact on the population over time. If CPUE is positively correlated with the magnitude of density depletion caused by derby fishing, it would provide a simple metric by which to track derby effectiveness without intensive field study across the region. We therefore calculated two measures of CPUE (fish participant⁻¹ day⁻¹ [CPUE₁] and fish participant⁻¹ day⁻¹ km⁻² [CPUE₂]) and total catch for each derby, and related these metrics to the magnitude of density depletion achieved by each event. To do this, we fitted generalized linear models (GLMs) with a binomial distribution for proportional reduction in density using the statistical software R (Zuur et al., 2009). As is the case with similar calculations for commercial fishing activities, our estimates of CPUE assume that fishing effort was distributed evenly across the area in which each team reported fishing.

3 | RESULTS

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Derby participation varied between 33 and 83 individuals per event, divided between a minimum of 9 and maximum of 22 teams per derby. In total, volunteers removed lionfish from an area ranging in size from 139 to 235 km² per derby between 2012 and 2014 (Table 1). As predicted, the majority of removal took place in habitats that were closest to the central derby scoring station, with fishing occurring consistently in the vicinity of the same study sites in consecutive years (Figure 1). The greatest distance from the central meeting point any team ventured to cull lionfish was 46 km in Green Turtle Cay, Bahamas, and 60 km in Key Largo, Florida. Removal activities in both regions captured a range of lionfish sizes, with landed lionfish ranging from 2 to 39 cm TL. The size distribution of lionfish observed at fished and unfished sites did not differ significantly between surveys immediately prior to and following each event, suggesting that culling activities were not significantly size selective (Figures 2E and F; t < -0.25; P > 0.15 for both regions).

The status of the invasion and biomass of native fish populations differed between Florida and the Bahamas at the outset of the study, resulting in large differences in the threshold densities at which lionfish were forecast to cause declines in native prey species in each region (Figures 2A and B). At the start, lionfish densities were an order of magnitude higher on Florida habitats compared with those in the Bahamas (131 \pm 60 and 32 \pm 16 individuals ha⁻¹, respectively; mean \pm SD; Figures 2A and B), and the population was composed of relatively smaller individuals in this higher density region $(61 \pm 37 \text{ and } 128 \pm 52 \text{ g}, \text{ respectively; mean } \pm \text{SD}; \text{ Figures } 2\text{E}$ and F). The standing biomass of prey-sized native fishes (i.e., those under 13 cm TL) was also much higher in Florida $(354 \pm 109 \text{ kg/ha}, \text{ compared with } 100 \pm 88 \text{ kg/ha} \text{ in the}$ Bahamas). As a result, we forecast that lionfish would begin to overconsume native fishes at densities above 10 individuals ha^{-1} (or 1.3 kg/ha, based on average lionfish size in the area) in the Bahamas, but not until 93 individuals ha^{-1} (or 5.7 kg/ha) in Florida (Figures 2A–D). Lionfish densities exceeded levels at which effects on prey biomass are forecast to occur across sites in both regions at the start of the study, with an initial reduction in density of at least 70% in the Bahamas and 41% in Florida required to reduce densities to the lower quartile of densities at which effects may occur (Table 1; Figures 2A and B).

We observed an average reduction of 53% (Bahamas) and 52% (Florida) in lionfish density and biomass at fished sites immediately following each derby between 2012 and 2014 (Table 1). Over time, different patterns of lionfish recolonization, and thus removal success, emerged in the two regions. In particular, lionfish size increased over time in Florida (Figure 2E; mean effect = 15.21 g/year, t = 1.787, P < 0.0001), but decreased in the Bahamas (Figure 2F; mean effect = 16.70 g/year, t = -11.051, P < 0.0001). Lionfish recolonized culled sites following all derbies, but at substantially different rates in the Bahamas and Florida (10 \pm 3 lionfish ha⁻¹ year⁻¹ and 62 \pm 10 lionfish ha⁻¹ year⁻¹, respectively; Figures 2A and B). The total biomass of lionfish remained suppressed at or below predicted levels of predation effect between events in the Bahamas, with densities on average 67% lower by the end of the study compared with the outset (Figures 2B and D). In contrast, the increasing body sizes of lionfish on Florida habitats meant that total biomass of the invader rebounded to nearly preculled levels after each derby (Figure 2C), despite sustained reductions in density between years (Figure 2A). Although lionfish densities on fished sites in Florida were on average 51% lower at the end of the study compared with the outset, lionfish biomass was within the distribution of predicted density at which lionfish begin to deplete prey (Figure 2C).

CPUE varied greatly between derbies, ranging between 8.5 and 31.7 lionfish participant⁻¹ day⁻¹ (CPUE₁; Table 1) or 0.04 to 0.13 lionfish participant⁻¹ day⁻¹ km⁻² (CPUE₂; Table 1). Interestingly, the proportion of lionfish removed at fished sites during derby events was not related to any metric of catch we calculated (total catch, CPUE₁ or CPUE₂; Figures 3A–C; $t_{catch} = 0.326$, $p_{catch} = 0.761$; $t_{CPUE1} = 0.134$, $p_{CPUE1} = 0.899$; $t_{CPUE2} = 0.405$, $p_{CPUE2} = 0.706$). However, CPUE was generally negatively related to the total number of volunteers who participated in the derby in both regions (Table 1).

4 | DISCUSSION

For invasions that are occurring at a scale precluding eradication, managers may instead choose to alleviate invasion effects through ongoing population suppression. Our analysis of removal derbies for invasive lionfish is the first to empirically demonstrate that engaging volunteers in invasive species control can affect and sustain local suppression to a level forecast to alleviate predation effects. Future work that gathers detailed spatial information on participant removal behavior would help to elucidate whether some areas within removal zones are affected to a greater extent than others, as well as correlates of participant removal success. However, such a study would likely require onboard and in-water observation, which may complicate derby activities on small



FIGURE 2 Effect of culling during annual derbies for invasive lionfish in Key Largo, Florida (A, C, E) and Green Turtle Cay, Bahamas (B, D, F). Points represent mean lionfish density (A and B), biomass (C and D), and body mass (E andF) at study sites bounded by 95% confidence intervals. Dashed lines = timing of derby events, light blue triangles = sites culled during at least one derby 2012–2014; dark blue circles = sites never culled during the derbies ($N_{Bahamas fished} = 40$ sites; $N_{Bahamas un-fished} = 20$ sites; $N_{Florida fished} = 32$, $N_{Florida un-fished} = 28$). Red lines = median predicted densities (A and B) and biomasses (C and D) at which lionfish are predicted to cause declines in native prey fishes, bounded by the first and third quartiles of predicted values (light red shading)

vessels. While lionfish were significantly depleted in fished areas immediately following all of the derby events we studied, the frequency needed to sustain suppression below a level predicted to alleviate predation effects differs between regions. Different patterns of lionfish recolonization emerged over time in each region, with lionfish sizes increasing in Florida but decreasing in the Bahamas in both culled and unculled areas. As a result, while annual derbies substantially suppressed lionfish densities in both regions, total lionfish biomass remained above levels at which the invasion is forecast to cause predation effects at fished sites in Florida. Increasing the frequency of derbies (i.e., to twice per year) in Florida may sustain suppression below densities at which predation effects occur. Alternatively, annual events like derbies could be supplemented with culling between events. Our study highlights the importance of bringing environmental monitoring data to bear in planning the timing of culling activities, and the need for coordination between management agencies, volunteer organizations, and marine tourism industries to ensure that culling effort is appropriately dispersed over time and across space.

There are several potential explanations for the difference in initial invader density, recolonization rates, and body sizes over time in the two study regions. First, invasive





FIGURE 3 The relationships between catch per unit effort (CPUE; A and C) and total catch (B and D) with initial lionfish density and reduction in lionfish density (expressed as a proportion) achieved during six lionfish derbies we studied between 2012 and 2014 in Florida and the Bahamas. Dashed lines represent the mean effect, bounded by 95% confidence intervals (gray shading), estimated from generalized linear models of the data

lionfish established in the Bahamas five years earlier than in the Florida Keys, and, as a result, local populations were likely at very different stages in their trajectory of population increase and stabilization. Boom and bust population trends at invasion fronts have been observed in a number of systems, with possible mechanisms including resource depletion, intensifying competition, and disease (e.g., Brown, Keleher, & Shine, 2013; Lovett, Canham, Arthur, Weathers, & Fitzhugh, 2006, and reviewed by Simberloff & Gibbons, 2004). Differences in level of competition for prey and habitat resources resulting from variable predator assemblages in each region could potentially affect population dynamics over time; however, recent studies show no detectable effect of native predator density on lionfish colonization intensity regionally (Hackerott et al., 2013), or habitat use (Raymond, Albins, & Pusack, 2012) and growth rates (Albins, 2012) experimentally. Second, many studies have identified a positive relationship between habitat complexity and fish density (e.g., Alvarez-Filip, Dulvy, Gill, Côté, & Watkinson, 2009; Chittaro, 2004); attributes that differed greatly between the two regions. In particular, nearshore marine habitats near Green Turtle Cay, Bahamas, are dominated by limestone ledges and seagrass meadows dimpled with "blowouts" at the sand–seagrass interface, which provide the majority of structural complexity. The biomass of native prey-sized fishes available to lionfish in these habitats was three times lower than at sites near Key Largo, Florida, where habitats are dominated by relatively high-complexity coral patch reefs and artificial structures.

Interacting effects of invasion stage, resource availability, and boom and bust dynamics of invasive populations could also explain differences in body size trajectories over time. First, differences in the timing of initial invasion could explain differences in average size at the outset of the study, with the relatively younger population of lionfish in the Florida Keys likely composed of a greater proportion of younger and thus smaller size classes (e.g., Edwards, Frazer, & Jacoby, 2014). Increases in body size structure-such as that observed for lionfish in Florida over time-have been observed for other fish invasions following range expansion by larval dispersal (e.g., the round goby; Gutowsky & Fox, 2011). Second, subsequent declines in body size over time at all sites in Bahamas, but increases Florida, could result from different patterns of resource depletion and intraspecific competition between the two regions; effects that have also been seen in other systems (e.g., cane toads in Australia [Brown et al., 2013] and signal crayfish in Europe [Hudina, Hock, Zganec, & Lucic, 2012]). In the absence of culling, the densities at which lionfish may respond numerically to resource depletion, and the timing of response is also likely to differ between regions as a result of resource availability and timing of the invasion.

While our model of lionfish predation identifies a range of densities at which predation effects could occur based on a subset of factors known to affect consumption and production rates, field research and monitoring to evaluate changes in native communities in relation to management interventions are urgently needed to understand the full extent of effects and improve our understanding of the factors that mediate effects. Our results show that tracking both invader body size and density over time and across space is important for understanding recolonization dynamics and the full scale of potential ecological change generated by the invasion. In the case of lionfish, increases in average body size at a given density serve to increase overall predation mortality by increasing total daily food requirements per individual (e.g., Côté & Green, 2012).

There is increasing interest in mobilizing volunteers to remove exotic species as a means to mitigate and reverse invasion effects, from Burmese python hunting "challenges" in Florida (FWCC, 2016), to invasive weed removal "days" in Australia (Sinden et al., 2004), and now invasive lionfish "derbies" across the Western Atlantic (Akins, 2012). We found that even when removal area is accounted for, CPUE was not related to the magnitude of population suppressionsuggesting that collecting removal data alone is not sufficient for tracking effectiveness (e.g., Malpica-Cruz et al., 2016). Variation in volunteer behavior and ability among teams and years may help to explain the lack of relationship between CPUE and removal success. Declining CPUE with increasing volunteer participation may indicate that the number of lionfish to be caught in the local environment is limited, suggesting that increased effort may not result in greater total catch at a derby event. Also, anecdotes from derby participants indicated that at least a few teams had knowledge of structurally complex sites known to be colonized by lionfish (i.e., potential "hot spots") where they focused effort. Thus, future work focused on tracking participant ability, individual effort, and local knowledge about the marine environment could also help to resolve some of the noise surrounding the relationship between catch, effort, and removal success, as well as differences in culling effects within fished regions. Requiring training ahead of the event, such as that conducted before lionfish derbies, may help to increase the quality and quantity of data available. The resources required to independently track removal success through before-after surveys of environmental abundance will also certainly vary between environments and invasions. At a minimum, coupling participant data collection with in situ density surveys prior to culling would allow managers to relate removal effort to environmental density over time.

The success of programs that engage volunteers in local suppression of invasive species will depend on a number of factors including: (1) characteristics of the invader and its populations, (2) the environment in which the invasion takes place, and (3) the availability of personnel to engage in culling. For example, rates of propagule supply and habitat connectivity are likely to vary between invaders (e.g., Lockwood, Cassey, & Blackburn, 2005) and environments (e.g., Sondgerath & Schroder, 2002). These rates, in turn, influence invader population densities and recolonization of culled areas, affecting the magnitude and frequency of removal required; effects likely at play in our study. Volunteers must also be able to reliably distinguish exotic species from native ones during culling activities to minimize the risk of incidental capture and negative effects on native biodiversity. While lionfish possess coloration and morphology that are unique among Atlantic reef fish species, accurate identification may be less reliable for other taxa (e.g., Somaweera, Somaweera, & Shine, 2010) and may vary among volunteers (e.g., Crall et al., 2011). In addition to successfully identifying invaders, volunteers also require the WILFY

means to safely remove them; appropriate tools and training are important elements of volunteer participation in culling for invaders that pose natural defenses (i.e., via bites, stings [e.g., from venomous fin spines in lionfish; Akins, 2012], or attacks). It also may not be practical for volunteers to access all invaded environments (e.g., remote areas or habitats that pose a safety risk). For example, habitats invaded by lionfish that are >30 m depth are unlikely to be safely accessed by volunteers while recreational scuba diving or snorkeling. In remote and inaccessible areas, other approaches to culling involving emerging technologies could aid in locating and removing invaders (e.g., Pitt & Trott, 2013; Rees, Maddison, Middleditch, Patmore, & Gough, 2014). Finally, personnel must be able to volunteer their time and perhaps contribute logistic support for culling activities (e.g., for the derbies we studied volunteers paid for boats, fuel, and culling supplies). For lionfish, volunteer derbies may be most appropriate in regions with relatively small coastal marine zones and large recreational dive communities (e.g., such as areas like the Cayman Islands; Bradley Johnson, personal communication).

Further research on the associated costs and relative benefits of culling by volunteers compared with other management tools, the ability of volunteer culling to suppress local populations' long term, and the response of native species to culling are needed. This research will help determine where volunteer assistance is best applied to reduce invasive species impacts. Field monitoring of both invasive and native populations in relation to removal activities is essential for addressing these needs. A key consideration for managers will also be how to effectively gauge and maintain volunteer interest and participation over time (e.g., Beirne & Lambin, 2013). In areas where culling by volunteers is deemed a viable option, we suggest that resource managers could guide volunteer efforts in at least two strategic ways. First, by encouraging volunteers to engage in culling events in areas that are most sensitive to impacts. In the case of lionfish, these may be areas with high densities of vulnerable native species and life stages (Green & Côté, 2014). Second, managers could guide volunteer efforts toward areas that are not normally culled by other sectors (e.g., resource management staff) to increase the spatial scale of invasion suppression achieved. Ultimately, while population suppression may alleviate local effects from widespread invasions, the resource-intensive nature of these efforts further highlights the urgent need for exotic species policy and practice reform that bolsters prevention, and early detection and rapid response before species become wide spread.

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