

Density-dependent colonization and natural disturbance limit the effectiveness of invasive lionfish culling efforts

Nicola S. Smith · Stephanie J. Green · John L. Akins ·
Skylar Miller · Isabelle M. Côté

Received: 15 September 2016 / Accepted: 28 April 2017
© Springer International Publishing Switzerland 2017

Abstract Culling can be an effective management tool for reducing populations of invasive species to levels that minimize ecological effects. However, culling is labour-intensive, costly, and may have unintended ecological consequences. In the Caribbean, culling is widely used to control invasive Indo-Pacific lionfish, *Pterois volitans* and *P. miles*, but the effectiveness of infrequent culling in terms of reducing lionfish abundance and halting native prey decline is unclear. In a 21-month-long field experiment on natural reefs, we found that culling effectiveness

changed after the passage of a hurricane part-way through the experiment. Before the hurricane, infrequent culling resulted in substantial reductions in lionfish density (60–79%, on average, albeit with large uncertainty) and slight increases in native prey species richness, but was insufficient to stem the decline in native prey biomass. Culling every 3 months (i.e., quarterly) and every 6 months (i.e., biannually) had similar effects on lionfish density and native prey fishes because of high rates of lionfish colonization among reefs. After the hurricane, lionfish densities were greater on all culled reefs compared to non-culled reefs, and prey biomass declined by 92%, and species richness by 71%, on biannually culled reefs. The two culling frequencies we examined therefore seem to offer a poor trade-off between the demonstrated conservation gains that can be achieved with frequent culling and the economy of time and money realized by infrequent culling. Moreover, stochastic events such as hurricanes can drastically limit the effectiveness of culling efforts.

Electronic supplementary material The online version of this article (doi:[10.1007/s10530-017-1449-6](https://doi.org/10.1007/s10530-017-1449-6)) contains supplementary material, which is available to authorized users.

N. S. Smith (✉) · S. J. Green · I. M. Côté
Earth to Ocean Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby, BC V5A 1S6, Canada
e-mail: nicolas@sfu.ca

Present Address:
S. J. Green
Center for Ocean Solutions, Stanford University, Monterey, CA 93940, USA

J. L. Akins
Reef Environmental Education Foundation, 98300 Overseas Highway, Key Largo, FL 33037, USA

S. Miller
Cape Eleuthera Institute, Rock Sound, Eleuthera, Bahamas

Keywords Coral reef fish · Hurricanes · Invasive predators · Invasive species control

Introduction

Culling is commonly used in conservation as a means to eradicate invasive species or to reduce their

populations to levels that minimize ecological effects (Zipkin et al. 2009). In such instances, culling can be an effective management tool. For example, culling has been used to completely remove introduced goats (Campbell and Donlan 2005), cats (Nogales et al. 2004) and pigs (Cruz et al. 2005) on islands. Likewise, the removal of non-native native predators via culling or translocation increased breeding performance and population sizes of a variety of vulnerable native bird species across six continents (Smith et al. 2010). Culling is also effective in aquatic environments. In temperate lakes, repeated removals of the introduced smallmouth bass, *Micropterus dolomieu*, resulted in a decrease in overall bass biomass and subsequent increases in the abundance of several native prey fishes (Weidel et al. 2007). Similarly, culling the invasive long-spined sea urchin, *Centrostephanus rodgersii*, in discrete areas along the Tasmanian coast substantially reduced its density and likelihood of the occurrence of ‘urchin barrens’ (i.e., bare areas of reef due to sea urchin overgrazing) (Tracey et al. 2015).

However, culling is also costly, labour-intensive, and sometimes has unintended ecological consequences. Both theoretical and empirical studies show that increased mortality, such as that caused by culling, can lead to greater variability in abundance and instability in the targeted population (Costantino et al. 1997; Benton et al. 2004; Cameron and Benton 2004; Abrams and Quince 2005; Zipkin et al. 2009). It can also result in overcompensation, i.e. an increase in the abundance of the targeted population with increases in mortality (Benton et al. 2004; Abrams and Quince 2005; De Roos et al. 2007; Zipkin et al. 2008, 2009). For example, Benton et al. (2004) showed that culling eggs of the soil mite *Sancassania berleseii* increased total soil mite population size in variable environments. They attributed this effect to changes in density-dependence dynamics: reducing egg number increased juvenile survival because intraspecific competition is typically intense during this early life stage (Benton et al. 2004).

Furthermore, culling can alter the behaviour of targeted species in ways that either impede the success of future culling efforts or have inadvertent impacts on native prey through behaviourally mediated indirect interactions. For example, invasive lionfish, *Pterois* spp. on regularly culled Bahamian reefs were less active and hid better than those on non-culled reefs—behaviours that can reduce their likelihood of capture

during culling events (Côté et al. 2014). Brook et al. (2012) showed that culling dingoes (*Canis lupus dingo*), an apex predator in Australia, effectively reduced their abundance, which likely reduced perceived predation risks (and increased activity levels) on feral cats, which are mesopredators that prey heavily on native species.

Culling is widely used in the Caribbean to control invasive Indo-Pacific lionfish, *Pterois volitans* and *P. miles*. These predators have colonized roughly 7.3 million km² of the western Atlantic, Caribbean Sea and Gulf of Mexico (Côté et al. 2013), and have substantially reduced native prey fish abundance and species richness on coral reefs (Albins and Hixon 2008; Green et al. 2012; Albins 2013, 2015; Benkwitt 2015; Ingeman 2016). Manual removal of individuals by spearing or netting is the most common form of lionfish culling (Akins 2012). Culling by concerned citizens or during organized tournaments currently occurs haphazardly throughout the region, but the effectiveness of these control efforts is unclear because lionfish and native prey abundances are rarely monitored (Côté et al. 2013). Empirical and theoretical studies, however, suggest that regular culling at targeted sites significantly reduces lionfish abundance and mean size (e.g., Arias-González et al. 2011; Barbour et al. 2011; Morris et al. 2011; Frazer et al. 2012; de León et al. 2013; Green et al. 2014; Johnston and Purkis 2015a), sometimes with concomitant stabilization of native prey fish biomass when lionfish are kept below threshold densities at which their ecological effects are predicted to be limited (Green et al. 2014).

It seems that culling lionfish must now be added to the portfolio of essential activities undertaken by Caribbean managers to maintain the native diversity and productivity of coral reef ecosystems (Morris 2012; Johnston and Purkis 2015a). Unfortunately, few small island states in the Caribbean have the resources to sustain the high culling effort required to drive and keep lionfish populations down and recover native fish populations over the long term. Theoretical models, for example, suggest that an annual exploitation rate of 35–65% many years in a row and at large spatial scales is needed to achieve recruitment overfishing of lionfish (Barbour et al. 2011). Such high mortality rate might be achievable with very frequent culling (e.g., at least monthly; Morris et al. 2011; Green et al. 2014; Johnston and Purkis 2015a), which is beyond

the financial means of many managers. Less frequent culling is more economically realistic but might also be less ecologically effective. For instance, culling lionfish three times per year on artificial reefs in the Gulf of Mexico was insufficient to stem the decline in native prey fishes, while lionfish densities quickly returned to pre-clearance levels on reefs that were cleared once a year (Dahl et al. 2016). The effectiveness of infrequent culling of lionfish on natural reefs is currently unclear.

Here, we assessed the effectiveness of culling lionfish at varying frequencies, some of which might be realistically in line with the financial constraints of long-term invasion management in small island states. Specifically, we compared the effectiveness of culling lionfish every 3 months (i.e., quarterly culls) versus every 6 months (i.e., biannual culls) in a 21-month-long field experiment on natural reefs. We used two criteria to evaluate whether culling lionfish was effective. First, culling should result in a decrease in lionfish density. Second, culling should also stem the decline of native prey fish biomass and species richness. We hypothesized that more frequent lionfish culls (i.e., quarterly culls) would result in larger reductions in lionfish density and larger gains in native prey fish biomass and species richness than less frequent culls (i.e., biannual culls). Beyond culling frequency, we also examined the effects of other factors that may influence lionfish abundance and native prey fishes, including: (1) culling efficiency (defined as the proportion of lionfish remaining on a reef immediately following a cull), (2) large-scale natural disturbance (i.e., the occurrence of Category 3 Hurricane Irene), and (3) seasonal changes in native fish recruitment.

Materials and methods

Study site

We conducted our study on 12 natural coral reef patches in Rock Sound, South Eleuthera, The Bahamas (24°50.000' N, 76°14.000' W; Fig. 1) over a period of 21 months, starting in December 2010. Reefs were at similar depths (i.e., 3–4 m), and of comparable size (mean \pm SD = 98.4 \pm 53.8 m²). The shortest distance between two adjacent reef patches was 200 m of sand and seagrass. This distance

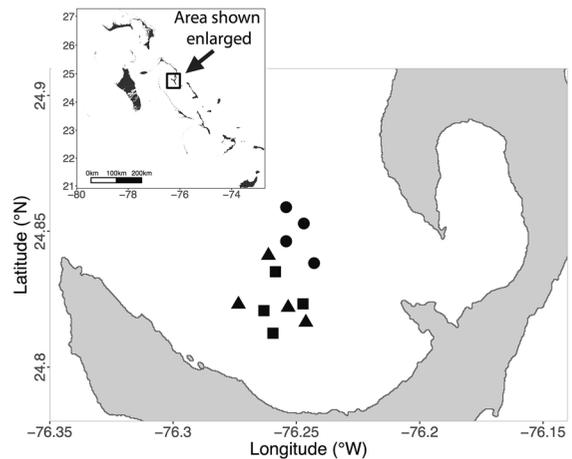


Fig. 1 Distribution of 12 coral reef patches at study site in Rock Sound, South Eleuthera, The Bahamas. Each patch was randomly assigned a lionfish culling treatment: biannual culls (squares), quarterly culls (triangles) and no culls (circles)

ensured limited movement of lionfish between patches because the majority (80%) of lionfish exhibit strong fidelity to their home patch (Tamburello and Côté 2015). We therefore considered reefs as independent samples in our analyses. Reefs also had similar live, hard coral cover (mean \pm SD = 9.36 \pm 4.38%) and structural complexity as determined by vertical relief, i.e., the height from the sea floor to the highest point on the reef (mean \pm SD = 1.3 \pm 0.5 m), and by reef rugosity (mean \pm SD = 2.2 \pm 0.3; see Supplementary Information). Lionfish were first observed in Rock Sound in 2005, and were prevalent throughout the study area at the time of our experiment (Green et al. 2014).

Experimental design

We randomly assigned reefs to one of three treatments: (1) control reefs, where no culling occurred ($n = 4$ reefs); (2) biannually culled reefs, where culling occurred once every 6 months ($n = 4$ reefs); and (3) quarterly culled reefs, where culling occurred once every 3 months ($n = 4$ reefs; Fig. 1). In a stroke of poor luck, most of the control reefs were grouped at the north-east end of the study area (Fig. 1). However, while this geographic bias might influence comparisons between culled and non-culled reefs, it would not affect the more important comparisons between biannually and quarterly culled reefs. Moreover, the fact that there was no difference in lionfish density, native

prey fish biomass, or native prey fish species richness among treatments at the start of the experiment (see “[Statistical analysis](#)” and “[Results](#)” sections for details) reassured us that geographic biases were unlikely to be severe.

We conducted surveys of lionfish and native prey fish on all 12 coral reef patches in December 2010 to provide a pre-experiment baseline, and then on a quarterly basis (i.e., every 3 months) until we concluded the experiment in September 2012. All surveys were conducted on SCUBA between 09:00 and 16:30, which was well outside crepuscular hours when lionfish are actively hunting, often off the reef patch (Benkwitt 2016a, b; Cure et al. 2012; Green et al. 2011). We therefore minimized the likelihood of failing to detect lionfish that are resident on a reef patch but were foraging in the surrounding areas at the time of our survey. All divers were trained to visually estimate fish lengths underwater (± 1 cm) with the aid of fish models prior to the start of the experiment.

We used detailed lionfish-focused searches to estimate lionfish sizes and abundance every 3 months on all study reefs (Green et al. 2013). During lionfish-focused searches, two or three divers slowly swam first around the perimeter of the patch and then over the reef in an S-shaped pattern, searching all crevices and overhangs for lionfish and noting their size and location (Green et al. 2013). A dive light was used when necessary, and survey time was approximately 15 min per 100 m². We visually estimated lionfish total length (TL) to the nearest cm with the aid of a 50 cm long PVC pipe demarcated by 1 cm marks. Divers discussed the size and location of all lionfish immediately following a survey to reduce the likelihood of double counting or missing individuals.

We used traditional belt transect surveys to estimate native prey fish sizes and abundances (Sale and Sharp 1983), which we also conducted every 3 months on all study reefs. During native fish surveys, divers placed two to four 8 m \times 2 m belt transects across the reef patch, depending on reef size. Divers waited approximately 5 min for fish to settle following the disturbance before swimming over the transect line to record the species and size (TL to the nearest cm) of every fish encountered.

We culled lionfish on treatment reefs immediately following fish surveys. During lionfish culls, a team of two or three divers manually removed as many lionfish as possible using hand nets and vinyl collection bags.

Pole spears were also sometimes used for particularly large lionfish that sheltered deep within reef crevices and overhangs (Akins 2012). All divers were trained in lionfish capture and handling prior to the start of the experiment. It was not always possible to remove all lionfish from a reef because some individuals evaded capture by retreating within the reef. Total time spent culling lionfish ranged from 14 to 110 min per reef, and we removed on average 93% (\pm SD = 13%) of all lionfish initially observed on a reef. All captured lionfish were humanely euthanized at the surface, typically by excess anesthesia in a bath of clove oil and seawater (Borski and Hodson 2003; Green et al. 2012). We weighed and measured captured lionfish in the lab. To estimate culling efficiency, two or three divers conducted lionfish-focused searches of the study reef immediately following each cull, noting the size (TL to nearest cm) and location of all remaining lionfish. Divers compared lionfish sizes, abundance and locations before and after each cull to reduce the likelihood of underestimating the number of lionfish that had evaded capture.

Statistical analysis

Although lionfish can consume prey up to half their own length in the invaded range (Morris and Akins 2009), lionfish prey are typically <5 cm TL (Morris and Akins 2009; Muñoz et al. 2011). For example, the mean size of prey consumed by lionfish in The Bahamas varied between 1.5 and 3.0 cm TL depending on lionfish size, which ranged from 6.2 to 42.4 cm TL (Morris and Akins 2009). Lionfish in our study ranged from 3 to 37 cm TL, with a median size of 20 cm TL (mean \pm SD = 19.4 \pm 6.5 cm TL). Our analyses therefore focused only on native fish ≤ 5 cm TL as these individuals are the main potential lionfish prey. We converted native fish size to biomass using the allometric function

$$B = aL^b$$

where B is biomass in g, L is TL in cm, and a and b are species-specific scaling constants derived from published literature (Froese and Pauly 2016). When species-specific parameters were unavailable, we used the scaling constants for closely related species with a similar body shape. To account for differences in reef sizes, we expressed lionfish abundance, native prey fish biomass and native prey fish species richness per

Table 1 Dummy coding for various hypotheses regarding the duration of the effect of Hurricane Irene on lionfish and prey fishes

Model	March 2011	June 2011	Sept. 2011	Dec. 2011	March 2012	June 2012	Sept. 2012
H1	0	0	1	1	1	1	1
H2	0	0	1	0	0	0	0
H3	0	0	1	1	0	0	0
H4	0	0	1	1	1	0	0
H5	0	0	1	1	1	1	0

Hurricane Irene was a Category 3 Hurricane that passed over the study area in late August 2011

unit area (m²). We conducted all statistical analyses in R (v. 3.2.3; R Development Core Team 2014). We also used the following add-on packages, where appropriate: (1) nlme, v. 3.1-127 (Pinheiro et al. 2016), (2) AICcmodavg, v. 2.0-4 (Mazerolle 2016) (3) reshape, v. 0.8.5 (Wickham 2007), (4) coefplot2, v. 0.1.3.2 (Bolker and Su 2011) and (5) MuMIn, v. 1.15.6 (Bartoń 2016).

Baseline surveys

To test if there were differences among treatments at the start of the experiment in lionfish density, native prey fish biomass and native prey fish species richness, we conducted one-way analyses of variance (ANOVA) on the natural log-transformed response variables. We used both visual (e.g., normal-quantile plots) and statistical methods (e.g., Levene's test for homogeneity of variance) to ensure that all assumptions of ANOVA were met (Whitlock and Schluter 2008).

Modeling hurricane effects

Large-scale natural disturbances like hurricanes and major storms are an important source of environmental stochasticity that can affect fish populations in a variety of ways (Woodley et al. 1981; Kaufman 1983; Walsh 1983; Harmelin-Vivien 1994; Johnston and Purkis 2015b). Category 3 Hurricane Irene passed over our study area in late August 2011, almost 9 months after the start of the experiment. We had no a priori expectation regarding the duration of the effect of Hurricane Irene on fishes. We therefore used dummy coding (Quinn and Keough 2002) in linear mixed-effects models, with an Akaike Information Criterion approach corrected for small sample sizes (AICc; Burnham and Anderson 2002), to select the

model(s) of hurricane effects best supported by our data. Specifically, we first used dummy coding to generate five hypotheses about how Hurricane Irene impacted fishes, ranging from a short-term effect that persisted only for several days to a longer-term effect that persisted for several months (Table 1). We assigned each survey period a '0' if there was no effect of Hurricane Irene and a '1' if there was an effect (Table 1). All survey periods before Hurricane Irene were coded as '0'. The null hypothesis that there was no effect of Hurricane Irene during any of the survey periods was represented in linear mixed-effects models that lacked hurricane as an explanatory variable.

We used linear mixed-effects models to assess the duration of the effect of Hurricane Irene on lionfish density and, separately, on native prey fish biomass. We included site (i.e., individual reef) as a random intercept in all models while the dummy variable hurricane was treated as a categorical, fixed effect. To meet the assumption of normality of residual variance, we transformed (natural log plus a constant) both lionfish density and native prey fish biomass for these and all subsequent analyses. We examined models within each set using maximum likelihood estimation (ML; following Zuur et al. 2009) and then compared them using AICc, in which AICc values represented a tradeoff between model complexity and model fit (Burnham and Anderson 2002). We considered the model with the lowest AICc value to be the best model (Burnham and Anderson 2002), and used the dummy coding of the best model in all subsequent analyses that included Hurricane Irene as an explanatory variable. We had no reason to assume that Hurricane Irene acted differently on native prey fish biomass than on native prey fish species richness. We therefore used the best model selected based on prey biomass to examine hypotheses about prey species richness.

Modeling the effects of culling and environmental factors on lionfish density

We constructed linear mixed-effects models to examine 17 a priori hypotheses regarding the effect of various factors (i.e., culling frequency, culling efficiency, Hurricane Irene, and seasonal changes in native prey fish recruitment) on lionfish density. We treated culling frequency as a categorical, fixed effect and hypothesized that more frequent lionfish culls would result in larger reductions in lionfish density than less frequent culls. The number of individuals removed during a cull can also affect lionfish density if leaving some lionfish behind influences colonization. We therefore accounted for differences in culling efficiency by including the proportion of lionfish remaining on a reef immediately following a cull as a numerical, fixed effect. We included the dummy variable from the best model for the impact of Hurricane Irene on lionfish density as a categorical, fixed effect (see “[Modeling hurricane effects](#)” section for details). Lastly, coral reef fish recruitment varies seasonally in the Caribbean (e.g., Caselle and Warner 1996; Green et al. 2014), thereby leading to predictable changes in lionfish food availability that may influence lionfish density. Native fish recruitment to reef patches is lowest during June in our study area (Green et al. 2014). We therefore used dummy coding to model the effect of June lows in native fish recruitment by assigning a ‘0’ to all survey periods except June surveys, to which we assigned a ‘1’. We treated the dummy variable for seasonal changes in native fish recruitment as a categorical, fixed effect.

We performed a series of tests on our most complex model for lionfish density before arriving at the structure of our final model, as described in Zuur et al. (2009). Specifically, we first fitted our most complex model with and without site as a random intercept using restricted maximum likelihood estimation (REML) and then compared them using AICc. The model with site as a random intercept had greater support than the model without. However, visual examination of the residuals plot indicated a violation of the assumption of homogeneity of residual variance. Hence, we allowed residual variance to differ by culling frequency, which improved model fit based on AICc and met the assumption of homogeneity of residual variance. Visual examination of the autocorrelation plot indicated temporal autocorrelation

between survey periods, i.e., non-independence with respect to time (Zuur et al. 2009). We therefore refitted the model with and without an auto-regressive model of order 1 (AR1) correlation structure, which is used with regularly spaced, time-series data and models the residual at time t as a function of the residual of time $t - 1$ plus noise (Zuur et al. 2009). Hence, the closer two residuals are to one another in time, the higher their correlation (Zuur et al. 2009). Re-examination of the residuals from our final model, which included site as a random intercept, allowed residual variance to differ by culling frequency and included AR1 correlation structure, indicated that all assumptions of linear models were met (i.e., homoscedasticity, independence and normality of residuals).

Next, we applied the structure of our final model to our candidate set of 17 models to identify the top model(s) that best explained the effect of various factors on lionfish density. We assessed the models using ML and then compared them using AICc. We then refitted the model with the lowest AICc value using REML to interpret parameter estimates (Zuur et al. 2009). Lastly, we performed model validation on our top model and subsequently calculated the marginal and conditional r^2 values to determine the amount of variation explained by fixed effects versus the combination of fixed and random effects, respectively (Nakagawa and Schielzeth 2013).

Modeling the effects of culling and environmental factors on native prey fishes

We generated 13 a priori hypotheses for the effects of culling frequency, Hurricane Irene and seasonal changes in native fish recruitment on native prey fish biomass and species richness. We assumed that lionfish culling efficiency would have an indirect and thus marginal effect on native prey fishes, hence we did not include it in models of native prey fishes. We followed the modelling procedure outlined above (see also Zuur et al. 2009). We used AICc to compare models of prey biomass and, separately, prey species richness, and selected our best models based on the lowest AICc value. The structure of the best model for native prey fish biomass included site as a random intercept, allowed residual variance to differ by seasonal changes in native fish recruitment, and included AR1 correlation structure. In contrast, the structure of the best model for native prey fish species

richness included site as a random intercept, allowed residual variance to differ by hurricane effect, and included AR1 correlation structure. Lastly, as previously described, we performed model validation on our top prey models and subsequently calculated the marginal and conditional r^2 values.

The trajectories of change in lionfish density, prey fish biomass and prey fish species richness are shown in Fig. S1.

Results

Baseline surveys

There was no difference among treatments in lionfish density (one-way ANOVA, $F_{2,9} = 0.08$; $P = 0.92$), native prey fish biomass ($F_{2,35} = 0.48$; $P = 0.62$) or native prey fish species richness ($F_{2,35} = 0.36$; $P = 0.70$) before the experiment.

Hurricane effects on fishes

The model that best described the effect of Hurricane Irene on lionfish density was different from that for native prey fish biomass. The model that indicated a long-term effect (i.e., approximately 12 months; H1 in

Table 1) of Hurricane Irene on lionfish density had approximately 2.3 times more support than the second-ranked model (Table 2a). In contrast, the model that indicated a shorter-term effect (approximately 3 months; H3 in Table 1) of Hurricane Irene on native prey fish biomass had 18.2 times more support than the second-ranked model in that set (Table 2b). The relevant top models were used in subsequent analyses of lionfish density and prey biomass and species richness.

Effects of culling and environmental factors on lionfish density

Our top model indicated that culling frequency, Hurricane Irene and the interaction between the two were important predictors of lionfish density (Table 3; Fig. 2). There was roughly 2.8 times more support in the data for our top model than for the second-ranked model in the candidate set (Table 3). Based on the marginal and conditional r^2 values of our top model, fixed effects explained 24% of variation in lionfish density in our study while the combination of fixed and random effects explained 51% (Fig. 2).

The effect of culling frequency on lionfish density depended on whether culling occurred before or after Hurricane Irene. Before the hurricane, culling reduced

Table 2 Results of model selection using AICc for five linear mixed-effects models that examine the effects of Hurricane Irene on (a) lionfish density (fish m^{-2}) and (b) native prey fish

biomass ($g\ m^{-2}$) on coral reef patches around Eleuthera Island, Bahamas ($n = 12$ reefs)

Model	K	AICc	$\Delta AICc$	w_i	Cumulative w_i	−Log likelihood
(a) <i>Lionfish density</i>						
H1	4	203.799	0.000	0.613	0.613	97.629
H4	4	205.500	1.701	0.262	0.875	98.480
H5	4	207.343	3.544	0.104	0.979	99.401
H3	4	210.786	6.987	0.019	0.998	101.123
H2	4	215.014	11.215	0.002	1.000	103.237
(b) <i>Prey biomass</i>						
H3	4	814.684	0.000	0.930	0.930	403.253
H5	4	820.486	5.802	0.051	0.981	406.154
H4	4	822.502	7.818	0.019	1.000	407.162
H1	4	833.442	18.758	0.000	1.000	412.632
H2	4	834.527	19.843	0.001	1.000	413.175

Both lionfish density and prey biomass were transformed (natural log plus a constant) prior to analysis. K is the number of model parameters. $\Delta AICc$ is the difference in AICc value between model i and the best-supported candidate model. w_i is interpreted as the probability that model i is the best model of the set given the data at hand. We considered the model with the smallest AICc value to be the best-supported model

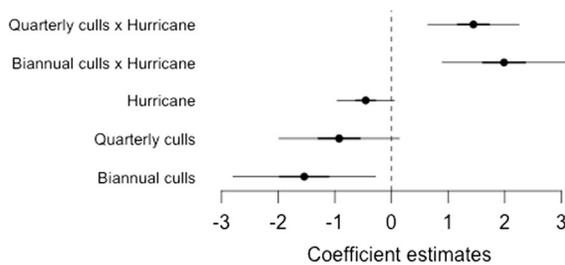


Fig. 2 Coefficients from the top linear mixed-effects model of the effects of various factors on lionfish density (fish m^{-2}) on coral reef patches around Rock Sound, South Eleuthera, The Bahamas ($n = 12$ reefs). Points are means bounded by 95% confidence intervals (*thin bars*) and 50% confidence intervals (*thicker bars*). Positive values (to the *right* of the *dashed line*) signify an increase in lionfish density while negative values (to the *left* of the *dashed line*) signify a decrease in lionfish density. Levels ‘biannual culls’ and ‘quarterly culls’ are compared against the baseline level ‘no culls’ (i.e., control reefs). Level ‘hurricane’ refers to the long-term effect of Category 3 Hurricane Irene on all survey periods following the disturbance and is compared against the baseline level ‘no hurricane effect’, i.e., all survey periods before the hurricane. Conditional r^2 of top model is 0.51 (i.e., proportion of variation in lionfish density among reefs explained by the combination of fixed and random effects in the model)

lionfish density on both biannually culled and quarterly culled reefs compared to the non-culled reefs, as evidenced by the negative effect sizes (Fig. 2). Specifically, lionfish density on reefs culled biannually before the hurricane was, on average, 0.22 times that on reefs where no culling occurred (Fig. 2). This translates to a 79% reduction in average lionfish density on biannually culled reefs compared to non-culled reefs. This reduction was significant, given that the 95% confidence interval does not overlap zero (Fig. 2). In contrast, lionfish density on reefs culled quarterly before the hurricane was, on average, 0.4 times that on non-culled reefs, i.e. 60% lower (Fig. 2). This decline was marginally non-significant. There was no difference in the effects of the two culling frequencies on lionfish density before the hurricane (Fig. S2).

After the hurricane, lionfish densities *increased* significantly on all culled reefs, and this effect persisted until the end of the study, roughly 12 months after the natural disturbance (Table 3; Fig. 2). Lionfish densities after the hurricane were, on average, 7.33 times (or 633%) higher on reefs culled biannually than on reefs where no culling occurred before the

Table 3 Results of model selection using AICc for 17 linear mixed-effects models that examine the effects of various factors on lionfish density (fish m^{-2}) on coral reef patches around Eleuthera Island, Bahamas ($n = 12$ reefs)

Model	K	AICc	Δ AICc	w_i	Cumulative w_i	–Log likelihood
CF, H, CF \times H	11	195.877	0.000	0.511	0.511	84.969
CF, CE, H, CF \times H	12	197.924	2.046	0.184	0.694	84.598
CF, H, S, CF \times H	12	198.289	2.412	0.153	0.847	84.781
CF, CE, H, S, CF \times H	13	199.975	4.098	0.066	0.913	84.188
Intercept only	6	201.778	5.901	0.027	0.940	94.306
H	7	201.908	6.031	0.025	0.965	93.165
S	7	203.591	7.713	0.011	0.975	94.007
CE	7	204.070	8.192	0.008	0.984	94.246
CF, CE, H, S, CF \times H, CF \times S	15	204.264	8.386	0.008	0.992	83.322
CF	8	206.350	10.473	0.003	0.994	94.147
CF, H	9	206.659	10.781	0.002	0.997	93.025
CF, S	9	208.311	12.434	0.001	0.998	93.851
CF, CE	9	208.565	12.688	0.001	0.999	93.978
CF, S, CF \times S	11	209.498	13.621	0.001	0.999	91.779
CF, H, S, CF \times S	12	210.348	14.471	0.000	0.999	90.810
CF, CE, H, S	11	210.861	14.984	0.000	1.000	92.461
CF, H, S, CF \times H	13	211.225	15.347	0.000	1.000	89.812

K is the number of model parameters. Δ AICc is the difference in AICc value between model i and the best-supported candidate model. w_i is interpreted as the probability that model i is the best model of the set given the data at hand. We considered the model with the smallest AICc value to be the best-supported model. CF culling frequency, CE culling efficiency (i.e., the proportion of lionfish remaining immediately after culling), H Hurricane Irene, S seasonal changes in native fish recruitment

Table 4 Results of model selection using AICc for 13 linear mixed-effects models that examine the effects of various factors on native prey fish biomass (g m^{-2}) on coral reef patches around Eleuthera Island, Bahamas ($n = 12$ reefs)

Model	K	AICc	ΔAICc	w_i	Cumulative w_i	–Log likelihood
CF, H, S, CF \times H	11	777.997	0.000	0.687	0.687	377.393
CF, H, S, CF \times H, CF \times S	13	780.394	2.397	0.207	0.894	376.354
CF, H, CF \times H	10	781.988	3.991	0.093	0.988	380.491
H, S	7	787.420	9.423	0.006	0.994	386.458
CF, H, S, CF \times S	11	788.432	10.435	0.004	0.998	382.611
CF, H, S	9	790.032	12.035	0.002	0.999	385.607
H	6	792.201	14.204	0.001	1.000	389.912
CF, H	8	794.706	16.709	0.000	1.000	389.027
Intercept only	5	801.186	23.189	0.000	1.000	395.459
S	6	802.508	24.511	0.000	1.000	395.065
CF	7	804.272	26.275	0.000	1.000	394.884
CF, S	8	805.703	27.706	0.000	1.000	394.526
CF, S, CF \times S	10	806.063	28.067	0.000	1.000	392.529

K is the number of model parameters. ΔAICc is the difference in AICc value between model i and the best-supported candidate model. w_i is interpreted as the probability that model i is the best model of the set given the data at hand. We considered the model with the smallest AICc value to be the best-supported model. CF culling frequency, H Hurricane Irene, and S seasonal changes in native fish recruitment

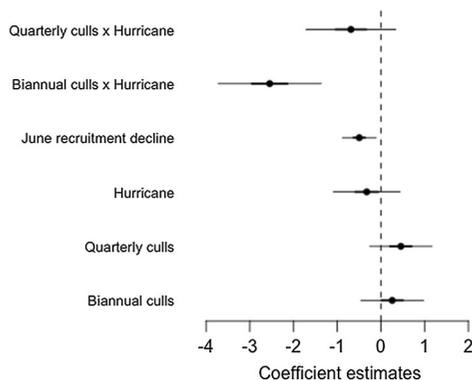


Fig. 3 Coefficients from the top linear mixed-effects model of the effects of various factors on native prey fish biomass (g m^{-2}) on coral reef patches around Rock Sound, South Eleuthera, The Bahamas ($n = 12$ reefs). Points are means bounded by 95% confidence intervals (*thin bars*) and 50% confidence intervals (*thicker bars*). Positive values (to the *right* of the *dashed line*) signify an increase in prey biomass while negative values (to the *left* of the *dashed line*) signify a decrease in prey biomass. Levels ‘biannual culs’ and ‘quarterly culs’ are compared against the baseline level ‘no culs’ (i.e., control reefs). Level ‘hurricane’ refers to the short-term effect of Category 3 Hurricane Irene on September and December 2011 surveys following the disturbance and is compared against the baseline level ‘no hurricane effect’, i.e., all other survey periods. Level ‘June recruitment decline’ refers to June lows in native fish recruitment to coral reef patches in our study area and is compared to all other survey months. Conditional r^2 of top model is 0.20 (i.e., proportion of variation in prey fish biomass among reefs explained by the combination of fixed and random effects in the model)

hurricane (Fig. 2). Similarly, lionfish densities on reefs culled quarterly after the hurricane were, on average, 4.27 times (or 327%) higher than on non-culled reefs prior to the hurricane (Fig. 2). There was again no difference between culling frequencies in their effect on lionfish density after the hurricane, as indicated by the considerable overlap in 95% confidence intervals (Fig. 2).

Effects of culling and environmental factors on native prey fishes

The top model for native prey fish biomass included culling frequency, Hurricane Irene, seasonal changes in native fish recruitment and the interaction between culling frequency and Hurricane Irene (Table 4; Fig. 3). This model accounted for 69% of model support using Akaike weights and was 2.40 AICc units lower than the second top model (Table 4). Fixed effects explained 17.3% of variation in native prey fish biomass while the combination of fixed and random effects explained 22.3% (Fig. 3).

As expected given the low rates of native fish recruitment in June at our sites, native prey fish biomass during June surveys was, on average, 0.61 times (39% lower) that of native prey fish biomass during any other survey month (Fig. 3). Culling had no

Table 5 Results of model selection using AICc for 13 linear mixed-effects models that examine the effects of various factors on native prey fish species richness (species m⁻²) on coral reef patches around Eleuthera Island, Bahamas (n = 12 reefs)

Model	K	AICc	ΔAICc	w _i	Cumulative w _i	–Log likelihood
CF, H, CF × H	10	445.051	0.000	0.667	0.667	212.023
CF, H, S, CF × H	11	446.855	1.804	0.271	0.938	211.822
CF, H, S, CF × H, CF × S	13	450.131	5.080	0.053	0.990	211.223
H	6	455.251	10.200	0.004	0.994	221.437
CF, H	8	455.913	10.861	0.003	0.997	219.630
H, S	7	457.314	12.263	0.001	0.999	221.405
CF, H, S	9	457.944	12.892	0.001	1.000	219.563
CF, H, S, CF × S	11	461.061	16.010	0.000	1.000	218.925
Intercept only	5	464.965	19.914	0.000	1.000	227.349
CF	7	465.633	20.582	0.000	1.000	225.564
S	6	465.764	20.712	0.000	1.000	226.693
CF, S	8	466.218	21.167	0.000	1.000	224.783
CF, S, CF × S	10	469.593	24.542	0.000	1.000	224.294

K is the number of model parameters. ΔAICc is the difference in AICc value between model *i* and the best-supported candidate model. w_i is interpreted as the probability that model *i* is the best model of the set given the data at hand. We considered the model with the smallest AICc value to be the best-supported model. *CF* culling frequency, *H* Hurricane Irene, and *S* seasonal changes in native fish recruitment

effect on native prey fish biomass, except on reefs culled biannually during the period in which Hurricane Irene affected prey fishes (i.e., Sept. 2011 and Dec. 2011; Fig. 3). In this instance, and contrary to our prediction, culling resulted in a significant 92% decrease in native prey fish biomass compared to non-culled reefs before the hurricane and after the effects of the disturbance had dissipated (i.e., after December 2011; Fig. 3).

Culling frequency, Hurricane Irene, and the interaction between the two were in the top model for native prey fish species richness (Table 5; Fig. 4). This model had 2.5 times more support than the second-ranked model (Table 5), and it explained 25.4% of variation in native prey richness (Fig. 4). Similar to prey fish biomass, the effect of culling frequency on native prey fish species richness depended on when culling occurred in relation to the impact of Hurricane Irene. On the one hand, before the hurricane and after the impacts of the disturbance had dissipated (i.e., after Dec. 2011), culling increased native prey fish species richness relative to control reefs, as predicted (Fig. 4). However, the increase in native richness on biannually culled reefs was marginally non-significant, and there was no difference between biannual and quarterly culls (Fig. 4). Native prey fish species richness on biannually culled and quarterly culled reefs was, on average,

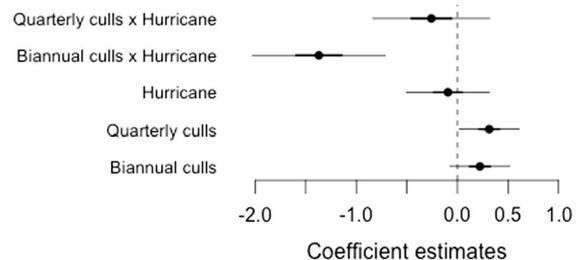


Fig. 4 Coefficients from the top linear mixed-effects model of the effects of various factors on native prey fish species richness (species m⁻²) on coral reef patches around Rock Sound, South Eleuthera, The Bahamas (n = 12 reefs). Points are means bounded by 95% confidence intervals (*thin bars*) and 50% confidence intervals (*thicker bars*). Positive values (to the right of the *dashed line*) signify an increase in prey species richness while negative values (to the left of the *dashed line*) signify a decrease in richness. Levels ‘biannual culls’ and ‘quarterly culls’ are compared against the baseline level ‘no culls’ (i.e., control reefs). Level ‘hurricane’ refers to the short-term effect of Category 3 Hurricane Irene on September 2011 and December 2011 surveys following the disturbance and is compared against the baseline level ‘no hurricane effect’, i.e., all other survey periods. Conditional r² of top model is 0.21 (i.e., proportion of variation in prey species richness among reefs explained by the combination of fixed and random effects in the model)

1.3 times (or 29% higher) to 1.4 times (or 41% higher) that of non-culled reefs, respectively, over the same time periods (Fig. 4). On the other hand, during the

period of hurricane impact on native prey fishes (i.e., September and December 2011), culling *decreased* prey species richness significantly, by 74%, on reefs culled biannually compared to non-culled reefs before the hurricane and after the impacts of the disturbance had dissipated, but had no effect on reefs culled quarterly (Fig. 4).

Discussion

Infrequent culling influenced invasive lionfish density, native prey fish biomass and native prey fish species richness on natural patch reefs. However, these effects did not vary systematically with culling frequency, and disturbance caused by the passage of a hurricane altered the effectiveness of these culling regimes as a management strategy. Before the hurricane, quarterly and biannual culling resulted in similar reductions in lionfish density and slight gains in native prey fish species richness relative to non-culled reefs. These effects, however, had large uncertainty and ranged from being statistically significant to marginally non-significant. Neither culling regime resulted in recovery of prey biomass. Importantly, after the hurricane, lionfish densities *increased* substantially on all culled reefs while both native prey fish biomass and species richness declined on reefs that were culled biannually.

In the absence of hurricanes, is culling an effective management tool for mitigating the impacts of invasive lionfish? The answer depends on how effective culling is in suppressing lionfish density and on the indicators managers use to assess the status of native fish communities (e.g., biomass or richness). In a previous experiment conducted in the network of reef patches we studied, culling reduced lionfish density and stemmed the decline of native prey biomass, but with substantial effort (i.e., monthly culls) that is unlikely to be financially sustainable in the long term (Green et al. 2014). These results are supported by population and biophysical models that suggest that intensive, frequent removals are required to control lionfish populations (Morris et al. 2011; Johnston and Purkis 2015a). Our results show that much less frequent culling can reduce lionfish density and promote marginal recovery of native prey fish species richness (Figs. 2, 4), but it had no effect on prey biomass (Fig. 3). The infrequent culling regimes examined here therefore did not mitigate the full

range of lionfish impacts on native prey fish, compared to more labour-intensive, monthly efforts (Green et al. 2014; Johnston and Purkis 2015a; Morris et al. 2011). The limited effectiveness of our less intense culling regimes is consistent with those of Dahl et al. (2016), who found that culling lionfish three times a year on artificial reefs reduced lionfish density, but had little impact on native prey fish recovery.

We expected more frequent culls to be more effective at suppressing lionfish density than less frequent culls. However, this was not the case. There was no difference between biannual and quarterly culls in their effect on lionfish density before the hurricane (Fig. S2). We suggest that negative density-dependent colonization of culled patches by lionfish, arriving from other patches in the network and perhaps via long-distance larval recruitment (e.g., see Andradi-Brown et al. 2017), might explain our finding. Previous work has shown that lionfish exhibit negative density dependence in movement (Tamburello and Côté 2015). Relocating lionfish preferentially move from high- to low-density patches, possibly in response to intraspecific competition for prey on high-density reefs. The likelihood of moving decreases as the difference in lionfish density between patches diminishes (Tamburello and Côté 2015). By reducing lionfish abundance, culling created low-density patches that were attractive to lionfish relocating from higher-density sites, an effect that ebbed over time as lionfish colonized culled patches and the density differences between culled and other patches in the network attenuated. Culling some patches more frequently than others temporarily ‘rejuvenated’ the attractiveness of these (quarterly culled) patches, until the density differentials disappeared once more. If lionfish exhibit negative density-dependent movement as we suggest—and as demonstrated by other invasive predators in response to culling (e.g., red foxes, *Vulpes vulpes*, Lieury et al. 2015; see also Doherty and Ritchie 2016 for an overview), we should expect that (1) the number of newly arriving lionfish (i.e., colonization rate) should be higher on culled than on non-culled patches, (2) that colonization rate should be higher on quarterly culled than biannually culled reefs, and (3) that, all else being equal, there should be a threshold lionfish density, determined by intraspecific interactions (e.g., competition for food), beyond which new arrivals to a patch nearly cease. In line with the first two predictions, we found that overall lionfish

colonization rates were significantly higher on culled reefs than on non-culled reefs, and nearly four times as high for quarterly culled than biannually culled reefs (Fig. S3). The third prediction is more difficult to test in the absence of more detailed records of colonization patterns but it is notable that all reefs had similar lionfish densities at the start of our experiment.

Even though there is some evidence that culling reduced lionfish density before the hurricane, especially on biannually culled reefs, it did not promote recovery of native fish biomass on reefs (Fig. 3). There are at least two possible explanations for this result, which are not mutually exclusive. First, there is evidence that lionfish exhibit density-dependent foraging habitat selection. At low density, they hunt mainly on coral reefs—their preferred foraging habitat (Benkwitt 2016a)—but at higher densities, they extend their foraging range to include seagrass and other habitats (e.g., isolated coral heads) away from their home reef—likely in response to intraspecific competition for prey (Dahl and Patterson 2014; Benkwitt 2016a, b). It is therefore possible that culling lowered lionfish density enough to reduce lionfish foraging, and perhaps curb prey decline, in seagrass and other surrounding habitats, but not on reef patches—the preferred hunting ground of lionfish (Benkwitt 2016a). Second, on small reefs, just a few lionfish can overwhelm the biomass production by resident fishes and deplete prey standing biomass. Benkwitt (2015), for example, showed that a single lionfish could substantially reduce native prey biomass on small, artificial reefs in The Bahamas. Similarly, Green et al. (2014) demonstrated that monthly removals of up to 96% of lionfish on natural reef patches were required to stem the decline of native fish populations. Thus, despite relatively high culling efficiency, our interventions may not have been sufficient to recover native prey biomass.

Surprisingly, lionfish density increased on all culled reefs after the hurricane. Storms can have major short-term as well as long-lasting effects on coral reef ecosystems. They can cause direct and indirect damage to benthic reef organisms (especially corals), change sedimentation processes, increase turbidity, lower salinity, and affect sea level (Harmelin-Vivien 1994). These changes subsequently impact reef organisms, from phytoplankton to reef-associated invertebrates and fish assemblages, in a variety of ways (Beecher 1973; Harmelin-Vivien 1994; Kaufman

1983; Walsh 1983; Woodley et al. 1981). Some species shift their distribution (e.g., by moving deeper) to seek more protected habitat (e.g. Walsh 1983), while others decline in abundance in response to habitat damage (e.g., Wantiez et al. 2006), remain unaffected (e.g., Cheal et al. 2002; Adams and Ebersole 2004) or even benefit if new habitat types are created (e.g., coral rubble fields, Kaufman 1983). In our study, there was no discernable damage to corals on patch reefs following the disturbance (SM, personal observations). Instead, the increase in lionfish abundance appears to be attributable to increased recruitment and/or movement of small lionfish, especially onto culled patches, after the hurricane. Indeed, lionfish were significantly smaller, by ~4–10 cm on average, depending on culling treatment in December 2011 (3 months after the hurricane) than in December 2010 (pre-experiment baseline) (Fig. S4, Fig. S5). This size reduction is not a consequence of culling (Dahl et al. 2016; Frazer et al. 2012) since we also saw smaller lionfish on non-culled reefs (Fig. S4, Fig. S5). In addition, the proportion of small/young lionfish (i.e., <10 cm TL) increased from 1 to 15% on non-culled patches and from 3 to 4% to 25 to 58% on culled patches after the hurricane (Fig. S6), with concomitant increases in abundance (Fig. 1). Note that, although hurricanes are thought to have contributed to increasing both the rate of spread and population sizes of lionfish throughout the Bahamian archipelago in the early years of the invasion (Johnston and Purkis 2015b), we cannot definitively ascribe the observed pulse in lionfish recruitment to Hurricane Irene.

Two important implications for the management of lionfish in the Caribbean emerge from our study. First, in the absence of hurricanes, infrequent culling can substantially reduce lionfish density but there is much unexplained variation in response among reef patches and no difference between quarterly and biannual culling. Infrequent culling also results in modest but inconsistent gains in prey richness but has no effect on prey biomass. The two culling frequencies we examined therefore seem to offer a poor trade-off between the demonstrated conservation gains that can be achieved with frequent culling (e.g., Green et al. 2014) and the economy of time and money achieved by infrequent culling. This conclusion might only apply to networks of coral reef patches with non-negligible rates of lionfish movement and recruitment. The effect of low culling frequencies on large,

continuous expanses of coral reef remains unclear. Second, stochastic processes such as hurricanes can substantially alter the outcome of conservation management interventions like culling. In our case, lionfish density increased substantially on culled reefs after the passage of a Category 3 hurricane. If the link between the two events is causal rather than coincidental and is unaffected by culling frequency, then managers might expect lionfish culling to have more predictable effects in areas that are less likely to experience such disturbances.

Acknowledgements We are grateful to Jocelyn Curtis-Quick and interns at the Cape Eleuthera Institute for assistance in the field, and to the Earth to Ocean Research Group and Stats-Beerz study group for discussions on statistical analyses. Administrative and logistical support was provided by The Bahamas Department of Marine Resources, The Centre for Agriculture and Bioscience International, and the Cape Eleuthera Institute. Funding was provided by a Global Environment Facility-United Nations Environment Program grant to The Bahamas Department of Marine Resources, an Organization of American States Academic Graduate Scholarship to NSS, a Canada Graduate Fellowship from the Natural Sciences and Engineering Research Council (NSERC) of Canada to SG, and an NSERC Discovery grant to IMC.

References

- Abrams PA, Quince C (2005) The impact of mortality on predator population size and stability in systems with stage-structured prey. *Theor Popul Biol* 68:253–266. doi:[10.1016/j.tpb.2005.05.004](https://doi.org/10.1016/j.tpb.2005.05.004)
- Adams AJ, Ebersole JP (2004) Resistance of coral reef fishes in back reef and lagoon habitats to a hurricane. *Bull Mar Sci* 75:101–113
- Akins JL (2012) Control strategies: tools and techniques for local control. In Morris JA (ed.) *Invasive lionfish: a guide to control and management*, pp. 24–50. Gulf and Caribbean Fisheries Institute Special Publication Series Number 1, Marathon, 133 pp
- Albins MA (2013) Effects of invasive Pacific red lionfish *Pterois volitans* versus a native predator on Bahamian coral-reef fish communities. *Biol Invasions* 15:29–43
- Albins MA (2015) Invasive Pacific lionfish *Pterois volitans* reduce abundance and species richness of native Bahamian coral-reef fishes. *Mar Ecol Prog Ser* 522:231–243. doi:[10.3354/meps11159](https://doi.org/10.3354/meps11159)
- Albins MA, Hixon MA (2008) Invasive Indo-Pacific lionfish *Pterois volitans* reduce recruitment of Atlantic coral-reef fishes. *Mar Ecol Prog Ser* 367:233–238
- Andradi-Brown DA, Vermeij MJA, Slattery M et al (2017) Large-scale invasion of western Atlantic mesophotic reefs by lionfish potentially undermines culling-based management. *Biol Invasions* 19:939–954
- Arias-González JE, González-Gándara C, Cabrera JL, Christensen V (2011) Predicted impact of the invasive lionfish *Pterois volitans* on the food web of a Caribbean coral reef. *Environ Research* 111:917–925
- Barbour AB, Allen MS, Frazer TK, Sherman KD (2011) Evaluating the potential efficacy of invasive lionfish (*Pterois volitans*) removals. *PLoS ONE* 6(5):e19666. doi:[10.1371/journal.pone.0019666](https://doi.org/10.1371/journal.pone.0019666)
- Bartoń K (2016) MuMIn: multi-model inference. R package version 1.15.6. <https://CRAN.Rproject.org/package=MuMIn>
- Beecher H (1973) Effects of a hurricane on a shallow-water population of damselfish, *Pomacentrus variabilis*. *Copeia* 1973:613–615
- Benkwitt CE (2015) Non-linear effects of invasive lionfish density on native coral-reef fish communities. *Biol Invasions* 17:1383–1395
- Benkwitt CE (2016a) Central-place foraging and ecological effects of an invasive predator across multiple habitats. *Ecology* 97:2729–2739
- Benkwitt CE (2016b) Invasive lionfish increase activity and foraging movements at greater local densities. *Mar Ecol Prog Ser* 558:255–266
- Benton TG, Cameron TC, Grant A (2004) Population responses to perturbations: predictions and responses from laboratory mite populations. *J Animal Ecol* 73:983–995
- Bolker B, Su YS (2011) Coefplot2: coefficient plots, R package version 0.1.3.2. <http://CRAN.Rproject.org/package=coefplot2>
- Borski RJ, Hodson RG (2003) Fish research and the institutional animal care and use committee. *ILAR J* 44:286–294. doi:[10.1093/ilar.44.4.286](https://doi.org/10.1093/ilar.44.4.286)
- Brook LA, Johnson CN, Ritchie EG (2012) Effects of predator control on behaviour of an apex predator and indirect consequences for mesopredator suppression. *J Appl Ecol* 49:1278–1286. doi:[10.1111/j.1365-2664.2012.02207.x](https://doi.org/10.1111/j.1365-2664.2012.02207.x)
- Burnham KP, Anderson DR (2002) *Model selection and multimodel inference: a practical information-theoretic approach*, 2nd edn. Springer, New York
- Cameron TC, Benton TG (2004) Stage-structured harvesting and its effects: an empirical investigation using soil mites. *J Anim Ecol* 73:996–1006
- Campbell K, Donlan CJ (2005) Feral goat eradications on islands. *Conserv Biol* 19:1362–1374. doi:[10.1111/j.1523-1739.2005.00228.x](https://doi.org/10.1111/j.1523-1739.2005.00228.x)
- Caselle JE, Warner RR (1996) Variability in recruitment of coral reef fishes: the importance of habitat at two spatial scales. *Ecology* 77:2488–2504
- Cheal AJ, Coleman G, Delean S et al (2002) Responses of coral and fish assemblages to a severe but short-lived tropical cyclone on the Great Barrier Reef, Australia. *Coral Reefs* 21:131–142
- Costantino R, Desharnais R, Cushing J, Dennis B (1997) Chaotic dynamics in an insect population. *Science* 275:389–391. doi:[10.1126/science.275.5298.389](https://doi.org/10.1126/science.275.5298.389)
- Côté IM, Green SJ, Hixon M (2013) Predatory fish invaders: insights from Indo-Pacific lionfish in the western Atlantic and Caribbean. *Biol Conserv* 164:50–61. doi:[10.1016/j.biocon.2013.04.014](https://doi.org/10.1016/j.biocon.2013.04.014)
- Côté IM, Darling ES, Malpica-Cruz L et al (2014) What doesn't kill you makes you wary? Effect of repeated culling on the behaviour of an invasive predator. *PLoS ONE* 9:e94248. doi:[10.1371/journal.pone.0094248](https://doi.org/10.1371/journal.pone.0094248)

- Cruz F, Josh Donlan C, Campbell K, Carrion V (2005) Conservation action in the Galapagos: Feral pig (*Sus scrofa*) eradication from Santiago Island. *Biol Conserv* 121:473–478. doi:[10.1016/j.biocon.2004.05.018](https://doi.org/10.1016/j.biocon.2004.05.018)
- Cure K, Benkwitt CE, Kindinger TL et al (2012) Comparative behavior of red lionfish *Pterois volitans* on native Pacific versus invaded Atlantic coral reefs. *Mar Ecol Prog Ser* 467:181–192
- Dahl KA, Patterson WF (2014) Habitat-specific density and diet of rapidly expanding invasive red lionfish, *Pterois volitans*, populations in the northern Gulf of Mexico. *PLoS ONE* 9(8):e105852. doi:[10.1371/journal.pone.0105852](https://doi.org/10.1371/journal.pone.0105852)
- Dahl KA, Patterson WF, Snyder RA (2016) Experimental assessment of lionfish removals to mitigate reef fish community shifts on northern Gulf of Mexico artificial reefs. *Mar Ecol Prog Ser* 558:207–221. doi:[10.3354/meps11898](https://doi.org/10.3354/meps11898)
- de León R, Vane K, Bertuol P et al (2013) Effectiveness of lionfish removal efforts in the southern Caribbean. *Endanger Species Res* 22:175–182
- De Roos AM, Schellekens T, van Kooten T et al (2007) Food-dependent growth leads to overcompensation in stage-specific biomass when mortality increases: the influence of maturation versus reproduction regulation. *Am Nat* 170:E59–E76. doi:[10.1086/520119](https://doi.org/10.1086/520119)
- Doherty TS, Ritchie EG (2016) Stop jumping the gun: a call for evidence-based invasive predator management. *Conserv Lett* 10(1):1–8. doi:[10.1111/conl.12251](https://doi.org/10.1111/conl.12251)
- Frazer TK, Jacoby C, Edwards M et al (2012) Coping with the lionfish invasion: can targeted removals yield beneficial effects? *Rev Fish Sci* 20:185–191. doi:[10.1080/10641262.2012.700655](https://doi.org/10.1080/10641262.2012.700655)
- Froese R, Pauly D (eds) (2016) FishBase. World Wide Web electronic publication. www.fishbase.org, version (10/2016)
- Green SJ, Akins JL, Côté IM (2011) Foraging behaviour and prey consumption in the Indo-Pacific lionfish on Bahamian coral reefs. *Mar Ecol Prog Ser* 433:159–167. doi:[10.3354/meps09208](https://doi.org/10.3354/meps09208)
- Green SJ, Akins JL, Maljković A, Côté IM (2012) Invasive lionfish drive Atlantic coral reef fish declines. *PLoS ONE* 7:e32596. doi:[10.1371/journal.pone.0032596](https://doi.org/10.1371/journal.pone.0032596)
- Green SJ, Tamburello N, Miller SE et al (2013) Habitat complexity and fish size affect the detection of Indo-Pacific lionfish on invaded coral reefs. *Coral Reefs* 32:413–421. doi:[10.1007/s00338-012-0987-8](https://doi.org/10.1007/s00338-012-0987-8)
- Green SJ, Dulvy NK, Brooks ALM et al (2014) Linking removal targets to the ecological effects of invaders: a predictive model and field test. *Ecol Appl* 24:1311–1322
- Harmelin-Vivien ML (1994) The effects of storms and cyclones on coral reefs: a review. *J Coast Res* 12:211–231
- Ingeman KE (2016) Lionfish cause increased mortality rates and drive local extirpation of native prey. *Mar Ecol Prog Ser* 558:235–245. doi:[10.3354/meps11821](https://doi.org/10.3354/meps11821)
- Johnston MW, Purkis SJ (2015a) A coordinated and sustained international strategy is required to turn the tide on the Atlantic lionfish invasion. *Mar Ecol Prog Ser* 533:219–235. doi:[10.3354/meps11399](https://doi.org/10.3354/meps11399)
- Johnston MW, Purkis SJ (2015b) Hurricanes accelerated the Florida–Bahamas lionfish invasion. *Glob Chang Biol* 21:2249–2260. doi:[10.1111/gcb.12874](https://doi.org/10.1111/gcb.12874)
- Kaufman SL (1983) Coral reefs effects of Hurricane Allen on reef fish assemblages. *Coral Reefs* 2:43–47
- Lieury N, Ruetten S, Devillard S et al (2015) Compensatory immigration challenges predator control: an experimental evidence-based approach improves management. *J Wildl Manag* 79:425–434
- Mazerolle MJ (2016) AICcmodavg: model selection and multimodel inference based on (Q)AIC(c). R package version 2.0-4. <https://cran.r-project.org/package=AICcmodavg>
- Morris J Jr (ed) (2012) Invasive lionfish: a guide to control and management. Gulf and Caribbean Fisheries Institute, Marathon
- Morris J, Akins JL (2009) Feeding ecology of invasive lionfish (*Pterois volitans*) in the Bahamian archipelago. *Environ Biol Fishes* 86:389–398. doi:[10.1007/s10641-009-9538-8](https://doi.org/10.1007/s10641-009-9538-8)
- Morris JA, Shertzer KW, Rice JA (2011) A stage-based matrix population model of invasive lionfish with implications for control. *Biol Invasions* 13:7–12. doi:[10.1007/s10530-010-9786-8](https://doi.org/10.1007/s10530-010-9786-8)
- Muñoz RC, Currin CA, Whitfield PE (2011) 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. doi:[10.3354/meps09154](https://doi.org/10.3354/meps09154)
- Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining R² from generalized linear mixed-effects models. *Methods Ecol Evol* 4:133–142. doi:[10.1111/j.2041-210x.2012.00261.x](https://doi.org/10.1111/j.2041-210x.2012.00261.x)
- Nogales M, Martín A, Tershy BR et al (2004) A review of feral cat eradication on islands. *Conserv Biol* 18:310–319
- Pinheiro J, Bates D, DebRoy S, Sarkar D and R Core Team (2016) nlme: linear and nonlinear mixed effects models. R package version 3.1-127. <https://CRAN.R-project.org/package=nlme>
- Quinn GP, Keough MJ (2002) Experimental design and data analysis for biologists, first. Cambridge University Press, Cambridge
- R Development Core Team (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>
- Sale PF, Sharp BJ (1983) Correction for bias in visual transect censuses of coral reef fishes. *Coral Reefs* 2:37–42. doi:[10.1007/BF00304730](https://doi.org/10.1007/BF00304730)
- Smith RK, Pullin AS, Stewart GB, Sutherland WJ (2010) Effectiveness of predator removal for enhancing bird populations. *Conserv Biol* 24:820–829. doi:[10.1111/j.1523-1739.2009.01421.x](https://doi.org/10.1111/j.1523-1739.2009.01421.x)
- Tamburello N, Côté LM (2015) Movement ecology of Indo-Pacific lionfish on Caribbean coral reefs and its implications for invasion dynamics. *Biol Invasions* 17:1639–1653
- Tracey SR, Baulch T, Hartmann K et al (2015) Systematic culling controls a climate driven, habitat modifying invader. *Biol Invasions* 17:1885–1896. doi:[10.1007/s10530-015-0845-z](https://doi.org/10.1007/s10530-015-0845-z)
- Walsh WJ (1983) Stability of a coral reef fish community following a catastrophic storm. *Coral Reefs* 2:49–63
- Wantiez L, Chateau O, Le Mouellic S (2006) Initial and mid-term impacts of cyclone Erica on coral reef fish communities and habitat in the South Lagoon Marine Park of New Caledonia. *J Mar Biol Assoc U K* 86:1229–1236

- Weidel BC, Josephson DC, Kraft CE (2007) Littoral fish community response to smallmouth bass removal from an adirondack lake. *Trans Am Fish Soc* 136:778–789. doi:[10.1577/T06-091.1](https://doi.org/10.1577/T06-091.1)
- Whitlock M, Schuller D (2008) *The analysis of biological data*, first. Roberts and Company Publishers, Greenwood Village
- Wickham H (2007) Reshaping data with the reshape package. *J Stat Software* 21:1–20
- Woodley JD, Chornesky EA, Cliffo PA, Sid EM (1981) Hurricane Allen's impact on Jamaican coral reefs. *Science* 214(80):749–755
- Zipkin EF, Sullivan PJ, Cooch EG et al (2008) Overcompensatory response of a smallmouth bass (*Micropterus dolomieu*) population to harvest: release from competition? *Can J Fish Aquat Sci* 65:2279–2292. doi:[10.1139/F08-133](https://doi.org/10.1139/F08-133)
- Zipkin EF, Kraft CE, Cooch EG, Sullivan PJ (2009) When can nuisance and invasive species control efforts backfire? *Ecol Appl* 19:1585–1595
- Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) *Mixed effects models and extensions in ecology with R*. Springer, New York