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ORIGINAL PAPER

Large-scale invasion of western Atlantic mesophotic reefs by lionfish potentially undermines culling-based management

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Abstract The detrimental effects of invasive lionfishes (*Pterois volitans* and *Pterois miles*) on western Atlantic shallow reefs are well documented, including declines in coral cover and native fish populations, with disproportionate predation on critically endangered reef fish in some locations. Yet despite individuals reaching depths >100 m, the role of mesophotic coral ecosystems (MCEs; reefs 30–150 m) in lionfish ecology has not been addressed. With lionfish control programs in most invaded locations limited to 30 m by diving restrictions, understanding the role of MCEs in lionfish distributions remains a critical knowledge gap potentially hindering conservation management. Here we synthesise unpublished and previously published studies of lionfish abundance and body length at paired shallow reef (0–30 m) and MCE sites in 63 locations in seven western Atlantic countries and eight sites in three Indo-Pacific countries where lionfish are native. Lionfish were found at similar abundances across the depth gradient from shallow to adjacent MCEs, with no difference between invaded and native sites. Of the five invaded countries where length data were available three had larger lionfish on mesophotic than shallow reefs, one showed no significant difference,

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while the fifth represented a recently invaded site. This suggests at least some mesophotic populations may represent extensions of natural ontogenetic migrations. Interestingly, despite their shallow focus, in many cases culling programs did not appear to alter abundance between depths. In general, we identify widespread invasive lionfish populations on MCE that could be responsible for maintaining high densities of lionfish recruits despite local shallow-biased control programs. This study highlights the need for management plans to incorporate lionfish populations below the depth limit of recreational diving in order to address all aspects of the local population and maximise the effectiveness of control efforts.

Keywords *Pterois volitans* · *Pterois miles* · Lionfish · Mesophotic · MCE · Invasive species · Twilight zone · Ontogenetic migration

Introduction

Fewer than 16% of marine environments are now considered to be free of invasive species and the threat to biodiversity they represent (Molnar et al. 2008). The major impacts they cause to natural ecosystem health and functioning, whether as predators, competitors, pathogens or parasites are well documented (Simberloff et al. 2013) and present an enormous dilemma for conservation practitioners. The ability to cross environmental barriers combined with high reproductive output facilitates the rapid spread of many marine invasive species (Côté et al. 2013) while the difficulties associated with removing individuals makes complete eradication almost impossible once invasives become established across a large geographical range (Thresher and Kuris 2004). Instead managers are often forced to limit their efforts to local control, and to focus on mitigating the most severe impacts rather than seeking complete eradication (Williams and Grosholz 2008).

The appearance of lionfish in the western Atlantic has led to one of the fastest marine invasions ever recorded (Schofield 2010). Native to the Indo-Pacific, the lionfishes *Pterois volitans* and *Pterois miles* (Family: Scorpaenidae) were introduced to the western Atlantic in the early 1980s and have since become a widespread conservation concern in the region (Côté et al. 2013). Lionfish have proved to be highly effective predators on invaded shallow coral reefs benefiting from young age of maturity combined with high fecundity, highly generalist feeding strategy, lack of natural predators and parasites, and prey naivety

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(Côté et al. 2013). Invasive population densities are consequently five times greater than those of lionfish in their native range, although the presence of additional co-occurring Indo-Pacific lionfish species may partially reduce this overall disparity (Darling et al. 2011). Invasive lionfish have been reported to reduce native fish recruitment by up to 79% (Albins and Hixon 2008) and drive declines in overall prey fish biomass of up to 65% (Green et al. 2012) on shallow patch reef systems. Their impacts on mesophotic reefs in The Bahamas have shown their potential to cause declines in coral cover (Lesser and Slattery 2011), while dietary analysis has suggested disproportionate predation on critically-endangered reef fish species in some locations (Rocha et al. 2015). Lionfish density appears limited by food availability (Benkwitt 2013), with invasive individuals 1.5 times longer and three times heavier on average than those in their native range (Darling et al. 2011).

Invasive lionfish are now established from North Carolina, USA in the north, throughout most of the Greater Caribbean and Gulf of Mexico (Schofield 2010), with an individual collected as far south as Brazil (Ferreira et al. 2015). This wide spatial distribution makes complete eradication impossible with current methods that focus on active culling to reduce local population densities. Culling efforts are often managed/regulated by government and conducted by volunteer recreational SCUBA divers using Hawaiian sling hand spears or pole spears (Morris et al. 2009). Evidence suggests that culling successfully reduces lionfish abundance on shallow reefs (Frazer et al. 2012), and such reductions aid the recovery of native fish communities (Green et al. 2014). However, continued culling is crucial as lionfish populations quickly recover after culling ceases (Arias-González et al. 2011).

It is vital that the ecology and distribution of the invasive species is fully understood to design the most effective form of control. If invasive species are widely dispersed habitat generalists, such as lionfish, then they will likely exhibit source-sink population dynamics, with individuals in certain areas disproportionately contributing to recruitment (Travis and Park 2004). Depth is recognised as a fish refuge from harvesting pressure, with major differences in biomass and species composition detected across even small depth gradients (Tyler et al. 2009; Bejarano et al. 2014a). Yet few studies have considered how control programs are affected by depth, despite several major shallow reef marine invasive species being recorded across wide depth ranges (Andradi-Brown et al. 2016).

Lionfish are found on mesophotic coral ecosystems (MCEs; reefs from 30 to 150 m) in their native range, having been reported at 65 m in the Red Sea (Brokovich et al. 2008), from trawl surveys at 75 m in New Caledonia (Kulbicki et al. 2012) and remotely operated vehicle (ROV) observations below 80 m in American Samoa (Wright 2005). Lionfish have also been anecdotally observed on MCEs throughout much of their invaded range, although comprehensive sampling at mesophotic depths remains lacking. For example, lionfish have been recorded down to 55 m in Puerto Rico (Bejarano et al. 2014a), over 100 m in The Bahamas (Lesser and Slattery 2011), 112 m in the northwestern Gulf of Mexico (Nuttall et al. 2014), and 120 m in Honduras (Schofield 2010). Even though many western Atlantic MCE observations report high abundances, logistical difficulties associated with accessing mesophotic reefs (Pyle 1998) mean that culling is largely restricted to shallow reefs. With active management interventions absent from most MCEs it is therefore feasible that deeper reefs are providing a refuge environment for invasive lionfish.

Many coral reef fish species are known to undergo ontogenetic migrations, typically from shallow habitats (mangroves, seagrass beds and nearshore reefs) to deeper reef habitats (Appeldoorn et al. 2003). These ontogenetic movements are believed to be driven by trade-offs between maximising food availability (and thus growth rates), while minimising predation risk (Kimirei et al. 2013). Some fish even demonstrate multiple stages of ontogenetic habitat shifts, incorporating transition habitats during intermediate life stages (Grol et al. 2014). Ontogenetic inter-habitat migrations by lionfish have been previously reported, with juveniles found in mangroves, seagrass beds and shallow sheltered reefs before migrating to reef slopes (10–30 m) (Claydon et al. 2012). It is not clear whether lionfish populations on MCEs represent a continuation of this ontogenetic migration, with lionfish primarily moving from the shallows to MCEs, or a less depth-structured population with lionfish movement in both directions between shallow reefs and MCEs.

This study synthesises data from multiple studies throughout the invaded and native range of lionfish, encompassing both shallow and mesophotic depths, in

order to explore the role of deeper reef environments in invasive lionfish ecology and to inform future management efforts. We use a meta-analysis approach to compare adjacent shallow-mesophotic paired reefs to identify whether anecdotal large-scale patterns in lionfish distributions are supported by available evidence. Specifically, we address: (1) the relative abundance of lionfish across the depth gradient in both native and invaded ranges; (2) whether body size varies between shallow and mesophotic reefs; and, (3) how these patterns with depth are affected by the availability of hard substrata, time since site invasion, and active management via culling.

Materials and methods

Study design

Study sites were identified through discussions at the Second International Mesophotic Workshop (Eilat, Israel, October 2014). Mesophotic researchers at the workshop, along with key collaborators, provided lionfishes (*P. volitans* and/or *P. miles*) abundance and/or body length data from reef sites shallower than 30 m (shallow) and adjacent deep reefs between 30 and 150 m (mesophotic). These depth zones follow the widely accepted definition of shallow and mesophotic reefs (Hinderstein et al. 2010), allowing broad patterns between the two to be tested. MCEs are broadly defined as reef communities harbouring zooxanthellate corals, though the dominant reef organisms can also be non-zooxanthellate corals, sponges or algae, that occur at depths from 30 m to >150 m (Hinderstein et al. 2010). Lionfish abundance measures were based on a variety of visual and video-transect techniques, but were consistent within each shallow-mesophotic pairing (summarised in Table 1). Fish length measurements used a combination of underwater visual estimates (broad size categories), post-dive measurement after spearing, and stereo-video in situ measurements (Table 1). Full details of all methods and site locations are included in the Electronic Supplementary Materials.

For inclusion, data from each site were required to include the following information for both shallow and mesophotic depths: (1) mean abundance and/or body length of lionfish; (2) standard deviation/standard error of mean; (3) number of replicates; (4) depths for all replicates; (5) survey year; and, (6) survey methodology. Where possible, we also recorded the following: (1) year of lionfish site invasion (non-native sites); (2) shallow and mesophotic percentage hard-substrata cover; and, (3) presence/absence of regular lionfish culling. Hard substrata included all benthic habitat types excluding mud, sand and rubble following Gratwicke and Speight (2005). Presence/absence of regular lionfish culling was based on information available from the data providers and, because of a general lack of intensity data, culling was treated as a categorical variable defined as regular local spearing of lionfish by divers.

In total, data incorporated lionfish abundance from 63 sites in seven western Atlantic (invasive) countries and eight sites from three Indo-Pacific/Red Sea (native) countries, with lionfish length data from 39 sites in six invasive countries and seven sites in three native countries (Fig. 1; Table 1). Shallow data ranged 5–30 m, while mesophotic data ranged 30–110 m. While the majority of data are previously unpublished, published data were also extracted from (1) broader fish community studies with no direct comparison of lionfish populations across depth gradients, specifically for The Bahamas (Lesser and Slattery 2011), Israel (Brokovich et al. 2008) and Puerto Rico (Bejarano et al. 2014a), and (2) a study on lionfish culling effectiveness for Bonaire and some Curaçao sites (de León et al. 2013). When a site had multiple survey depths within a single zone, data were combined and mean depth (weighted by replication) used. Western Atlantic studies were totals of both invasive lionfishes (*P. volitans* and *P. miles*), while Indo-Pacific studies were for *P. volitans* (Micronesia, Philippines) and *P. miles* (Israel) separately, as these species do not co-occur in these locations. While *P. volitans* and *P. miles* are distinct species, they seem to be ecologically and morphologically analogous (Freshwater et al. 2009).

Data analysis

To compare sites surveyed using different methods, summary data from each site were converted into a standardised effect size, Hedges' *d* (Hedges and Olkin 1985; Koricheva et al. 2013). Hedges' *d* (Eq. 1) is based on the standardised mean difference (SMD)

Table 1 Numbers of individual shallow-mesophotic paired sites used in analysis for each country, along with the mean shallow and mesophotic survey depth, maximum mesophotic survey depth, and methods used for lionfish abundance and length surveys

Country	Abundance					Length				
	Number of sites	Mean shallow depth (m)	Mean mesophotic depth (m)	Maximum mesophotic depth (m)	Methods	Number of sites	Mean shallow depth (m)	Mean mesophotic depth (m)	Maximum mesophotic depth (m)	Methods
Western Atlantic										
The Bahamas	2	13	54	91	Visual transects	2	13	54	91	Visual estimation
Bermuda	4	15	50	60	Visual transects	1	15	70	65	Spearing
Bonaire	33	19	35	35	Visual transects	21	19	35	35	In water measurement
Cayman Islands	3	20	61	91	Visual transects	0	–	–	–	–
Curaçao	12	19	38	90	Visual transects	9	21	35	35	In water measurement, spearing
Honduras	5	13	45	91	Visual transects, stereo-video transects	2	14	57	110	Spearing, stereo-video camera drops
Puerto Rico	4	25	55	70	Visual transects	4	25	50	70	Visual estimation
Indo-Pacific										
Israel	2	7	46	65	Visual transects	1	5	49	65	Visual estimation
Federated States of Micronesia	3	17	46	61	Visual transects	3	17	46	61	Visual estimation
Philippines	3	12	46	61	Visual transects	3	12	46	61	Visual estimation

See Electronic Supplementary Materials for further details

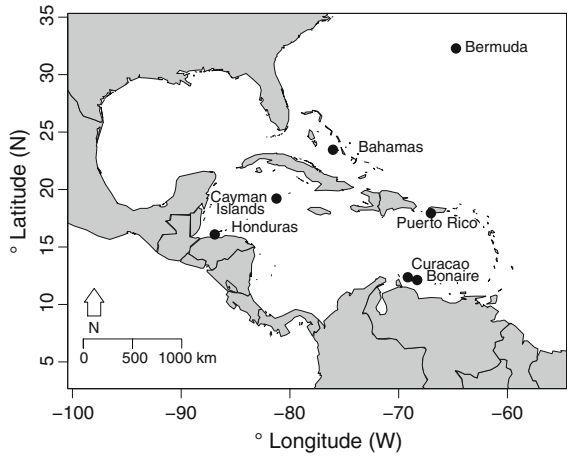

Fig. 1 Western Atlantic lionfish survey locations included in this study, and surveyed between 2009 and 2014. Multiple paired shallow-mesophotic sites were located within the marked region for each country (see Electronic Supplementary Materials for individual sites)

between two groups (here depth zones), where $\overline{X_s}$ and $\overline{X_m}$ represent mean lionfish abundance or body length at a single shallow-mesophotic pairing (respectively). Hedges' d values can be positive or negative indicating the direction and magnitude of effect, with $d = 0$ representing no difference. Negative effect sizes indicate greater abundances or larger lionfish at mesophotic depths, while a positive effect size indicates the reverse. Pooled standard deviation (s_{pooled}) was calculated from the standard deviation of means for shallow and mesophotic depths (Eq. 2), where s_s and s_m represent standard deviation, and n_s and n_m represent number of replicates within a site for shallow and mesophotic reefs respectively. J (Eqs. 1 and 3) is a correction for small sample sizes, allowing Hedges' d to be reliable with small numbers of replicates.

$$d = \frac{\overline{X_s} - \overline{X_m}}{s_{pooled}} J \tag{1}$$

$$s_{pooled} = \sqrt{\frac{(n_s - 1)(s_s)^2 + (n_m - 1)(s_m)^2}{n_s + n_m - 2}} \tag{2}$$

$$J = 1 - \frac{3}{4(n_s + n_m - 2) - 1} \tag{3}$$

The variance of each Hedges' d estimate was calculated using Eq. 4.

$$v_d = \frac{n_s + n_m}{n_s n_m} + \frac{d^2}{2(n_s + n_m)} \tag{4}$$

When fitting models using data obtained using different methods, between-site heterogeneity in effect sizes must be considered (Koricheva et al. 2013). Under standardised methods, heterogeneity between replicates tends to be from sampling variance alone. To account for sampling variation within and between sites, we fitted random-effects models based on Hedges' d estimates and variance. Random-effects models were fitted to calculate summary effects for sites with and without lionfish culling for each country, and overall for all sites within the invasive and native ranges. Mixed-effects models were then used to test the influence of potential effect modifiers on effect sizes and direction. Mixed and random-effects models were fitted using the DerSimonian-Laird estimator (Koricheva et al. 2013), with sites weighted by the inverse of their effect size variance for calculations of summary effects. To identify within-study heterogeneity I^2 and H^2 statistics were calculated. I^2 quantifies the percentage of heterogeneity that can be explained by between-study variance. By calculating heterogeneity as a percentage, it is possible to directly compare I^2 values between meta-analyses with different numbers of studies and effect metrics (Higgins and Thompson 2002). H^2 is another related measure of heterogeneity with $H^2 = 1$ indicating homogeneity of treatment effects and larger values providing increasing evidence of heterogeneity (Higgins and Thompson 2002). For testing the amount of heterogeneity accounted for when fitting mixed-effects models, a *pseudo-R^2* value was calculated following Raudenbush (2008). All analyses were conducted in the statistical program R (R Core Team 2013) with effect sizes calculated using the 'escalc' function and models fitted and heterogeneity estimated with the 'rma.uni' function in the metafor package (Viechtbauer 2010).

Results

Variation in lionfish abundance with depth

We found no overall difference in the abundance of lionfish between shallow and mesophotic depths at invaded sites without culling (Fig. 2a, SMD = −0.06,

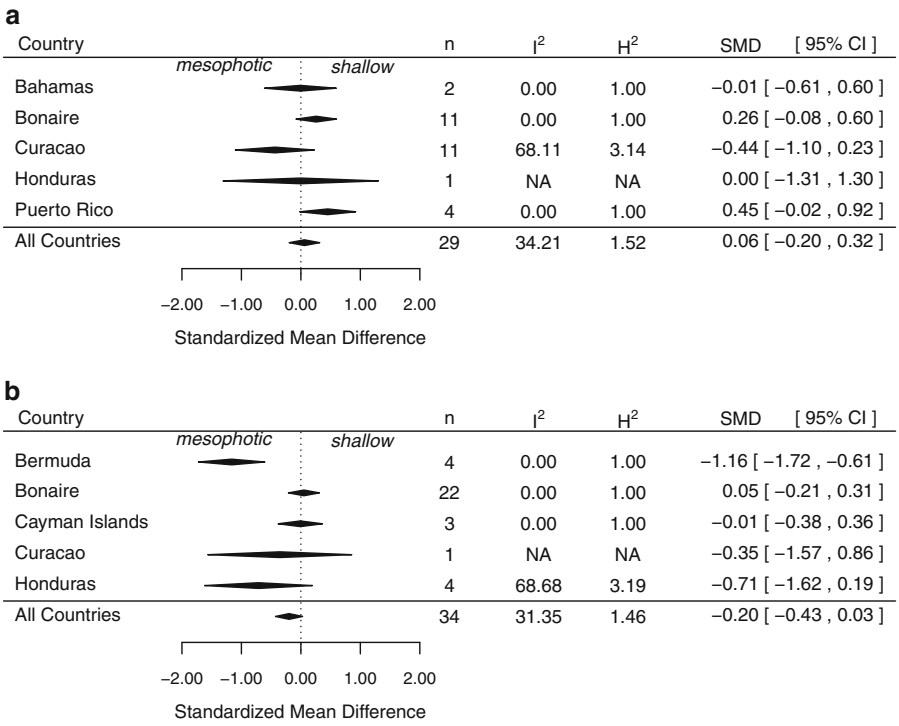

Fig. 2 Summary random-effect models for lionfish abundance at western Atlantic sites with countries presented individually and grouped, showing **a** sites without active lionfish culling and, **b** sites with active lionfish culling. *Diamonds centre* represent the mean summary effect, and the width the 95% confidence interval (CI). Diamonds intersecting the *dashed vertical line* indicate the summary effect is not significantly different to zero, while n = number of study sites (each site contains multiple replicate surveys—see Electronic Supplementary Materials for individual site information), I^2 = residual heterogeneity/unaccounted variability, H^2 = unaccounted variability/sampling variability, *SMD* Standardized Mean Difference, and *NA* values not able to be calculated due to small sample sizes. Positive effect sizes (SMD) indicate greater lionfish abundance on shallow reefs than mesophotic reefs, while negative effect sizes indicate the reverse

95% CI −0.20, 0.32), or those with culling (Fig. 2b, SMD = −0.20, 95% CI −0.43, 0.03). No individual invaded country exhibited differences in abundance between depth ranges at sites without culling (Fig. 2a). Differences were found in Bermuda where culling takes place (Fig. 2b), with abundance higher at mesophotic depths (SMD = −1.16, 95% CI −1.72, −0.61).

Native range sites exhibited similar abundance patterns to the western Atlantic (Fig. 3a; SMD = −0.14, 95% CI −0.46, 0.17). When tested in a fixed-effects model, there was no difference between the overall summary effect for Indo-Pacific sites and either non-culled western Atlantic sites ($z = -1.32, p = 0.19$) or culled western Atlantic sites ($z = 0.38$, $p = 0.70$). Invasive lionfish populations therefore appear to exhibit a similar depth-distribution pattern to those in their native range in terms of abundance.

Despite no overall difference in lionfish abundance between shallow and mesophotic reefs, the magnitude and direction of each site's observed effect size (SMD) was significantly correlated with both time since invasion and availability of hard substrata (Table 2). There was a negative relationship between SMD and time since invasion ($t = -2.07, p = 0.038$), meaning surveys conducted soon after initial invasion found a greater abundance of lionfish on shallow reefs compared to those conducted at increased time intervals after invasion. Time since first lionfish observation at our study sites ranged from 2 to 14 years. Shallow hard-substrata cover also negatively correlated with effect size ($t = -2.14, p = 0.032$), indicating that at sites with greater shallow hard-substrata availability a greater abundance of lionfish was found at mesophotic depths. Mesophotic hard-substrata cover was positively correlated with effect size ($t = 2.76$, $p = 0.006$), suggesting that at sites with lower

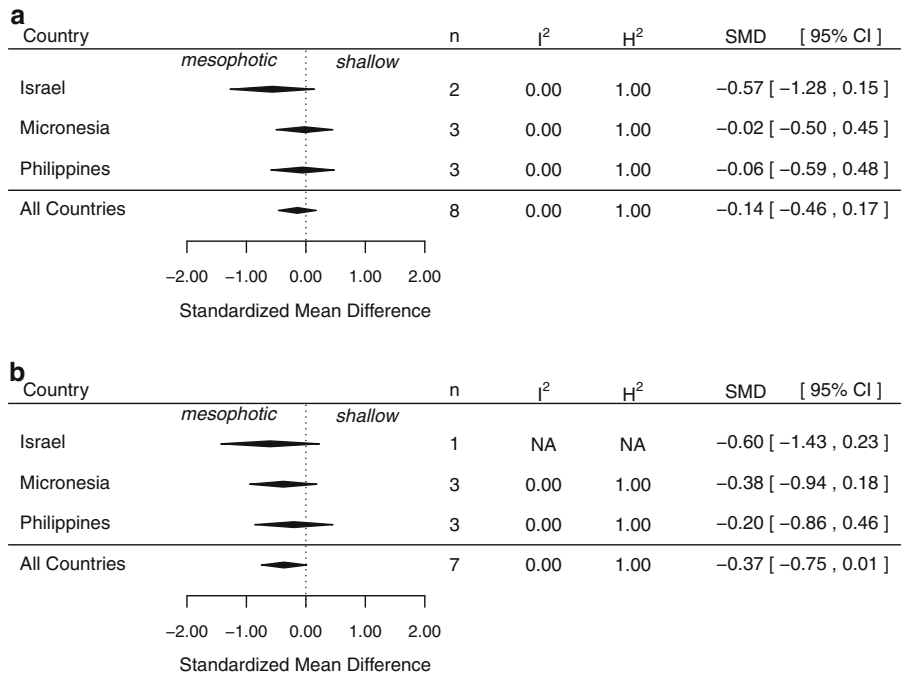

Fig. 3 Summary random-effect models for **a** lionfish abundance and **b** mean lionfish body length at Indo-Pacific reef sites, with countries presented individually and grouped. Positive effect sizes (SMD) indicate greater abundance or larger mean body length of lionfish on shallow reefs than mesophotic reefs, while negative effect sizes indicate the reverse. See Fig. 2 legend for full description

Table 2 Mixed-effect model testing effect modifiers impacting western Atlantic lionfish abundance effect sizes

Parameter	Estimate	SE	t value	*p* value
Intercept	0.904	0.517	1.749	0.080
Time since first lionfish observation	−0.204	0.099	−2.073	0.038*
Culling	0.001	0.191	0.004	0.997
Shallow hard substrate % cover	−0.019	0.009	−2.140	0.032*
Mesophotic hard substrate % cover	0.018	0.007	2.764	0.006**

Effect modifiers fitted as fixed-effects in the random-effects model. Positive estimates indicate a positive correlation between individual studies' Hedges' d and the variable, where $n = 54$, $I^2 = 21.50\%$, $H^2 = 1.27$ and $R^2 = 27.79\%$

Asterisks indicate significance level, with * indicating $p < 0.05$ and ** indicating $p < 0.01$

mesophotic hard-substrata availability, a greater abundance of lionfish was found at mesophotic depths. The presence of culling (Table 2) had no impact on the mean difference in abundance between shallow and mesophotic sites. The addition of these effect modifiers to the model accounts for 27.79% of the between-study variation observed, with I^2 reduced from 40.79% (all sites random-effect model with no effect modifiers) to 21.50%.

Variation in lionfish body size with depth

We found no overall difference in mean lionfish body length between shallow and mesophotic invaded sites for all sites without culling combined (Fig. 4a). However, at the country level, those sites without culling in The Bahamas, Curaçao and Honduras showed larger lionfish at mesophotic depths than shallow depths (Fig. 4a). Bonaire data showed no

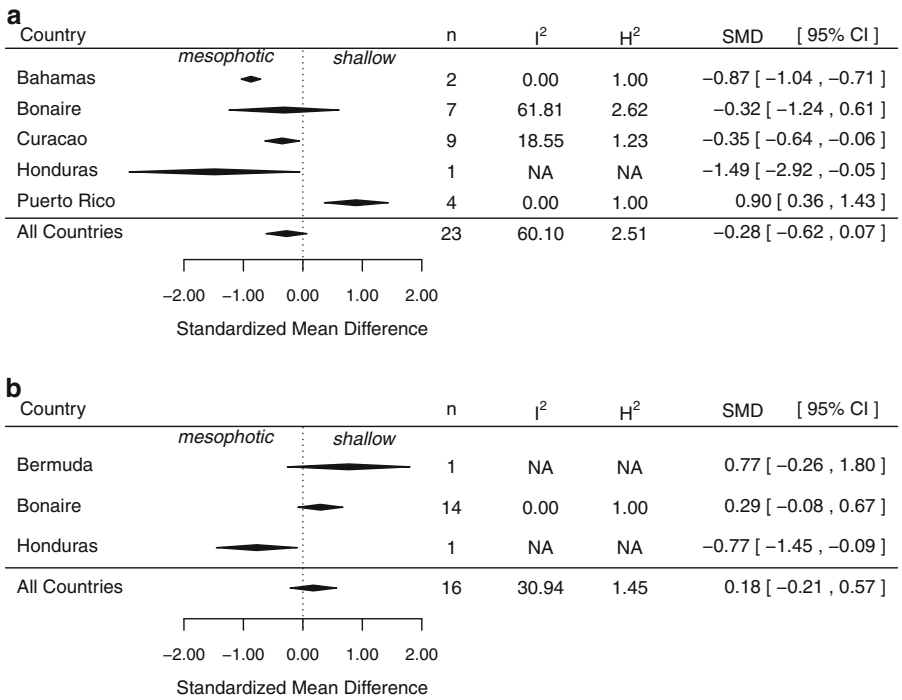

Fig. 4 Summary random-effect models for lionfish body length at Caribbean sites with countries presented individually and grouped, showing **a** sites without active lionfish culling and **b** sites with active lionfish culling. Positive effect sizes (SMD) indicate larger mean lionfish body length on shallow reefs than mesophotic reefs, while negative effect sizes indicate the reverse. See Fig. 2 legend for full description

difference (SMD = −0.32, 95% CI −1.24, 0.61), while Puerto Rico had larger lionfish in the shallows (SMD = 0.90, 95% CI −0.36, 1.43). At sites where culling takes place, there was no difference in mean body length between depth ranges (Fig. 4b, SMD = 0.18, 95% CI −0.21, 0.57). Comparisons within their native-range found no difference in body length between shallow and mesophotic depths (Fig. 3b, SMD = −0.37, 95% CI −0.75, 0.01). This native range summary effect was not different to non-culled invaded sites ($z = -0.45$, $p = 0.65$), but was different to invaded sites with culling ($z = -2.19$, $p = 0.028$).

The differences in mean lionfish body length between invaded depth ranges were affected by the time since first lionfish observation and the presence/absence of culling (Table 3). Time since invasion had a negative relationship with effect size ($t = -3.42$, $p = 0.001$), indicating more initial similarity in fish lengths between depths, but progressively larger fish on mesophotic and/or smaller fish on shallow reefs with time. Presence or absence of culling was also highlighted as an important modifier affecting length distributions ($t = 3.05$, $p = 0.002$), with different overall summary effects for invaded sites with and without culling ($z = -2.03$, $p = 0.04$). Neither shallow nor mesophotic hard-substrata cover had an effect on lionfish body lengths. Including these factors in the model accounted for 83.39% of the between-study heterogeneity, with I^2 in a random-effects model for all sites without effect modifiers reduced from 44.75 to 10.57%.

Lionfish length distributions have generally been found to be unimodal, however, cohort effects can occasionally be observed, particularly as new invasions occur (Trégarot et al. 2015). To incorporate lionfish length data from all sites, mean length had to be used. To test for potential bimodality, we tested the variance of lionfish lengths against depth for all shallow and mesophotic western Atlantic sites using Spearman's rank correlation coefficient. Our results do not suggest any consistent difference in unimodal or bimodal length distributions in either depth zone, as we found no relationship between length variance and

Table 3 Mixed-effect model testing effect modifiers impacting western Atlantic lionfish body length effect sizes

Parameter	Estimate	SE	t value	p value
Intercept	0.778	0.626	1.243	0.214
Time since first lionfish observation	−0.343	0.100	−3.415	0.001**
Culling	0.721	0.236	3.054	0.002**
Shallow hard substrate % cover	−0.010	0.011	−0.944	0.345
Mesophotic hard substrate % cover	0.007	0.007	0.968	0.333

Effect modifiers fitted as fixed-effects in the random-effects model. Positive estimates indicate a positive correlation between individual studies' Hedges' d and the variable, where $n = 30$, $I^2 = 10.57\%$, $H^2 = 1.12$ and $R^2 = 83.39\%$

Stars indicate significance level, with * indicating $p < 0.05$ and ** indicating $p < 0.01$

depth for non-culled ($\rho = <0.01$, $p = 0.99$, $n = 92$) or culled ($\rho = -0.191$, $p = 0.13$, $n = 64$) western Atlantic sites.

Discussion

Invasive lionfish have widely colonised mesophotic reefs throughout the western Atlantic and at the time of surveying exist at densities similar to those on nearby shallow reefs, which have to date received the vast majority of research and management attention. Importantly, we also show that individual lionfish in some locations are larger on mesophotic reefs than their shallow counterparts. These findings raise important questions about the role of MCEs in lionfish life history, such as whether MCEs are acting as depth refuges for invasive populations, and so providing a local source of recruits despite removal efforts. Our results also indicate that without direct human intervention via culling the relative abundance and length distributions between shallow and mesophotic depths appear similar for invaded and native sites, suggesting a similar role for MCEs between the two regions.

Mesophotic reefs as a potential refuge for invasive lionfish

Across the western Atlantic region, we found no difference in lionfish abundances between shallow and mesophotic depths, highlighting an urgent need to integrate deeper reefs into lionfish management plans, which currently focus almost exclusively on removal from shallow environments. Supported by previous shallow-reef research (e.g. Claydon et al. 2012), combined with our results of (1) no difference in lionfish abundance between depth zones in most locations, (2) larger lionfish on MCEs in three locations, and (3) increasing proportional abundance and mean length of lionfish found on MCEs with greater time since invasion, we propose that lionfish population resilience benefits from substantial mature mesophotic lionfish populations (Fig. 5). Specifically, lionfish invade new sites at shallow depths via larval settlement from floating egg bundles, with juveniles and then adults subsequently migrating to greater depths, which happen to be below the range of lionfish control programs.

At first glance, this presents a major challenge to lionfish managers, as culling programs are often restricted to shallower depths through a reliance on volunteer recreational divers to achieve sufficient effort and by the financial and logistical complications of technical diving (Pyle 1998). Lionfish culling is most effective if adults of all age classes are targeted (Arias-González et al. 2011), with shallow culling resulting in reduced average lengths and abundance of shallow individuals (Frazer et al. 2012), while work on other species has shown that fishing at restricted depth zones can cause fine-scale length-distribution changes (Lindfield et al. 2014).

Previous research into lionfish depth distributions at invaded locations absent of culling has proved inconclusive. Claydon et al. (2012) reported greater sightings of lionfish, per unit effort, at 10–30 m than at 0–5 m in the Turks and Caicos Islands, and Lee et al. (2012) found greater abundances of lionfish with larger body lengths on surveys deeper than, compared to shallower than, 13 m in Jamaica. In contrast, in their native ranges, McTee and Grubich (2014) found

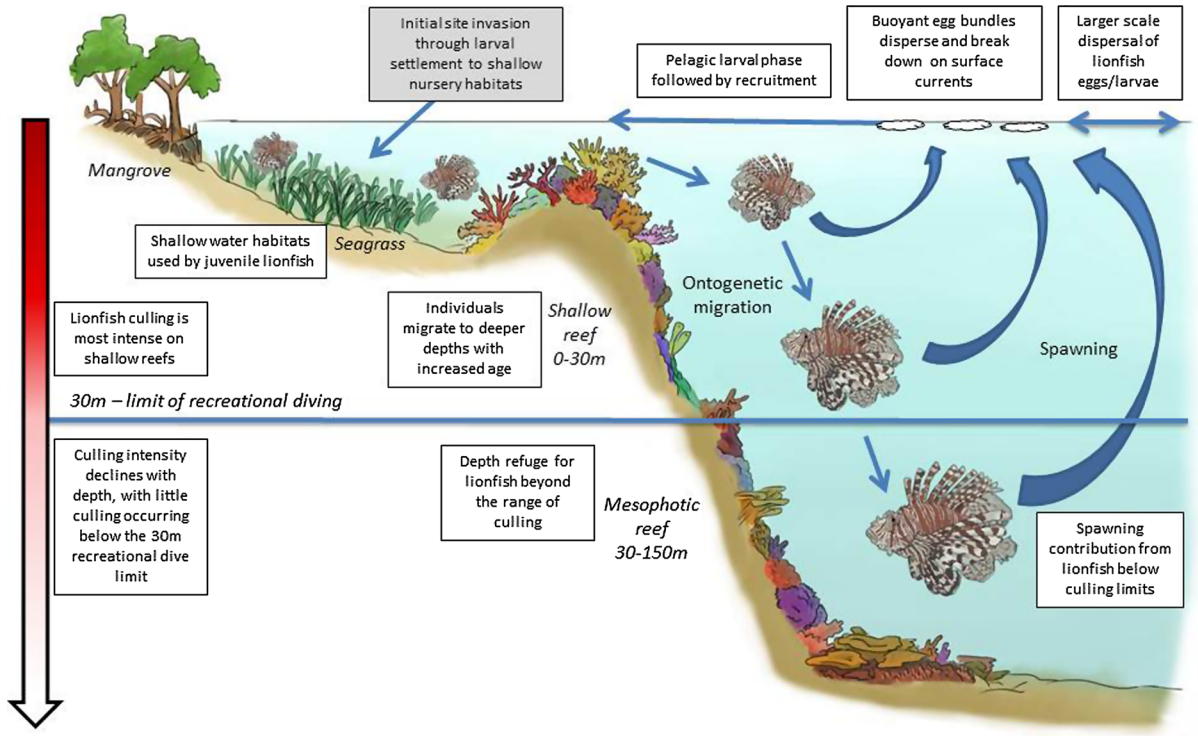

Fig. 5 Schematic diagram of the proposed lionfish distribution across the shallow-mesophotic depth gradient. Lionfish initially invade new sites at shallow depths, before moving to deeper reef areas beyond the range of lionfish control measures (culling)

lionfish abundance to be highest at shallow depths in the Red Sea, as did Kulbicki et al. (2012) in their review of Indo-Pacific literature. Our data suggest these differing patterns are likely partially driven by varying availability of hard substrata and linked factors (e.g. structural complexity), which have been shown to be important in lionfish aggregations (Bejarano et al. 2014b). Although lionfish abundance is significantly higher in the western Atlantic than in their native range (Darling et al. 2011; Kulbicki et al. 2012), we identified similar patterns in relative abundance and mean body length distributions across the depth gradient at native sites as we found at invaded sites without culling. This suggests lionfish are using MCEs in their invaded range in similar ways as their native counterparts and, thus native-range studies can support and inform our understanding of the western Atlantic invasion.

Lionfish populations in their native and invaded geographical range limits are likely to face different structuring processes affecting their abundance and distribution. In Bermuda, it has been noted that lionfish are rarely observed in shallow reef habitats, but are much more common on deep fore-reef slopes (Smith et al. 2013). While all sites in our study from Bermuda were culled, it is possible that, at higher latitudes, physical factors such as temperature and wave energy may be the most significant factors driving lionfish-abundance distributions across depth gradients. For example, work by Whitfield et al. (2014) in North Carolina, USA, at the northern limit of the established populations, suggests that lionfish abundance across the shallow-mesophotic depth gradient correlates strongly with minimum winter water temperatures. In Bermuda, inshore shallow habitats experience lower winter water temperatures than deeper sites further offshore (Coates et al. 2013). These low winter inshore temperatures are below the temperature threshold at which experimental lab studies have suggested lionfish cease feeding (Kimball et al. 2004). This potentially drives the larger abundances observed on MCEs compared to shallow habitats. We suggest that further studies on lionfish ecology in Bermuda should focus on the interaction between culling-based management and seasonal water-temperature variation in order to better

understand whether temperature has a more significant role at the invasion range limit.

Lionfish body size and depth

The idea of a deep refuge for invasive lionfish was previously modelled by Arias-González et al. (2011), who found that if larger lionfish exist below depths accessible to culling programs, it will be harder to reduce and control the overall population. There are several possible explanations for larger lionfish being found below culling depths. When spawning, lionfish produce buoyant egg bundles that drift on the ocean's surface for several days before breaking down (Morris et al. 2009), leaving the embryos/larvae free floating with a pelagic larval duration of between 20 and 35 days (Ahrenholz and Morris 2010). Settlement is then believed to primarily occur in mangroves, seagrass beds, and shallow reef environments (<5 m) (Claydon et al. 2012). These shallow ecosystems are used by juvenile lionfish, before individuals migrate to intermediate depth reefs (10–30 m) as they mature (Claydon et al. 2012) (see Fig. 5), and this migration could extend into MCEs. Alternatively, the presence of larger lionfish on deeper reefs could be caused by culling biases at shallow depths, disproportionately reducing the number of larger lionfish and so giving the appearing of increasing body size with depth. This could be driven by higher detection rates for larger lionfish than smaller lionfish in culling programs (Green et al. 2013).

While we did not find consistent patterns in lionfish body size with depth, additional factors such as time since invasion are likely to explain this discrepancy. In three invaded countries we found larger lionfish at mesophotic depths (The Bahamas, Curaçao, Honduras), in Bonaire, we found no difference in lionfish body lengths with depth, while in Puerto Rico, we found larger lionfish in the shallows. Puerto Rican studies were conducted 2 years after lionfish invasion, the shortest time interval after invasion of any included studies, so it is possible these studies do not represent the natural length distribution with depth for an established lionfish population. We found a negative correlation between time since invasion and the SMD in lionfish body length, suggesting this short time since invasion explains why we did not find larger lionfish at mesophotic depths in Puerto Rico. Individual country results must be interpreted with caution before generalisation, as some countries are only represented by several sites within the analysis (see Table 1). However, these broad country-level results provide support to the hypothesis that invasive lionfish on MCEs are an extension of the established mangrove, seagrass and shallow reef (>5 m) to intermediate depth reef (10–30 m) ontogenetic migrations (Claydon et al. 2012). However, research studying movement patterns through tagging, stable isotope or otolith age-structure analysis in lionfish across the depth gradient are needed to confirm these ontogenetic movements. These studies should be conducted to allow comparisons between areas with regular culling and those without to establish the influence on culling at finer scales than has been possible in this analysis.

Culling changes lionfish movement and behaviour

Our data suggest shallow culling (<30 m) leads to increased similarity in lionfish body lengths across the depth gradient, or even to an increase in larger individuals at shallow depths compared to MCEs. As we treated culling as a categorical variable, many subtle impacts of differing culling effort may be hidden. Future work would benefit from detailed culling records (e.g. frequency, intensity, time of day, experience of cullers) to better understand its impacts. A likely response to shallow culling would be changes in movement patterns of lionfish. It has previously been hypothesised that ontogenetic fish migrations may be reduced when competition between individuals in shallow habitats is limited (Appeldoorn et al. 2003), meaning those lionfish that avoid culling may mature at shallower depths. Yet this hypothesis is based on consistent mortality rates, whereas applying culling increases shallow lionfish mortality. However, we found similar lionfish abundance effects when comparing shallow and mesophotic reefs regardless of the presence of culling. This could suggest that culling on shallow reefs did not cause a significant decline in shallow lionfish abundance, but there is strong evidence to suggest this is not the case (Frazer et al. 2012). There are several biological explanations possible, for example: (1) individuals may be recolonising shallow reefs from adjacent deeper reefs; (2) an established mesophotic lionfish population may have been absent before shallow culling was effectively implemented; or alternatively (3) this was simply caused by low power in our analysis. Previous

studies of lionfish movement have focused within the shallows and, while the majority were found to have high site fidelity, there are multiple records of individuals moving more than 1 km (Côté et al. 2013; Akins et al. 2014). This would suggest that the relatively small distance between adjacent shallow and mesophotic reefs is within their natural movement range. However, movement from deeper areas without culling into shallow areas under continued culling runs counter to expected fish behaviour, as we would expect individuals to avoid areas with increased mortality risk (Werner and Gilliam 1984; Kimirei et al. 2013), although a large reduction in competition could outweigh the potential mortality risk. Further research is required to address this, focusing on specific movement studies of individual fish in culled areas across the depth gradient.

Lionfish culling reduces the number of lionfish in culled areas (Frazer et al. 2012), but also affects lionfish behaviour, making lionfish more cautious during daylight hours (Côté et al. 2014). Therefore, this combination of active removal combined with increasingly cryptic behaviour suggests we should observe greater relative lionfish abundances at deeper depths at culled sites than sites without culling. However, we do not see an effect of culling on lionfish relative abundance distribution across the depth gradient. When lionfish engage in increased cryptic behaviour, smaller lionfish become more easily hidden than larger individuals leading to greater detection rates for larger lionfish on lower structural complexity sites (Green et al. 2013). This process could explain our observations that higher abundance was correlated with areas of lower hard substrata, and that following culling we found similar mean body sizes at shallow and mesophotic depths, yet in the absence of culling we saw three countries with larger lionfish at depth.

While organised culling has been the focus of most lionfish management efforts, there is increasing interest in developing fisheries for lionfish and promoting market demand for invasive lionfish consumption (Bogdanoff et al. 2014). Switching focus from a government-led invasive species control effort to a market-based fisheries approach could bring substantial increases in lionfish removal (Bogdanoff et al. 2014). For example, in The Bahamas at the Cape Eleuthera Institute, a small marine research centre, their 2011–2015 invasive lionfish-culling program resulted in the collection of 55 kg of lionfish, whereas a locally developed lionfish fishery collected 680 kg of lionfish in 2015 alone (J Curtis-Quick personal communication). Larger lionfish on MCEs could potentially be a target for future fisheries, especially as fishers have previously reported them from MCEs in lobster traps and by hook and line (Bogdanoff et al. 2014). While hook and line is not considered appropriate for widespread lionfish collection (Bogdanoff et al. 2014), there has been much interest in developing a lionfish trap that can be deployed while minimizing bycatch (Pitt and Trott 2015). Traps can remove substantial numbers of MCE lionfish—for example, over 1,200 lionfish were removed from 40 to 80 m depth around Bermuda as bycatch in commercial lobster traps between September 2013-March 2014 (Pitt and Trott 2015). However, in many locations, lionfish trapping has not been achieved effectively at a large scale (Morris et al. 2011) and further research and development of traps is required before trapping can be widely adopted. When developing lionfish fisheries as a conservation management strategy it is important to concentrate on keeping lionfish populations low, as there is a risk that established fisheries could become focused on managing for continued lionfish harvests. With these current technological limits most current MCE lionfish removal is carried out by technical divers using hand spears. With recent reduced costs, and increased interest from the recreational dive community in technical diving (Mitchell and Doolette 2013), it is becoming possible to incorporate deeper culling depths into lionfish management programs. For example, in 2016 the Bay Islands Conservation Association (the organisation with responsibility for lionfish management on Utila, Honduras) began to include a technical diving category in their annual lionfish derby to encourage technical divers to become involved in lionfish removal efforts and specifically target MCEs (M Arteaga personal communication).

Our results raise critical questions about the role of MCEs as a refuge for lionfish from culling and whether shallow culling program impacts are limited to shallow reefs or able to affect deeper populations. With increased interest from technical divers combined with technological development in lionfish traps, it is becoming possible to incorporate deeper culling depths into lionfish management programs. In addition, if mesophotic lionfish populations are

dependent on lionfish recruitment in shallow marine habitats for new individuals, then infrequent deep reef culling combined with intense regular shallow culling could be sufficient to reduce the overall population and maximise the chances of complete localised eradication where culling intensity is sufficient.

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