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Multiple drivers of invasive lionfish culling efficiency in marine protected areas

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Abstract

Designing effective local management for invasive species poses a major challenge for conservation, yet factors affecting intervention success and efficiency are rarely evaluated and incorporated into practice. We coordinated regional efforts by divers to cull invasive lionfish (*Pterois* spp.) on 33 U.S. Atlantic, Gulf of Mexico, and Caribbean protected coral reefs from 2013 to 2019 and estimated removal efficiency and efficacy as a function of environmental and habitat conditions, invasion status, and personnel expertise. Highly experienced individuals culling during crepuscular periods (<2 hr from sunrise/sunset) are three times more efficient (in terms of minutes) than novice divers during midday, suggesting: (a) retention of experienced individuals is key for efficient programs, and (b) planning culls with personnel and time of day in mind increases the number of sites covered with the same effort. Lionfish behavior and habitat characteristics had little effect on removal efficiency and efficacy, but divers had higher capture success at reefs with higher lionfish densities. We suggest reefs with persistently <20 fish ha^{-1} as low priority, given that impacts to native fauna are unlikely and culling effectiveness declines to <50% below this level. Incorporating efficiency factors in spatial management planning along with density estimates derived from remotely sensed data can ensure limited resources for control are extended across a greater range of invaded habitats.

KEYWORDS

Atlantic, Caribbean, citizen science, conservation planning, functional eradication, Gulf of Mexico, invasive species, marine protected areas, population control, population suppression, protected area management, removal efficacy

1 | INTRODUCTION

Rates of biological invasion and range expansion are increasing with climate change and habitat loss, making invasive species a threat to global biodiversity and a major conservation concern (Mooney & Cleland, 2001). Because of the widespread impacts of many invasive species, particularly in aquatic ecosystems, intervention that involves removal or mitigation activities are a priority within many countries' conservation and natural resource management plans (David et al., 2017; Gallardo, Clavero, Sanchez, & Vila, 2015). Invasive species management is a large economic strain; globally, managers spend over a trillion dollars annually on removal and mitigation efforts (De Poorter, Darby, & MacKay, 2009; Diagne et al., 2021; Larson et al., 2011; Pimentel, Lach, Zuniga, & Morrison, 2000). For many established invaders, eradication is not possible due to their geographic scale, population densities, or the challenges associated with accessing the invaded habitat. In such cases, managers may conduct suppression in priority locations, with the goal of achieving "functional eradication," or sustained reduction of the invader below levels that cause unacceptable changes in the system (Green & Grosholz, 2021). Criteria for identifying priority locations are likely to be numerous and varied depending on local priorities and may include factors such as invasion intensity; the economic, cultural, or ecological value of a location's natural resources (e.g., within protected areas or areas of high tourism value); and the presence and abundance of sensitive species (Baker, 2017; Davidson, Fusaro, & Kashian, 2015; Rohal, Cranney, & Kettenring, 2019). Alongside these criteria, managers must estimate what resources are required to achieve and maintain sufficient suppression at priority locations.

Many factors are likely to affect both removal efficiency (e.g., time, financial, or other resources required per unit intervention) and efficacy (e.g., removal or intervention success per unit effort). For example, habitat and environmental conditions (weather, time of day, remoteness, and season) likely affect access to removal locations. Density and distribution of the invader across its range (Taylor & Hastings, 2004) and the species' body size, behavior, or life-stage likely also affect removal success (Münzbergová, Hadincová, & Kindlmaová, 2013; Pichancourt, Chadès, Firn, van Klinken, & Martin, 2012). If removal requires special skill or gear, training or equipment costs can be high. Finally, for invaders removed by hand with no chemical or automated means, search and handling time are likely to affect efficiency. Previous studies of invasive species removal have primarily examined factors affecting cost and success through modeling and/or in theoretical contexts (e.g., Bonanno, 2016; Jardine & Sanchirico, 2018; Taylor & Hastings, 2004). Amidst growing calls for holistic management plans for invasive species (Larson et al., 2011), factors affecting removal efficiency and efficacy have begun to be evaluated empirically in terrestrial systems (e.g., Mehta et al., 2007; Baker, 2017 [general examples]; Carrion, Donlan, Campbell, Lavoie, & Cruz, 2011; Donlan, Muque, & Wilcox, 2014; Bode, Baker, & Plein, 2015 [island examples]; Hauser & McCarthy, 2009; Epanchin-Niell, Haight, Berec, & Liebhold, 2012 [mainland terrestrial examples]). However, progress has been very limited for marine and aquatic invasive species (but, see Hastings, Hall, & Taylor, 2006 in seagrass), perhaps due to the logistic challenge posed by depth and pressure restrictions when accessing many invaded aquatic habitats.

Here, we focus on the invasive Indo-Pacific red lionfish (*Pterois* spp.) in the Atlantic Ocean, Gulf of Mexico, and Caribbean Sea to examine the efficacy and efficiency of population control activities across multiple jurisdictions in the invaded region. Over the past two decades, lionfish have quickly established as a persistent invader due to many physiological and behavioral traits (Andradi-Brown et al., 2017; Bernal, DeAngelis, Schofield, & Sealey, 2015; Cure, Mcllwain, & Hixon, 2014; Gress et al., 2017; Johnston & Purkis, 2011; Jud, Nichols, & Layman, 2015). In general, it is unknown if lionfish densities are decreasing across the invaded range because few studies have been conducted. However, there have been reports of decline in the Bahamas (Benkwitt et al., 2017), and in 2018, there was a reported decrease in lionfish recruitment of up to 80% after an ulcerative skin disease across the entire northern Gulf of Mexico (Harris, Fogg, Allen, Ahrens, & Patterson, 2020). Despite these regional decreases in populations, lionfish consume a multitude of economically and ecologically important reef fish species (Peake et al., 2018) and pose a major challenge to marine managers (Graham & Fanning, 2017; Mizrahi et al., 2017). This has led to a large effort in most countries of the invaded range to remove lionfish, and currently, efforts by humans are the only way to *ensure* removal and reduction of densities on reefs (Anderson et al., 2013; Graham & Fanning, 2017).

Lionfish are primarily removed with spears and nets by divers while on scuba or snorkeling. However, there has been work in recent years to improve traps (Harris et al., 2020; Pitt & Trott, 2013; Pitt & Trott, 2015) as well as development of underwater robots used to spear and collect lionfish in areas too deep for recreational divers (Andradi-Brown et al., 2017; Sutherland et al., 2017). Additionally, more than 1,000 kg of lionfish are also often caught as bycatch in lobster traps every year (Harris, Fogg, Gittings, et al., 2020). Several studies have documented the effects of culling on lionfish densities and invasion impacts. Green et al. (2014) found that reducing lionfish densities to a predicted threshold (25–92%) increased native fish biomass in the Bahamas. Local depletion of this magnitude by scuba divers is feasible in shallow coastal areas (e.g., Usseglio, Selwyn, Downey-Wall, & Hogan, 2017) and may keep local populations of lionfish from reaching densities that affect native fish communities (Harms-Tuohy, Appeldoorn, & Craig, 2018). Sustained local removal through volunteer lionfish "derbies" can maintain lionfish below levels predicted to cause impacts to native species (Green, Underwood, & Akins, 2017). Taken together, these studies suggest that scuba-based culling activities can be an effective means to suppress lionfish populations locally. However, culling is labor intensive and removal efforts are usually limited to a subset of frequented locations and habitats within recreational diving depths (i.e., most of the culling occurs at easily accessible dive spots), which can lead to lack of reduction in lionfish densities despite culling efforts (Bayraktarov, Alarcón-Moscoso, Polanco, & Wild, 2014; Smith, Green, Akins, Millar, & Côté, 2017). Ultimately, resource managers must direct lionfish culling efforts toward areas that maximize density reduction with available resources (i.e., personnel, time, and funding) for control.

Our goal is to quantify the effort and success of invasive lionfish culling efforts in relation to a suite of environmental and biological characteristics of the invaded system and characteristics of the personnel engaged in culling activities. Specifically, we ask: (1) What factors affect the efficiency (time) and efficacy (likelihood of removing individuals, and proportion of individuals removed per event) of invasive lionfish culling events? and (2) How do capture efficiency and efficacy change

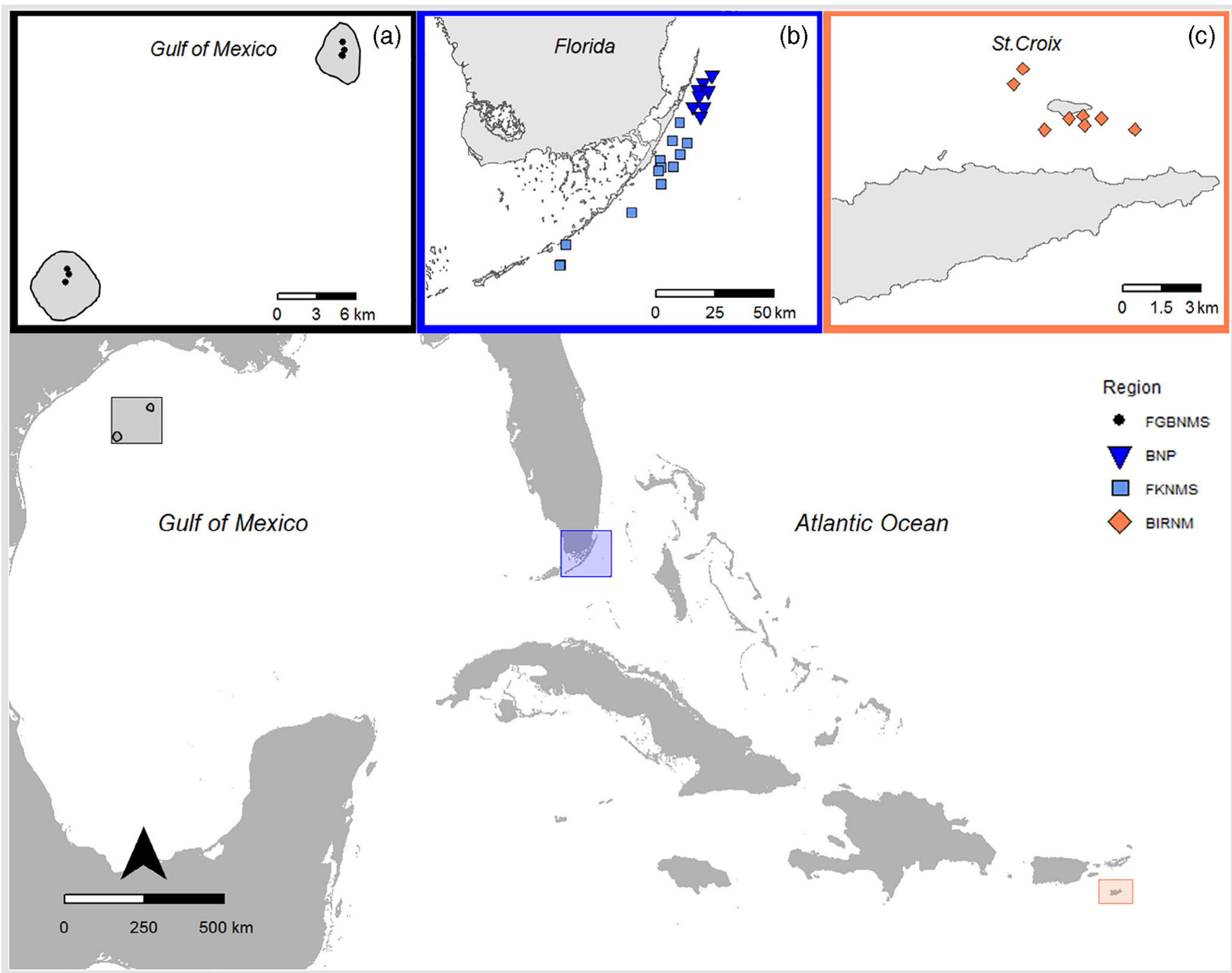

FIGURE 1 Locations of coral reefs where lionfish culling took place for this study in the four marine protected area (MPA) management zones within three regions: (a) Flower Garden Banks National Marine Sanctuary, in the Northwest Gulf of Mexico, United States, (b) Florida Keys National Marine Sanctuary and Biscayne National Park, in South Florida, United States, and (c) Buck Island Reef National Monument, St. Croix, U.S. Virgin Islands

over time during culling programs? The goal of our analysis is to illustrate how key variables affecting invasive species control activities can be incorporated into management planning to increase the efficiency and efficacy of ongoing suppression activities at local priority locations impacted by broadly distributed invaders.

2 | METHODS

2.1 | Study system

We tracked lionfish removal efforts on 33 individual invaded coral reefs in four distinct marine protected area (MPA) management zones within three regions of the Western Atlantic, Gulf of Mexico, and Caribbean from 2013 to 2019 (Figure 1). The Flower Garden Banks National Marine Sanctuary (FGBNMS; $n = 6$ reefs) in the Northwestern Gulf of Mexico, Biscayne National Park (BNP; $n = 7$ reefs) and Florida Keys National Marine Sanctuary (FKNMS; $n = 12$ reefs) in South Florida, and Buck Island Reef National Monument (BIRNM; $n = 8$ reefs) in the U.S. Virgin Islands (USVI). Studying removal at this scale allowed us to examine how regional variation in physical abiotic characteristics, biotic composition, invasion dynamics, and the characteristics of personnel involved in removal influenced the efficacy and efficiency of invader suppression.

Habitat structure and biotic composition varied greatly among and within the four zones (Figure 2). Lionfish removal within FGBNMS took place at seven locations on two continuous reef tracts atop seamounts between 18 and 25 m in depth and approximately 180 km from the coast of Texas and Louisiana,

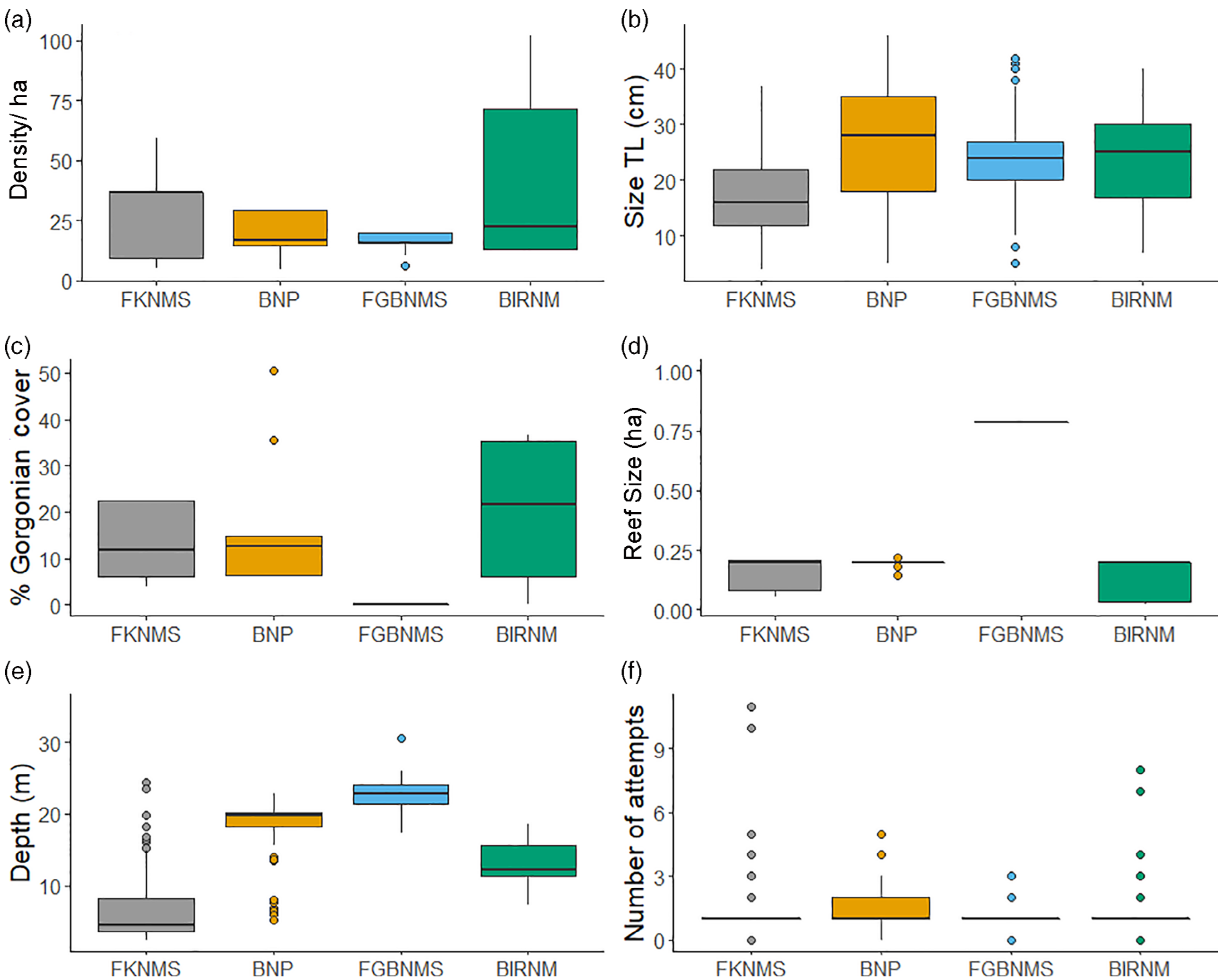

FIGURE 2 Box plots comparing the continuous predictor variables: (a) density ($n = 33$ reefs), (b) size ($n = 867$ fish), (c) gorgonian cover (n = 33 reefs), (d) depth (n = 33 reefs), (e) reef size ($n = 33$ reefs), and (f) number of attempts to spear an individual fish ($n = 867$ fish) between the four management zones

United States (Figures 1a and 2). Sites in FKNMS and BNP included discrete patch reef habitats between 2.5 and 23 m depth and 1 and 2 km from shore, and continuous reef habitats between 9 and 25 m depth and 4 and 5 km from shore along the Florida Reef Tract (Figures 1b and 2). Sites in BIRNM included patch reef habitats at 15–20 m depth, fringing reef habitats at 8–20 m depth, and continuous hard bottom areas ranging from 15 to 25 m depth (Figures 1c and 2). The area for patch reefs was calculated to be the total size of the reef. For fringing and continuous reefs in Florida and the USVI the survey site was standardized to two transects each 20 m × 50 m, and the area for the FGBNMS sites was a circle with a 50 m radius.

2.2 | Tracking invader removal

Scuba divers in all regions carried out lionfish monitoring and removal using standardized protocols but at varying frequencies: sites in FKNMS and BNP were monitored multiple times per year from 2013 to 2016 (up to 18 visits/site total), sites in BIRNM were monitored approximately four times per year from 2013 to 2016 (up to six visits/site total), and sites in FGBNMS were monitored twice per year from 2016 to 2019 (six visits/site total). During each visit, two pairs of divers worked independently to conduct a systematic search for lionfish within a defined survey area at each site following the protocols of Green (2012). Specifically, on continuous reef sites divers surveyed and removed lionfish along two 50 × 20 m transects laid parallel to the reef crest, conducting a roving S-shaped search pattern within 10 m of either side of the transect line (Green, 2012). At patch reef sites, divers laid out one transect line along the longest axis of the reef, spaced to divide the reef into two areas of equal width, with surveyors searching for lionfish in an S-shaped roving pattern between the reef edge and transect line (Green, 2012). On patch reefs, survey length and width varied from 18 m × 12 m to 49 m × 25 m per site depending on patch reef size. During surveys, one diver from each pair attempted to remove all lionfish sighted using a spear, while the second diver recorded data on lionfish location and position on the reef, size, behavior, and the removal effort of their dive partner, including number of attempts at capture, the time spent in removal efforts per fish, and whether the fish was caught (Table 1; invasion characteristics).

2.3 | Personnel characteristics

Removals were conducted by a range of volunteer divers, non-profit staff and interns, and natural resource management agency staff and interns coordinated by local partners in each zone. Data on diver experience including dive certification level, number of dives prior to volunteering, and number of lionfish captured prior to the project were used to determine if volunteer experience affected capture efficiency. These metrics were amalgamated into one experience variable rated as "High" (individuals with rescue diver certification equivalent or higher, extensive lionfish removal experience, and 300 + dives) "Medium" (combinations of high remover experience but low dive experience [e.g., removed 100 lionfish but only has 50 logged dives], high dive experience and low removal experience [e.g., has 300 + logged dives but no removal experience]), "Low" (certifications below rescue diver, little to no prior lionfish removal experience, and fewer than 300 dives), or "None" (no experience removing lionfish and fewer than 50 dives; Table 1; removal characteristics).

2.4 | Habitat and environmental conditions

We evaluated several characteristics of the physical habitat and environmental conditions predicted to influence efficiency and efficacy of culling activities by scuba divers. Habitat variables including depth (m), average vertical relief (cm), and live substrate coral and gorgonian cover (%) were measured at each site. Average vertical relief per site was calculated by taking the mean of measurements made every 2 m along two transect lines laid out at each site. At the continuous reef sites, transects were 50 m in length, while on patch reef sites transect length varied from 18 to 49 m depending on patch size (n = 18–140 measures per site depending on transect length and number). Relief at each point was measured as the difference in height (to the nearest 1 cm) between the highest and lowest points of hard reef structure within a 0.5 m radius around the central point on the transect line. Live coral and gorgonian cover at each site were calculated from photo quadrats of the benthos taken at the same frequency as relief measurements along the same transect lines, with each quadrat covering an area of 1 m^2. Images were imported into the software CPCe (Coral Point Count with Excel extensions) and overlaid with 25 random points at which benthic habitat type (e.g., live coral) was assessed. Percent live coral cover per site was calculated as the proportion of points containing live coral divided by the total number of points analyzed across all photos of each site, multiplied by 100. Depth (to the nearest 0.1 m) was measured at the start of each transect line per visit using a dive computer as part of survey metadata, and the average computed

TABLE 1 Variables related to invasion, habitat, removal, and environment characteristics, and their hypothesized effect on lionfish removal efficiency (reduced time) and efficacy (proportion removed and likelihood of removal)

Variable	Hypothesis	Description/units
Invasion characteristics (lionfish):		
Lionfish density	Higher densities of lionfish will increase removal efficiency (type II functional response). Variance in proportion removed may decrease with higher densities (i.e., at low densities have either 0 or 1)	#/ha
Lionfish size	Increased lionfish body size will increase efficiency and efficacy due to larger bodies creating larger targets	Total length, cm
Lionfish position of reef	Position may have no effect, however sheltered lionfish may increase search time, but may also increase proportion removed by being an easier target with a spear	Sheltered or exposed
Lionfish behavior	Behavior may have no effect, however fish that are active may be easier to identify, and resting fish may be easier to spear (increase efficiency)	Active or resting
Removal characteristics (gear and personnel):		
Number of attempts	The number of attempts to capture each lionfish will reduce efficiency and efficacy by increasing time spent on an individual fish	# of discrete attempts per fish
Volunteer experience	Efficiency and efficacy will increase will increased volunteer experience	None, low, med, high
Habitat characteristics (reef):		
Vertical relief	Higher vertical relief will decrease efficiency and efficacy in removing lionfish due to physical complexity providing increased habitat (refuge)	cm
% Coral cover	Coral cover may have no effect, but may decrease efficiency and efficacy by adding to the physical complexity of the reef	$\%/m^2$
% Gorgonian cover	Soft corals will reduce efficacy and efficiency by interfering with removal efforts by reducing visibility and creating physical obstacles	$\%/m^2$
Depth	Increasing depth will decrease efficiency and efficacy due to time (air) restrictions	m
Reef size	Increasing reef size will reduce efficiency and efficacy due to time (air) restrictions	ha
Environmental characteristics (conditions):		
Time of day	Efficiency and efficacy will both increase during crepuscular hours, versus mid-day hours due to lionfish being more active at this time	Crepuscular (±2 hr before and after sunset and sunrise)

Note: Data on each variable was collected from 33 sites in four invaded regions of the Caribbean from 2013-2019. Italicized variables (vertical relief and coral cover) were eventually excluded from our model analyses due to high collinearity with reef size.

across all visits to obtain a value per site. Vertical relief, coral cover, and gorgonian cover were only measured during one of the visits at each site, as they were unlikely to change during the study period. Time of day was recorded for every survey by divers and was subsequently divided into crepuscular hours (± 2 hr before and after sunset and sunrise) and mid-day hours for analysis (Table 1; habitat and environmental characteristics).

2.5 | Statistical analyses

All statistical analyses were run using *R* version 3.5.3 (R Core Team, 2013). We evaluated change over the duration of the study in average time spent attempting removal for each lionfish (seconds), proportion of lionfish caught, density of lionfish, and lionfish size during dives in each region using a repeated measures ANOVA

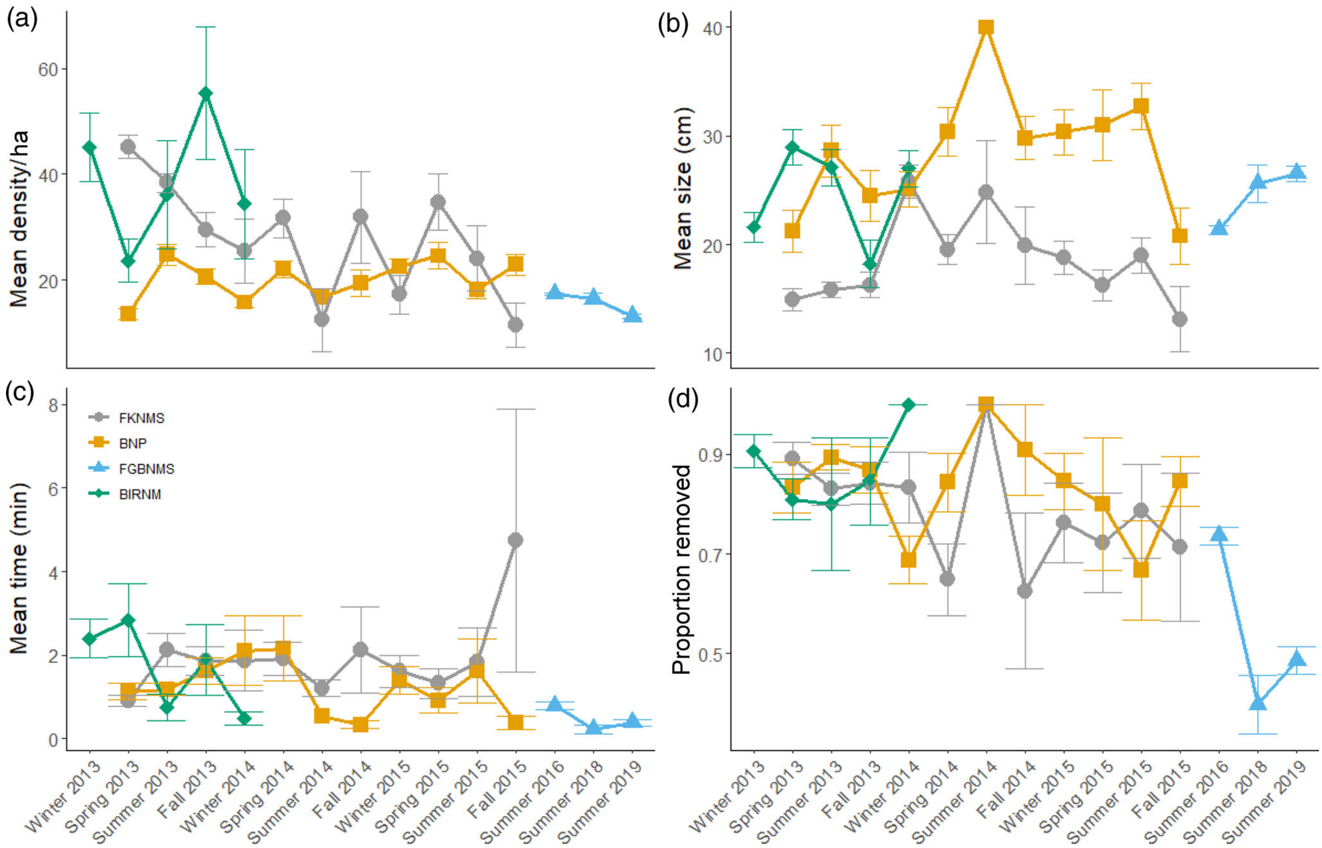

FIGURE 3 Time series of (a) mean lionfish density, (b) mean lionfish body size, (c) mean time to remove invasive lionfish, and (d) proportion of lionfish removed from coral reefs in four U.S. Caribbean marine protected areas. Line colour represents the individual management zones. Points represent means bounded by standard error. The data point for BNP Summer 2014 represents one fish and has no error bars

(rstatix package) to account for any temporal autocorrelation. We then used multiple comparisons pairwise Tukey HSD post hoc tests to evaluate change in removal efficacy and lionfish demographics over time. We also compared these metrics between regions using ANOVA and Tukey HSD post hoc pairwise tests.

To evaluate our hypotheses (Table 1) about the effects of variables describing habitat, environment, invasion characteristics and remover characteristics on the efficacy and efficiency of invasive lionfish removal we constructed generalized linear mixed effects models (GLMMs). Specifically, we modeled three response variables: the probability of each lionfish being captured (0/1 binary), total proportion of lionfish removed (0—1 continuous), and time (seconds) spent attempting to capture each lionfish (0—infinity, continuous) during a site visit. We used a binomial (link = logit) distribution for likelihood of removal, an exponential (family = gamma, link = log, dispersion = 1) distribution for time, and a beta distribution (link = logit) for the proportion removed. All GLMMs were created using the lme4 (for likelihood and time) and glmmTMB (for proportion) statistical packages (Bates, Maechler, Bolker, & Walker, 2014; Brooks et al., 2017). We also included an interaction between lionfish size and position on the reef in the models to test if larger lionfish sheltering in the reef might be more visible to personnel, and thus more likely to be removed in less time, than small individuals. Lionfish density, coral cover, and reef area were scaled to match the range of the other continuous predictor variables. Site ID (33 levels) and management zone (4 levels) acted as random variables in each model. We evaluated collinearity among our predictor variables in the global model for each response variable using the VIF function in the car package for *R* (Fox & Weisberg, 2019). A VIF value greater than 5 indicates potentially severe correlation between predictor variables (Petrie, 2016). Any variables that were collinear were assessed and removed from the model. Coral cover, vertical relief, and site area were all highly correlated (r = .75–.8). To identify which variable to keep in the global model for each response variable, Akaike Information Criterion (AICc) between models with just vertical relief or site area or coral cover were compared. The models with site area were kept due to an AICc that was six

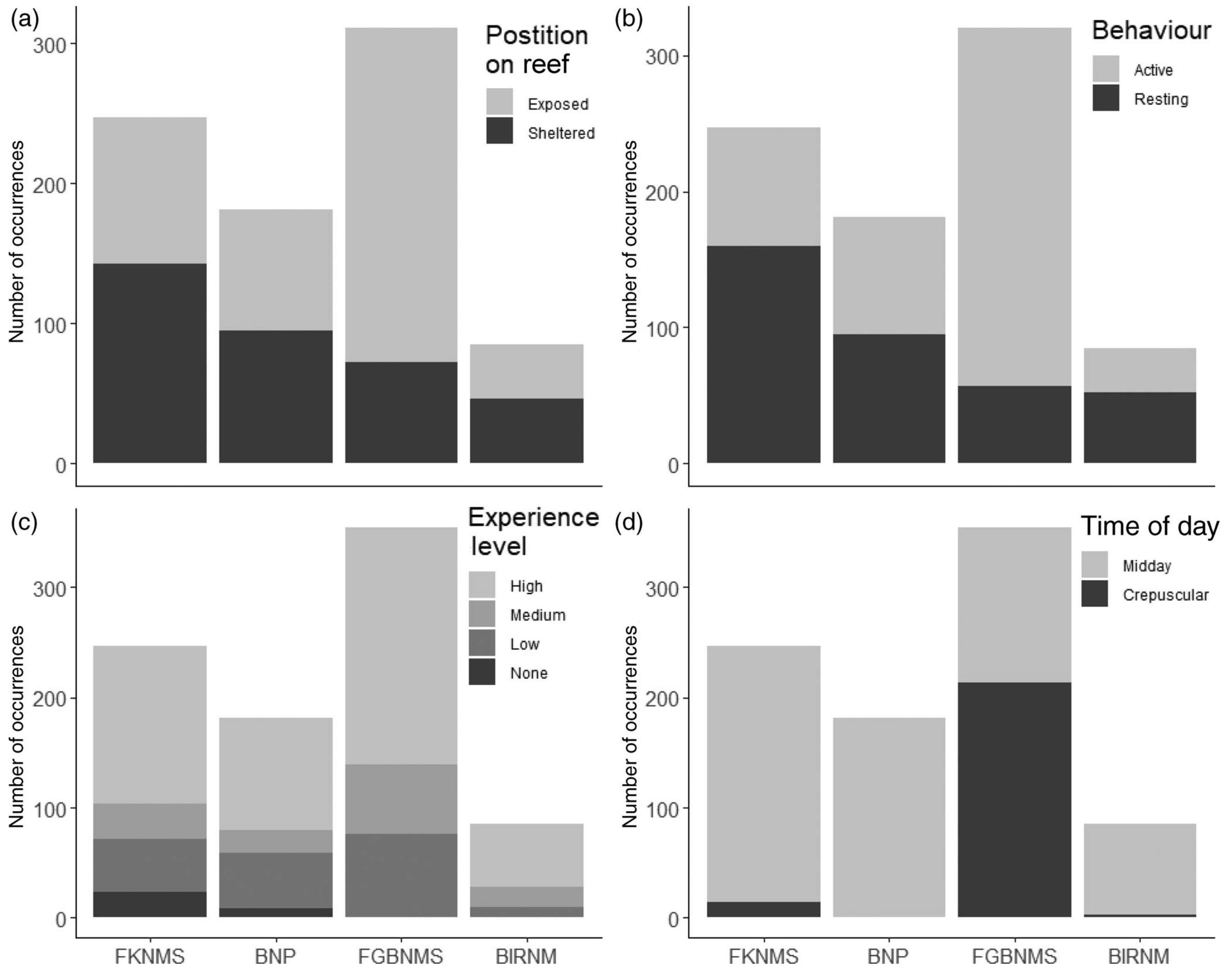

FIGURE 4 Difference in the frequency of (a) lionfish position on the reef, (b) behavior of the lionfish, (c) experience level of the remover, and (d) time of day at which removal was conducted (all categorical variables) between the four management zones

below that of the other models. The global model for each response variable (i.e., containing all predictors) was assessed using QQ plots and examining the distribution of the residuals.

We then ran the global model for each response variable (likelihood of removal, time [seconds] spent attempting to remove each fish, and proportion of fish removed) through an automated model selection tool, "dredge," in the *R* package MuMIn (v1.43.15). This process iteratively runs and compares models containing all combinations of the predictor variables for the given response variable using AICc, with the top model set (i.e., combinations of predictor variables) being those with the lowest AICc and with <4 delta AICc between them. Average parameter estimates are these calculated for each for predictor variable appearing among in the top models for a given response variable; this "natural average" method (Burnham & Anderson, 2002; Grueber, Nakagawa, Laws, & Jamieson, 2011; Green & Côté, 2014) only averages variables across models in which they appear, eliminating bias in model selection toward parameters of interest. Model average parameter estimates were used to create predictions to illustrate how the change in predictor variables affected the response variable (proportion removed, time for removal, or likelihood of capture) across values seen in the study.

3 | RESULTS

3.1 | General trends in lionfish invasion characteristics

Lionfish densities and body sizes varied within and between all four management zones (Figure 2a,b) and over time (Figure 3a,b), with surveyors reporting an average of 23.75 ± 0.59 lionfish ha^{-1} (range: 5–102 lionfish ha^{-1}) across all site visits for the study. Though variable through time, and for a shorter period, reefs in BIRNM had the highest average and maximum densities at 39.16 ± 53.74 fish ha^{-1} (mean ± *SD*) and 102 fish ha^{-1}, respectively (Figures 2a and 3a) and was statistically higher than both BNP and FKBNMS (ANOVA and Tukey HSD $p = .003$ and .004 respectively). Lionfish densities were significantly lower at the final survey in FKNMS and FGBNMS compared with the first survey in each region (repeated measure ANOVA and Tukey HSD post hoc test, $p < .001$; Figure 3a). Lionfish densities neither increased nor decreased by the end of the study period in the BIRNM, and densities were higher in BNP compared to at the start of the study (repeated measure ANOVA and Tukey HSD post hoc test $p = .399$ and .018, respectively; Figure 3a). The average size of lionfish sighted across all regions was 22.4 ± 8.7 cm total length (TL; mean ± *SD*), with the largest fish found in BNP (average 27.2 cm ± 10.13 cm TL, and maximum of 40 cm TL; Figures 2b and 3b). However, the average size in BNP was only statistically higher than in FKNMS (ANOVA and Tukey HSD $p < .001$). The average size of lionfish sighted also varied through time, with trends differing in each management zone (Figure 3b). In FKNMS and BNP (where the longest time series were available) average lionfish size increased initially and declined over time in both zones. This increase in size followed by a decrease was significant in FKNMS ($p < .001$) and non-significant in BNP ($p = .95$) and the average size of fish at the end of the study was the same as at the beginning in both places ($p = .06$ and .95, respectively).

Lionfish position on the reef and behavior during the removal also varied between management zones (Figure 4a,b). A higher proportion of lionfish observed in FGBNMS were exposed on the reef (77%) and active (82%) than in the other three management zones. In the other three management zones lionfish were sheltered and resting for over 50% of the occurrences (i.e., observations).

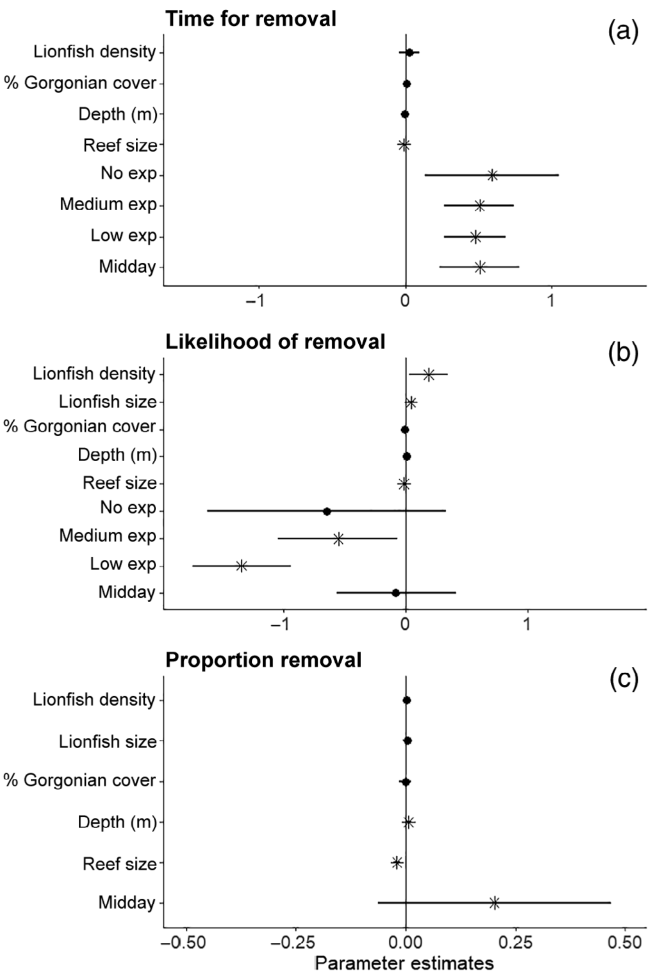

FIGURE 5 Parameter estimates for standardize covariates (averaged from top models where Δ AIC < 4) for (a) time spent attempting removal for individual lionfish, (b) likelihood of removal for each fish, and (c) proportion of lionfish removed during a site visit from 56 sites in four zones of the study area. Positive values (to the right of the vertical line) indicate that variable increases the time spent, likelihood of removal, or proportion removed, respectively. Negative values (to the left of the vertical line) indicate that variable decreases the time spent, likelihood of removal, or proportion removed, respectively. All points are bounded by a 95% confidence interval and are only significant (indicated by a *) if they do not cross the vertical line. Variables are grouped by status of the invasion, habitat, removal characteristics, and environment characteristics

3.2 | Variation in removal site condition, remover experience, and time of day

The reef sites examined in this study varied greatly in biotic composition and structure (Figure 2c; 2d; 0–50% gorgonian cover, and 0.021–0.785 ha in size), and environmental condition (Figure 2e; depths from 2.4 to 30.3 m) both within and between the four jurisdictions. The average number of attempts per lionfish was 1.27, and there was no difference in the average number of attempts at capturing lionfish when they were encountered between the regions (Figure 2f) except in the FGBNMS where it was slightly lower (1.13 attempts, ANOVA and Tukey HSD post hoc test $p = .04$). Diver experience ranged from 18 to 10,000 dives and 0 to 2,000 lionfish removed prior to the project. More than half of participants (58%) fell into the “high” experience category, while only 6% of participants fit into the category of “none,” with no lionfish removal experience (Figure 4c). While 27% of individuals in the “Low” and “No” categories had not collected any lionfish prior to the study, this group still had an average of 197 dives prior to the project, far beyond the minimum number of dives required for open water certification. Most removals took place during midday hours (637) compared to crepuscular

TABLE 2 Top models for time spent in removal, likelihood of capture, and proportion of lionfish removed describing lionfish removal efficacy and efficiency for the study area

Model	Parameters in top ranked models	*df*	AICc	ΔAIC	Weight
Time					
1	**Experience** + **site area** + **time of day**	9	1857.24	0.00	0.24
2	**Experience** + depth + **site area** + **time of day**	10	1858.57	1.34	0.12
3	Gorgonian + **experience** + **site area** + **time of day**	10	1858.84	1.60	0.11
4	**Experience** + **site area** + density + **time of day**	10	1859.02	2.03	0.10
5	**Experience** + **site area** + lionfish size + **time of day**	10	1859.27	2.77	0.09
Likelihood					
1	**Experience** + depth + **site area** + **lionfish size** + **density**	10	858.25	0.00	0.27
2	**Experience** + **site area** + **lionfish size** + **density**	9	858.81	0.56	0.20
3	**Experience** + depth + **site area** + **lionfish size** + **density** + time of day	11	860.21	1.95	0.10
4	Gorgonian + **experience** + depth + **site area** + **lionfish size** + **density**	11	860.30	2.04	0.10
5	Gorgonian + **experience** + **site area** + **lionfish size** + time of day	10	860.73	2.48	0.08
Proportion removed					
1	**Depth** + **site area** + **density**	7	−5,595.42	0.00	0.21
2	**Depth** + **site area** + **density** + time of day	8	−5,595.40	0.03	0.21
3	**Depth** + **site area** + **density** + lionfish size + time of day	9	−5,594.28	1.14	0.12
4	**Depth** + **site area** + **density** + lionfish size	8	−5,594.22	1.20	0.11
5	Gorgonian + **depth** + **site area** + **density**	8	−5,593.39	2.03	0.08

Note: AIC, *df*, and the weight of top models are presented along with the parameters used in the model. Bolded variables were significant in the model.

hours (230), except in FGBNMS where approximately two thirds of the removals were done in crepuscular hours (Figure 4d).

3.3 | General trends in removal efficacy and efficiency

Removing data points with missing variables yielded a total of 867 removal attempts during the study. The amount of time spent attempting to remove each lionfish, and the proportion of lionfish removed during a site visit varied over time and among regions (Figure 3c,d). The mean time spent attempting removal time for each lionfish across all sites was 1.35 min; however, the median removal time was less than a minute (Figure 3c). On average, 75% of lionfish sighted were removed across all sites in all management areas (Figure 3d). The highest mean proportion of lionfish removed per site visit was from BIRNM (0.87 ± 0.24; mean ± *SD*) and the lowest from FGBNMS (0.65 ± 0.30; mean ± *SD*). Removal time was highest in FKNMS and BIRNM with a mean of 2.03 min per capture attempt, and lowest in FGBNMS with 0.64 min. The longest time per fish was 27 min in BNP. The mean time spent attempting to capture lionfish decreased significantly over time in FGBNMS (0.78 min at the start and 0.33 min in the final period; Figure 3c, repeated measure ANOVA and Tukey HSD post hoc test $p = .006$). While variable between study periods, the time spent removing lionfish showed no significant trend over time in the other three zones (repeated measure ANOVA and Tukey HSD post hoc test $p = .15$, .12, and .59).

3.4 | Drivers of removal efficacy and efficiency

The top models predicting likelihood of capture for each lionfish, time spent attempting capture for each fish, and proportion of lionfish removed during each site visit all contained lionfish density, % gorgonian cover, depth, reef size, and time of day (Figure 5; Table 2). Reef size was significant in top models for all three response variables (Figure 5). For example, it decreased the proportion

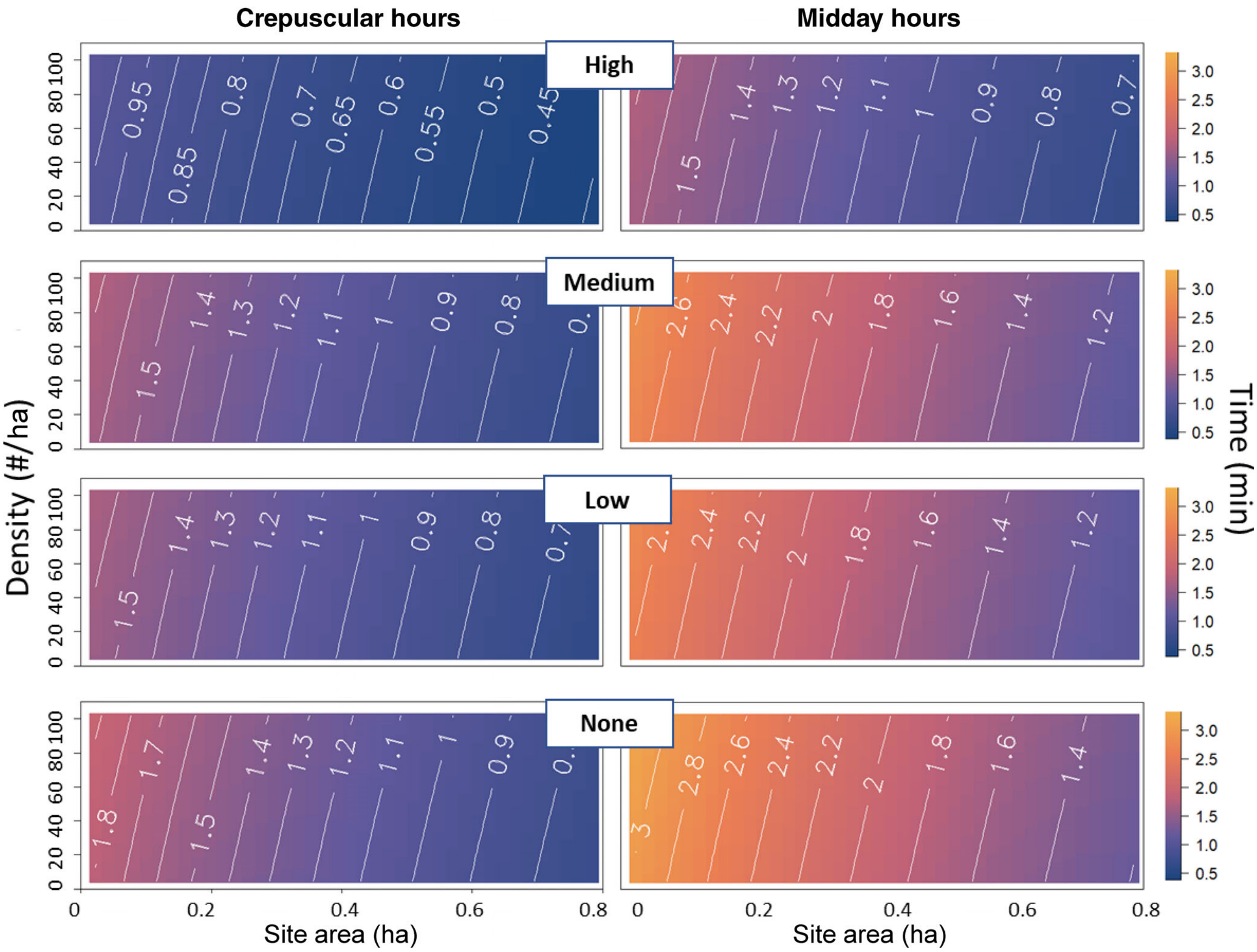

FIGURE 6 Heat plot showing the predicted amount of time to remove an individual lionfish during midday and crepuscular hours for all experience levels (high, medium, low, and none) across all site area and lionfish density combinations. All other variables from the model are held constant at their mean

removed by 2% for every 1,000 m^2 increase in reef size, but it also decreased the time for removal by 15 seconds/fish.

Time of day and remover experience had a significant effect on the amount of time spent attempting to capture individual fish across all regions, with removers taking 1 min more per fish during midday site visits compared with crepuscular visits (Figures 5a and 6). Removers with medium, low, or no experience all spent significantly more time attempting to capture individual lionfish (0.5–1.3 min/fish) when compared to those with "High" experience (Figures 5a and 6; Table 2).

The density of lionfish observed during a site visit significantly increased the likelihood of catching individual lionfish during the dive by 2% for every fish/ha increase (Figure 5b). Lionfish size also increased the likelihood of capture, and with every cm increase in size (TL) the likelihood of capture increased by 5% (Figure 5b). Removers with low and medium experience were significantly less likely to catch individual fish compared with those in the High experience group (Figure 5b). In general, individuals with No experience tended to be less likely to capture individual lionfish than those with High experience, though this effect was highly variable (Figure 5b).

The proportion of fish removed during each site visit was positively influenced by lionfish density and site depth, increasing the proportion removed by 0.3% and 0.02% respectively per unit increase. (Figure 5c). Lionfish behavior (active or resting) and position on the reef (sheltered or not), and number of capture attempts had no significant effect on capture efficacy or efficiency across the three regions and did not appear in any of the top models.

Predictions on the scale of the response show that there is an average of 1 min difference between the time spent attempting to catch an individual fish between crepuscular and midday surveys, holding all other variables at their mean. However, this difference is not equal across experience classes (Figure 6). The difference in time spent attempting removal for each fish between midday and crepuscular decreased the more experienced divers were divers in the none, low, and medium categories were comparably efficient during crepuscular culls as High experience divers during midday culls (Figure 6; Figure S1).

4 | DISCUSSION

Lionfish culling is now a regular activity occurring in most jurisdictions across the invaded range by natural resource management agencies, dive operators, non-profit organizations, and private citizen groups (Alemu, 2016; Malpica-Cruz et al., 2016; Pearson, 2019). There is growing interest in directing culling activities to effectively suppress lionfish populations (Bogdanoff et al., 2020; Chapman, Green, Solomon, Bogdanoff, & Fruitman, 2019; Green et al., 2017), necessitating estimates of factors affecting lionfish removal efficacy and efficiency. Our study is the first to quantify factors affecting the efficiency and efficacy of divers engaged in lionfish culling over multiple years and in four invaded regions. Of the 10 factors we examined, site-specific lionfish densities and body sizes, reef size, remover experience, and the time of day during which culling took place had the largest effects on removal efficiency across all study regions. The success of culling activities varied little on reef sites varying greatly in biotic composition and structural complexity (range of gorgonian cover (0–50%) and complexity values (0.2–4 m relief, 0–95% coral cover). Culling efficiency (proportion removed and likelihood of catching each fish) generally decreased as the size of the site increased (in this study, ranging from 0.02 to 0.78 ha), while time spent attempting to cull each fish declined as reef area increased. It is possible that information on the size of the site divers were meant to cover during their limited bottom time during each dive altered their removal behavior, perhaps making them more willing to “give up” on fish that were not quickly captured to move on to new parts of the reef, thus decreasing average time spent attempting removal and decreasing likelihood of capture and proportion removed. Further studies of diver behavior would be needed to test this potential effect on removal decision making. However, counter to our expectations, the proportion of lionfish culled during a dive increased with the depth of the site (in this study, ranging from 2.4 to 30.3 m), suggesting that restrictions on dive time at depth alone do not influence culling success.

We found that the time of day culling took place significantly influenced the time divers spent attempting to catch lionfish, but not the likelihood of capture. On average, divers spent 1 min longer attempting capture on dives conducted during midday (i.e., >2 hr from sunrise or sunset) compared with crepuscular dives. Lionfish exhibit strong daily patterns of behavior, most actively foraging during crepuscular dawn and dusk periods, and sheltering within habitats during the middle of the day (Benkwitt, 2016; Green, Akins, & Côté, 2011). Our results support the notion that lionfish are likely easier to locate during these near-crepuscular periods, though studies in other habitat types (i.e., hard bottom ledges and artificial reefs in the Gulf of Mexico) surveying lionfish using methods including diver surveys and remotely operated vehicles (which have a lower detection rate for the species overall) did not detect an effect of time of day on detectability (Harris, Patterson, Ahrens, & Allen, 2019).

Experience with scuba diving and capturing lionfish prior to this project also significantly affected the time divers spent attempting removal and the likelihood of each fish being successfully captured. Planning culling activities with time of day and diver experience in mind could dramatically increase removal efficiency, enabling managers to control a larger portion of the habitat within their jurisdiction with the same resources. Our results suggest that divers with no experience are more efficient if they plan their removal dives during crepuscular hours, approaching the time spent by highly experienced divers during a midday dive. However, the effect of time spent underwater adds up when teams target multiple sites per day and over repeated days, which is the nature of ongoing suppression programs for lionfish (e.g., Chapman et al., 2019). For example, a pair of divers with little prior experience culling lionfish on a 2,500 m^2 coral reef site with 12 lionfish (48 individuals ha^{-1}, the mean density seen in this study) would spend 28 min attempting removal during an average daytime visit and 17 min during crepuscular dives. In comparison, highly experienced divers would spend 17 min attempting this same removal during a daytime dive and only 9 min during crepuscular periods. Given the limited bottom time available to scuba divers during a day of repetitive diving, this extra time accrued by experienced divers (i.e., approximately 19 min/dive) could be allocated to culling additional dive sites per day. Thus, strategically planning culling activities in the 2 hr immediately following sunrise and prior to sunset and prioritizing retention of skilled divers could enable culling programs to cover far greater areas with the same effort.

Lionfish culling by divers will not lead to the complete eradication of the species from the invaded region. However, there is mounting evidence that culling is essential to achieve local functional eradication, that is, ongoing suppression below densities likely to cause ecological impacts to native fauna (Green & Grosholz, 2021). Our results suggest that targeting high density areas is not only important for mitigating invasion impacts, but also increases the efficiency of removal. Lionfish predation effects are non-linear, with lionfish density strongly linked to the magnitude of their predation impact on native reef species (Albins, 2015; Benkwitt, 2016; Green et al., 2014). Benkwitt (2015) conducted a study on isolated artificial reefs that total 1 m^3, where single lionfish caused declines in prey. However, lionfish density on these tiny patches equate to approximately 10,000 lionfish ha^{-1}, orders of magnitude beyond the range observed on natural reef environments. Recent synthesis of empirical data suggests that maintaining lionfish densities below 25 individuals ha^{-1} would reduce the likelihood that densities exceed non-linear thresholds for predation impacts to native fishes (Green & Grosholz, 2021). Predator–prey modeling to estimate threshold densities of lionfish that cause prey decline for reefs in BIRNM (one of the study regions in this paper) estimate densities in this same range, with reductions to 20–32 fish ha^{-1} sufficient to prevent declines in native fish biomass (Green et al., 2015). Considering our work alongside these impact studies reveals density levels that managers can use to identify site-specific priorities for culling. We found that the proportion of lionfish removed on a dive begins to drop below 50% for divers when they cull on reefs harboring less than 20 lionfish ha^{-1}. Taken together, these results suggest that managers would be well served by allocating effort away from sites with persistently low densities (i.e., <20 lionfish ha^{-1}) and toward higher densities in terms of increasing efficiency and protecting against impacts. The average density of lionfish observed at the reefs for this study (which were each culled 2–4 times per year) was approximately 24 fish ha^{-1} and ranged from 5 to 102 ha^{-1}, suggesting that some sites within the system had densities persistently lower than this value and could be culled less frequently, with resources allocated to additional visits at sites with higher densities.

How might managers select areas with sufficiently high lionfish densities, without having already conducted extensive in-water monitoring or culling? Predictive estimates of lionfish abundance based solely off remotely sensed data have been shown to accurately reflect in-water estimates for reefs in the Bahamas (Davis, 2019). Remote sensing techniques could enable managers to create planning maps without ever entering the water that target areas likely to harbor populations above these density levels. For example, BNP staff have previously determined that lionfish densities and sizes vary across habitat types and depths within the park (V McDonough unpublished data); combining those findings with those of this study will allow managers to more effectively allocate their limited resources for lionfish removal efforts. The new Caribbean Marine Maps data set (CaribbeanMarineMaps.tnc.org) created by The Nature Conservancy is a free and publicly available resource for detailed benthic maps of the entire Caribbean, Florida, and USVI that could be used for spatial planning in this way across regions.

Our results also support the notion that fully extirpating broadly distributed invasive species such as lionfish from sites (i.e., culling every lionfish sighted) is an endeavor with diminishing returns. As more lionfish are removed from a site, it will be more challenging to cull the final few that remain. As seen in our study, divers remove lower proportions of fish and have a decreased likelihood of capturing each fish at low densities. Depletion studies by Usseglio et al. (2017) and Harris et al. (2019) also show that high numbers of removal events at the same site are required to achieve complete extirpation. There is the possibility for exploited populations to become more productive when culled, that is, the fundamental theory and mechanism that allows fisheries harvest to be possible (Hilborn & Walters, 1992). Such density-dependent overcompensation could be problematic and has been demonstrated for invasive species management in other species (Grosholz et al., 2021; Zipkin, Kraft, Cooch, & Sullivan, 2009). However, low densities of lionfish are less likely to cause impacts to native fauna (e.g., Hackerott, Valdivia, Cox, Silbiger, & Bruno, 2017), suggesting that suppression rather than extirpation is still an ecologically relevant goal. Lionfish densities and body sizes varied greatly between regions and over time, potentially due to differences in invasion status, and environmental and biotic features such as larval supply and habitat connectivity fueling colonization to reef sites. While lionfish densities in FGBNMS and BNP were consistently lower compared with FKNMS and BIRNM, abundance showed variable trajectories over the course of the study with regions increasing, remaining stable, or declining (Figure 2). Data from reference sites (i.e., where culling is not regularly occurring) are required to fully evaluate the "successes" of culling interventions across these four jurisdictions. Natural variation in lionfish larval supply and adult recolonization to reefs between removals may mask the effects of culling, so that lionfish densities may potentially increase, remain stable, or decline over time depending on local environmental and biotic processes at play.

We also found that an increase in lionfish body size increases the likelihood of catching an individual fish. For all size classes we observed, there was at least a 50% chance of capture, and the size at which probability of capture is >75% is 16 cm (approximately the size at which female lionfish become sexually viable [Gardner, Frazer, Jacoby, & Yanong, 2015]; Figure S2). Given that lionfish predation impact is also strongly linked to lionfish body size (with prey consumption rates increasing with increases in size [Cerino, Overton, Rice, & Morris, 2013]), this is good news for the long-term success of culling programs that seek to minimize impacts to native fauna. In our collective experience, divers are unlikely to want to "leave fish behind" during their removal activities. However, there is strong evidence that while lionfish which are initially curious around divers, they quickly grow wary of diver presence following unsuccessful capture attempts and may be subsequently much harder to remove (Côté et al., 2014). In our study, lionfish 10 cm or smaller were exclusively captured by divers with high levels of experience. We suggest that a tactic of targeting individuals above 10 cm TL can be employed "on the fly" by divers in the water and would require no pre-planning or prior surveys from managers. Emphasizing such a strategy during training, especially for inexperienced divers that are less likely to capture fish and spend more time attempting removal on average, could increase the proportion of fish that are successfully captured and reduce the risk that remaining fish will be harder to cull into the future.

Managers are likely to prioritize locations for culling based on a range of factors including the importance of reef resources (e.g., high coral cover and fish biomass; the presence of rare or sensitive species); visitation for recreation, tourism, and fishing; ease of access; and the magnitude of invasion across locations (i.e., lionfish density, body size, and recolonization rates). Our study provides quantitative evidence that variation in lionfish density and body size across invaded reefs, the time of day at which culling occurs, and site characteristics such as depth and size have important implications for the success of removal activities. Environmental and biotic factors influencing lionfish density, recolonization rates, and body sizes across the reef-scape are outside the scope of this analysis. Nevertheless, our results suggest that prioritizing smaller sites with high lionfish density (i.e., >20 lionfish ha^{-1}) and targeting visits within a few hours of dawn and dusk will greatly increase the efficiency of culling teams (of all experience levels). Our work also highlights the importance of ongoing training for divers to increase their culling efficiency and effectiveness, which may also have the benefit of reducing any effects of learned diver avoidance by lionfish on effectiveness over time. These data can be combined with spatially explicit information on the reef-scape (native fish density and biomass, reef value and status, ease of access) to estimate resources required to achieve functional eradication of lionfish at priority locations and sustain culling efforts for the long term.

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CONFLICT OF INTEREST

The authors declare no potential conflict of interest.

AUTHOR CONTRIBUTIONS

Stephanie J. Green and Lad Akins conceptualized the study and data collection methodology. Michelle

A. Johnston: coordinated data collection in FGBNMS; Clayton Pollock, Bernard Castillo II, and Kynoch Reale-Munroe coordinated data collection in BUIS; Vanessa McDonough and Shelby Moneysmith coordinated data collection in BNP; and Lad Akins coordinated data collection in FKNMS. Alexandra C. D. Davis cleaned and quality controlled the data, performed all statistical analyses, and created the figures and tables. Alexandra C. D. Davis and Stephanie J. Green wrote the manuscript, Ian Lundgren and all other authors edited and contributed to manuscript revisions.

DATA AVAILABILITY STATEMENT

The data and *R*-code for the analysis presented in this paper are available in the open-access repository: https://github.com/CHANGE-Lab/CSP-lionfish-efficacy.

ETHICS STATEMENT

This manuscript is solely the work of the authors. Lionfish removals and field work at FGBNMS were carried out under permits FGBNMS-2009-001, FGBNMS-2011-002, FGBNMS-2014-001, FGBNMS-2018-002, and FGBNMS-2019-008. Lionfish removals and field work at BUIS were carried out by NPS resource management staff as a management action and by researchers and collaborators authorized under the following permits: BUIS-2016-SCI-0004, BUIS-2017-SCI-0014, and BUIS-2019-SCI-0002. Lionfish removals and field work at BNP were done so under permission granted internally as part of program activities. Lionfish removals and field work at FKNMS were carried out with permission under research permit FKNMS-2013-018.

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