AQUATIC CONSERVATION: MARINE AND FRESHWATER ECOSYSTEMS
Aquatic Conserv: Mar. Freshw. Ecosyst. (2015)
Published online in Wiley Online Library
(wileyonlinelibrary.com). DOI: 10.1002/aqc.2549

Enhancing management effectiveness of invasive lionfish using distance sampling and detection probability

ALEXANDER TILLEY[a,b,c,*], ELLIOTT CARTER[c,d], SOPHIA WASSERMANN[c] and JULIANA LÓPEZ-ANGARITA[a,e]
[a]*Fundación Talking Oceans, Bogotá, Colombia*
[b]*Smithsonian Marine Station, Fort Pierce, FL, USA*
[c]*School for Field Studies, Center for Marine Resource Studies, South Caicos, Turks and Caicos Islands*
[d]*Davidson College, 204 Ridge Road, Davidson, NC, USA*
[e]*Environment Department, University of York, UK*

ABSTRACT

1. Invasive lionfish *Pterois volitans* and *Pterois miles* are one of the greatest threats to coral reef fisheries in the Caribbean. Management currently relies solely on removal, however, there is little understanding of spatial ecology of lionfish to inform management strategies and thus, increase their effectiveness.
2. The use of detection probability and population density estimates from distance sampling as a method to: (a) estimate spatial and depth variations in detectability of lionfish to prioritize removal efforts; (b) reduce costs related to removal in the Caribbean; and (c) provide quantifiable baseline data against which management success can be measured was evaluated.
3. Underwater visual transect surveys were conducted at varying depths at four coral reef sites in the Turks and Caicos Islands using perpendicular distance sampling. Detection functions were fitted to distance data from 299 lionfish sightings across 37 transects to explore variation in detectability among survey sites and depths.
4. Lionfish were detected with a 15.9% (12.2–20.6%) (mean ± 95% CI) probability across all sampling. Detection probability was significantly higher in depths < 15 m, however, lionfish density and mean size increased with depth. Population density on South Caicos reefs was estimated at 1679 (1140.4–2473.1) individuals per km^2. Increased detection probability in shallower depths implies caution is needed in assessing management success at depth, and that removal methods and effort should be related specifically to depth and habitat factors.
5. Distance sampling is an effective method for accurate estimation of lionfish population density and detection probability, providing metrics by which to identify priority management areas, and track population changes along with the success of removal efforts. As a result its integration into initial planning and continued monitoring aspects of lionfish management throughout the Caribbean is recommended.

Received 7 July 2014; Revised 26 October 2014; Accepted 13 December 2014

KEY WORDS: coral; reef; conservation evaluation; ecological status; fish; alien species

*Correspondence to: A. Tilley, Fundación Talking Oceans, Bogotá, Colombia. E-mail: alex@talking-ocens.org

INTRODUCTION

Invasive species are one of the leading causes of biodiversity loss, and cost the global economy more than $US1.4 trillion annually (Burgiel and Muir, 2010). When strong predatory effects combine with high population densities, invasive species are detrimental to native organisms and their habitats (Benkwitt, 2013). Most likely introduced to the western Atlantic via accidental or intentional aquarium releases, Indo-Pacific red lionfishes *Pterois volitans* (Linnaeus, 1758) and *Pterois miles* (Bennett, 1828) were first spotted in 1985 off the south-western coast of Florida (Ruiz-Carus *et al.*, 2006; Green *et al.*, 2012). Since then they have successfully spread across the western Atlantic, Gulf of Mexico, and Caribbean reaching densities far exceeding those of native lionfish populations in the Indo-Pacific (Darling *et al.*, 2011). Their invasive success is attributed to a lack of natural predators and their exploitation of unwary prey, especially herbivores and cleaner fish (Morris and Akins, 2009; Burgiel and Muir, 2010). They are voracious, generalist predators, feeding on a wide variety of reef fishes (Layman and Allgeier, 2012; Benkwitt, 2013), with up to 41 different teleost prey species identified in 10 different families, accounting for around 54% of all potential prey species (Ruiz-Carus *et al.*, 2006; Morris *et al.*, 2009; Green *et al.*, 2012; Côté *et al.*, 2013). The wide trophic niche of lionfish may disrupt interspecific interactions at various trophic levels (Darling *et al.*, 2011; Côté *et al.*, 2013), and can cause up to 79% decreased recruitment of native reef fishes (Albins and Hixon, 2008).

Although lionfish exhibit generalist feeding behaviours, individuals typically have specialized diets, often preying upon specific assemblages, owing to their high site fidelity (Layman and Allgeier, 2012). One estimate of home range from an estuarine study in Florida suggests that lionfish have an average range of only 28 m over an extended period of time (Jud and Layman, 2012), with limited movements across open spaces between habitat patches. It is suspected that movement across continuous three-dimensional habitat may be at larger scales, however, previous studies by Côté and Maljkovic (2010) and Green *et al.* (2011) suggest that lionfish do not travel more than ~15 m to forage, and exhibit crepuscular peaks in foraging activity (Morris and Akins, 2009). These ecological attributes are important management considerations because they provide an insight into dispersal speeds and the impacts of lionfish predation on prey assemblages (Green *et al.*, 2012), as well as informing effective removal strategies.

The potential role of Caribbean groupers as 'biocontrollers' of invasive lionfish has been suggested but is contentious, with contrasting results recently published (Mumby *et al.*, 2011; Bruno, 2013; Valdivia *et al.*, 2014). Lionfish remains have been found in the stomachs of Nassau and tiger groupers (Maljković *et al.*, 2008), and while Mumby *et al.* (2011) purport possible biocontrol of lionfish by grouper in no-take marine reserves, Hackerott *et al.* (2013) and Valdivia *et al.* (2014) found no such relationship. Hence, 30 years after the arrival of this alien species, physical removal continues to be the mainstay of management efforts to combat the spread of lionfish.

Using a simulation model of physical lionfish removal, Barbour *et al.* (2011) estimated that 35–65% of the population must be removed annually to have an effect, and that even after 50 years of culling, lionfish would rebound to 90% of the original population after a six year suspension. However, Green *et al.* (2014) suggest that complete eradication of invasive lionfish is not necessary to reverse their ecological effects, but rather that reducing the population density by 75–95% allows for native prey fish biomass to increase by 50–70%, presenting a reduction in ecological effects equivalent to complete removal. As such, reliable estimations of species density and population size are paramount to ecological management (Newey *et al.*, 2003).

The impact of invasive species can be defined quantitatively as the product of the distribution, abundance, and per capita effect of individuals, so calculating these figures is essential to control the spread of lionfish (Parker *et al.*, 1999). Capture–mark–recapture methods are commonly used to assess population abundance and density in fisheries management, but these labour-intensive methods are susceptible to sampling bias, especially for dispersed populations (Thomas *et al.*, 2010), and returning tagged lionfish to the system seems illogical at best. In addition, lionfish tend to be highly cryptic in reef habitat, making traditional underwater visual censuses involving a fixed transect width or point counts unreliable (Kulbicki and Sarramégna, 1999), with one estimate suggesting that only 1/8 of the population is detected (Kulbicki *et al.*, 2012).

In small island nations and territories such as the Turks and Caicos Islands (TCI), scientific capacity and environmental resources are limited, so effective management must be balanced with associated effort and the costs involved. Distance sampling provides an alternative method to traditional fixed width or point count census methods by detecting individuals and measuring their distance from a predetermined line or point (Thomas *et al.*, 2010). However, it is seldom utilized in visual surveys of fish or benthic organisms (Ensign *et al.*, 1995; Kulbicki and Sarramégna, 1999), so the efficacy of distance sampling as a method to enhance removal success and efficiency by providing accurate density estimates, still needs to be evaluated.

Local livelihoods on South Caicos (the southernmost island of the TCI's Caicos Bank) rely heavily on fishing (Hall and Close, 2007) and target potentially important biocontrol species such as Nassau grouper, whose populations are declining rapidly with a recorded 60% decrease in the past 30 years (Tewfik and Béné, 2004; Landsman *et al.*, 2009). With mesopredator populations like Nassau grouper already in decline, the deleterious effects of invasive lionfish on native fish recruitment (Albins and Hixon, 2008) may generate serious ecological and economic impacts in years to come. As physical removal remains the only viable control for invasive lionfish and yet most Caribbean nations lack appropriate budgets and resources to consider undertaking such broad-scale removal programmes, there is a pressing need to identify spatial parameters of lionfish distribution with which to target and prioritize removal efforts and maximize management efficiency.

The aims of this study were to test the efficacy of using distance sampling as a method to estimate density and abundance of invasive lionfish, to quantify their 'catchability' (i.e. likelihood of detection) in varying depths using detection probability, and to provide quantifiable baseline data against which management success can be measured.

MATERIALS AND METHODS

Study site

Visual transect surveys were carried out at four sites on the contiguous reef wall to the south of South Caicos, Turks & Caicos Islands (Figure 1). Survey sites were chosen as representative habitat and structure of the 2.2 km^2 reef in this area. Surveys were carried out at approximate depths of 2 m, 12 m, 18 m, and 25 m, though actual depth measurements were more continuous due to the natural variability in substrate rugosity. At each site, substrate structure dictated the survey trajectory, precluding precise and balanced depth sampling, causing certain depths to be constrained to narrow bands owing to flat shelf bathymetry (e.g. 15–20 m). Sites of 2 m depth were surveyed by snorkelling.

Field surveys

Underwater visual transect survey methods were adapted from Tilley and Strindberg (2013) following distance sampling methods developed by Buckland *et al.* (2001). At each study site, transects began at a specified depth with divers swimming parallel to the reef wall at a spacing of ~4 m, actively searching for lionfish along their personal 'zero-line' (Figure 2). Transect length varied according to current, visibility, diver air consumption, and no-decompression limits. Upon sighting a lionfish, observers measured the perpendicular distance from the fish to their zero-line with a tape. If a lionfish was sighted between two observers, the first diver to notice the individual measured the perpendicular distance, in order to produce accurate detection probability results.

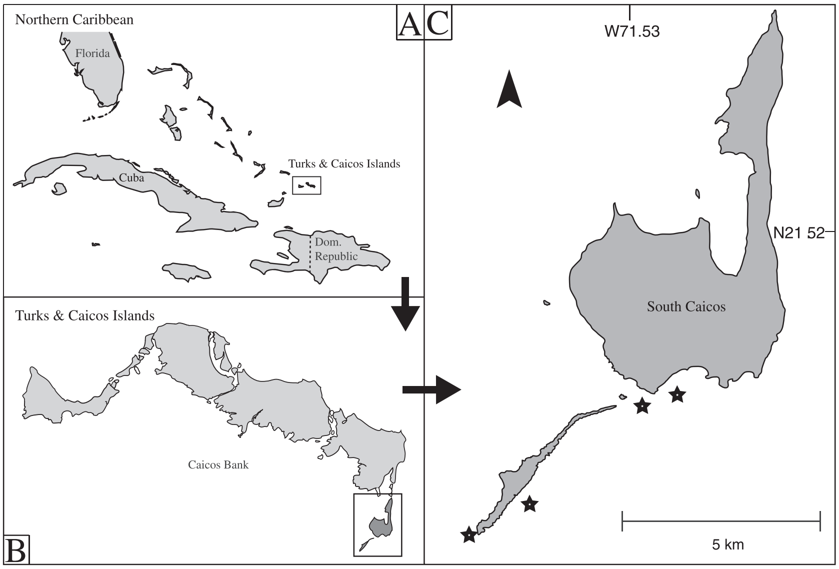

Figure 1. Map depicting (A) the location of the Turks and Caicos Islands within the northern Caribbean region; (B) the Turks and Caicos Islands, British West Indies (excluding outlying islands) showing South Caicos boxed and shaded dark grey; and (C) the islands of South Caicos and Long Caye with survey sites illustrated by stars along fringing reef.

Time, depth, size, habitat, and behaviour of sighted lionfish were recorded. To prevent duplicate counts, observers signalled when a lionfish was spotted and the line halted while measurements were recorded. These procedures were repeated for all shallow (<5 m) transects, except that observers were snorkelling.

To ensure unbiased results, the main assumptions of the distance sampling method were met during the field surveys (following

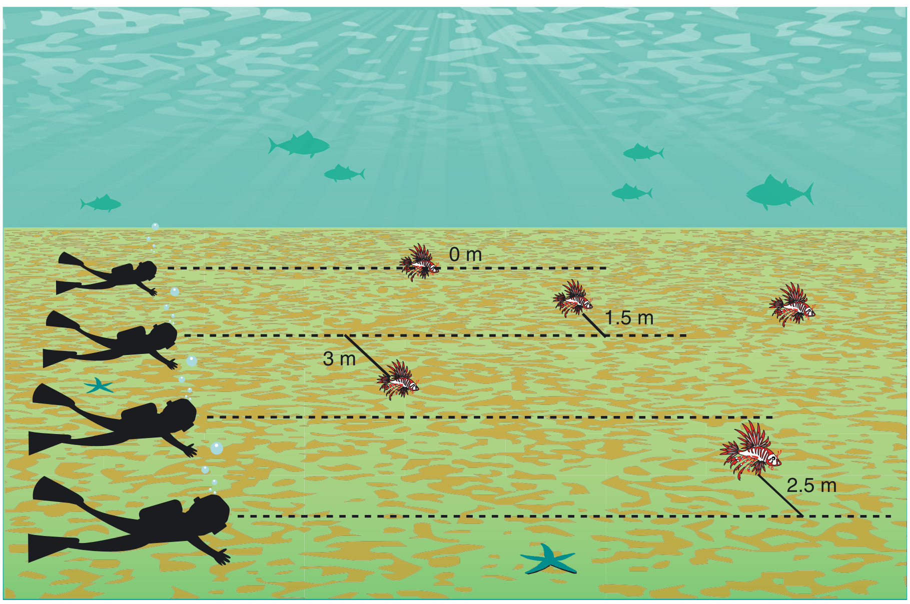

Figure 2. Diagram of the distance sampling survey design used on forereef habitat in South Caicos, Turks and Caicos Islands. Four observers follow a zero-line (dotted black lines) and measure perpendicular distances to individual lionfish sighted (solid black lines with distance measurements).

Buckland *et al.* (2001), Thomas *et al.* (2002) and Newey *et al.* (2003):

1. *Individuals on the transect line, or zero line with multiple observers, are detected with certainty.* Although lionfish are difficult to detect, observers assume that they sight all lionfish directly beneath them, where the probability of detection remains at or close to one initially and decreases with distance away from zero (Thomas *et al.*, 2002).
2. *Objects do not move.* Lionfish are diver-neutral, only moving when threatened at very close range. As long as any movement is slow relative to the observer, errors can be avoided (Thomas *et al.*, 2010).
3. *Measurements are exact.* If distances from the individual to the zero line are estimated or measured inaccurately, then results will be biased. Given the slow movement of lionfish, accurate measurements of distance to the fish can be taken with transect tapes rather than estimating distances.

Data analysis

Perpendicular distance data from underwater visual surveys were analysed using Distance 6 software (Thomas *et al.*, 2010). Transect length was multiplied by the number of observers (4) to give total sampled length. Encounter rate was stratified into four categories by survey depths ($<$ 5 m, 5–15 m, 15–20 m, and $>$ 20 m) and its standard error was estimated empirically using the replicate transects as samples. Maximum likelihood methods were used to estimate the variance of the effective strip width, a simple measure of detectability. Exploratory analyses were first conducted to examine options for truncation and grouping intervals of pooled data and depth-stratified data, to improve model fit for the detection function. Analyses were conducted to determine an ideal interval grouping for best model fit for the detection function. Following Buckland *et al.* (2001), a variety of key functions and adjustment term combinations were considered to model the detection function (e.g. uniform + simple polynomial, half-normal + cosine, etc.) for pooled perpendicular distance data and for the depth-stratified data. A goodness of fit test was used for model selection using the highest Akaike's Information Criterion (AIC) value, with particular attention paid to model fit at distances near zero, important for robust estimation (Buckland *et al.*, 2001).

Post hoc comparisons were made between depth-specific detection probabilities and overall detection probability. Estimates of lionfish density and abundance were obtained by taking the mean of the depth estimates weighted by effort at depth, with each survey at a certain depth treated as a replicate.

RESULTS

In total, 299 lionfish were detected during 37 transect surveys covering 8.8 km from March to November 2013. Transects lasted approximately 35 min travelling a distance of 237 m $\pm$ 16.7 m (mean $\pm$ SE), varying with depth and diver air consumption. Lionfish were sighted at depths between 2 and 30 m and were observed in coral heads, coral overhangs, and sand channel habitats. Most lionfish sighted were solitary or in loose pairs, and only occasionally seen in groups of three or more individuals. Time and field resources availability constrained balanced sampling of depth categories, so encounter rates and densities were weighted by sampling effort at each depth.

Perpendicular distance data were divided into 12 equal intervals with truncation at 15 m and a hazard-rate function with no adjustment terms showed the best fit according to AIC, so it was used for the detection model function (Figure 3). For all observations of lionfish combined, effective strip width was approximately 2.38 m (1.83–3.10) (mean $\pm$ 95% CI). The overall detection probability of lionfish was estimated at 0.159 ($\pm$0.122–0.206) indicating that ~16% of all lionfish were observed within a 15 m wide transect cut-off. Utilizing an estimated total area of 2.2 km^2 of continuous South Caicos reef habitat, density of lionfish was calculated at 1679 (1140.4–2473.1) lionfish per km^2, with a total population size of 3695 (2509.0–5441.0) lionfish.

Post-stratification by depth showed that detection probabilities were higher in shallower water depth ($<$ 15 m) than in deeper surveys $>$ 15 m depth (Table 1). Similarly, effective strip widths were wider in depths $<$ 15 m than they were in depths $>$ 15 m (Table 1). The lionfish

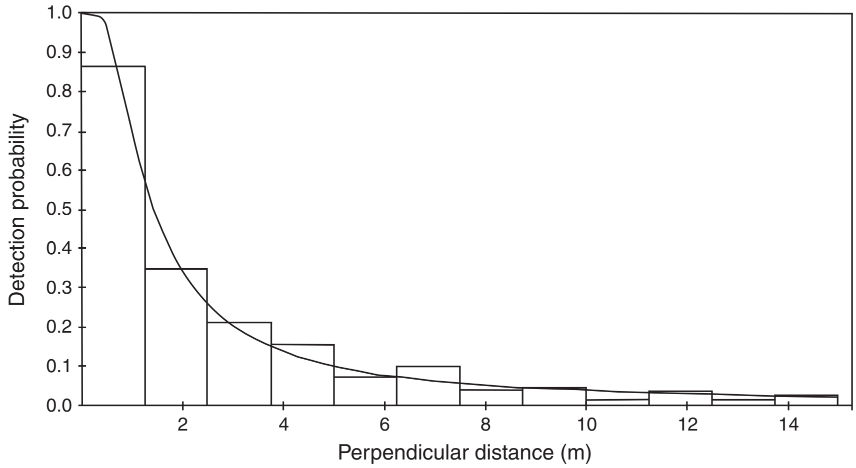

Figure 3. Detection function (hazard rate no adjustment) fitted to perpendicular distances of lionfish (*Pterois volitans*) observations from South Caicos, Turks and Caicos Islands.

Table 1. Summary of distance sampling surveys for invasive lionfish by depth category in South Caicos, Turks & Caicos Islands. SE = standard error

Depth	Number of transects	Detection probability	Effective strip width (m)	Encounter rate ± SE (lionfish km^{-1})	Mean lionfish size ± SE (cm)	Number of lionfish
<5 m	6	0.185	2.96	13.8 ± 14.0*	16.7 ± 1.5	15
5–15 m	8	0.208	3.33	20.5 ± 4.8	21.7 ± 1.1	62
15–20 m	13	0.157	2.53	18.9 ± 4.6	24.8 ± 0.8	84
>20 m	10	0.114	1.82	43.3 ± 11.2	26.3 ± 0.6	138

*High error value owing to two transects resulting in zero sightings.

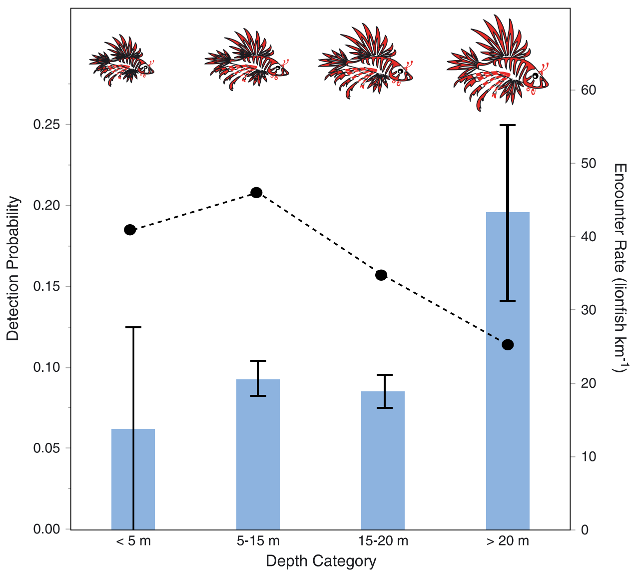

Figure 4. Detection probability (black dots, left y-axis), encounter rate ± SE (blue bars with error bars, right y-axis) and mean lionfish size (proportionally scaled fish illustrations) according to depth categories of distance sampling surveys in South Caicos, Turks and Caicos Islands. Black dotted line between detection probabilities is for visualization only and does not represent a statistical trend.

encounter rate (lionfish km^{-1}) was higher at the deepest survey stratum of > 20 m than it was for all shallower depths, suggesting that within the sampled range, abundance increases with depth in contrast to detection probability (Figure 4). Mean lionfish size showed a positive correlation with depth (Spearman's $\rho = 0.2802$, $P < 0.0001$), with the largest individuals being seen at the greatest depth (Table 1) (Figure 4).

DISCUSSION

This study provides evidence that distance sampling is a method that can be used effectively to determine population density of lionfish; moreover, this method reveals priority areas of higher lionfish densities at particular depths that allow the focusing of removal actions to achieve more effective results. Distance sampling and the stratification of abundance and detection probability data by depth, show lionfish are smaller yet easier to detect at shallower depths, but are larger and more abundant in deeper water (Figure 4). Hence, although detection probability was higher in shallower water, encounter rate was lower, with the highest encounter rate seen at depths > 20 m. This suggests that lionfish abundance is greatest at the deepest depth, but the likelihood of detecting them is lower.

Surveys in shallow water (< 15 m) exhibited less complex habitat with fewer holes, overhangs, and coral heads in which lionfish could hide compared with deeper sites. Green *et al.* (2013) showed that lionfish detectability is lowest on reefs with high rugosity and may approach zero in the most rugose reefs. The lack of complexity in shallow TCI habitats is likely to have produced the higher detection probability and the greater effective strip width for these depths. The overall detection probability of lionfish across all survey sites in South Caicos was 15.9%. This figure is comparable with that of Kulbicki *et al.* (2012) who estimated that only 12.5% of lionfish were spotted during visual counts using non-specialized methods. The slight increase in detection probability suggests that distance sampling alone does not vastly improve the low detection rates for lionfish, given their preference for resting under or within coral heads. This is further supported by Green *et al.* (2013) who suggest that conventional survey methods underestimated lionfish biomass by ~200%, and that while detection probability increases with fish size, it decreases with reef rugosity. The arrival and speed of distribution of lionfish in the TCI documented by Claydon *et al.* (2012), also showed a general increase in body size with depth, where lionfish initially colonized shallow seagrass and mangrove habitats, before spreading to deeper reefs. Claydon *et al.* (2012) utilized an encounter rate (individuals per observer per hour) as a proxy for density in 2010, stating figures of 9.51 ± 5.37 lionfish per observer per hour (mean ± SD). Since methodologies are different, direct comparisons of density cannot be made, but utilizing the same units as Claydon *et al.* (2012) our surveys below 10 m produced similar densities (27.1 lionfish per hour or 6.8 per observer per hour in all transects). Despite mean lionfish size increasing with depth, the results show detection probability decreasing with depth (Figure 4), suggesting that reef rugosity may be a better predictor of detectability than fish size.

Low parasite loads in invaded Atlantic habitats could translate to higher growth rates and greater fecundity in invasive lionfish (Albins and Hixon, 2011). Given the linear relationship between fecundity and body size in lionfish (Priyadharsini and Manoharan, 2013) the culling of lionfish at depth may have significantly greater regional management effects in terms of limiting reproduction, as opposed to removing greater numbers of smaller lionfish in the shallows. Hence, despite the lower detection probabilities seen at depth, the much higher encounter rates indicate that focusing removal efforts at depths greater than 20 m would have the dual benefits of larger culls, made up of larger (more fecund) individuals.

This study provides important baseline data for the density and population size of lionfish on South Caicos reefs over time, and allows for comparisons between similar areas. Since their introduction off the coast of Florida (Ruiz-Carus *et al.*, 2006), lionfish have become distributed throughout the Caribbean, and are thought to have moved to the TCI from the Bahamas (Whitfield *et al.*, 2007). A density of 1679 lionfish per km^2 is low compared with the Bahamas, where density estimates range between 10 000 lionfish per km^2 (Darling *et al.*, 2011) and ~40 000 per km^2 (Green and Côté, 2008) for the same area. Lionfish are expected to continue to spread throughout the Caribbean (Schofield, 2009) with densities in the TCI likely to increase rapidly if left unchecked.

The effective strip width across all surveys was 2.38 m, suggesting that every individual lionfish within this width of the zero line was detected 95% of the time. This effective strip width is narrow relative to the 4 m separation between observers, and to the truncated perpendicular distance of 15 m, so future sampling should consider reducing observer spacing given the low detection probability of cryptic lionfish. While these results suggest that distance sampling is only slightly more effective at detecting lionfish than non-specific underwater visual counts, distance sampling requires fewer transects and less overall effort (Kulbicki and Sarramégna, 1999), and allows for identification of priority removal areas by generating specific habitat and depth attributes of lionfish distribution. Focused, localized lionfish culls have been shown to be effective, with Green *et al.* (2014) suggesting that partial culling is as effective as full culling in reducing loss of native fish biomass, yet using 30% less time and effort. The strategy of aiming removal efforts towards lionfish population thresholds such as those proposed by Green *et al.* (2014), may be more suitable for developing territories such as TCI, where budget constraints hinder effective environmental monitoring and management. Greater efficiency provided by distance sampling in both prioritizing areas for removal, and monitoring population density, will reduce the costs related to conducting large-scale removal and monitoring programmes in the field (boat time, fuel, personnel, diving).

Green *et al.* (2013) suggest that removal efforts should be directed towards complex corals and overhangs where lionfish are known to reside, rather than swimming along a predetermined transect and waiting for individuals to appear. Our results show that detection probability of lionfish in the TCI is highest in depths of 5–15 m, a depth at which free-diving spear fishermen are active, providing an opportunity to introduce culling as a resource alternative for these fishermen while utilizing them to enhance management threshold objectives. The effectiveness of management exploiting the greater 'catchability' of lionfish in shallow habitats will be negated by the presence of denser populations of larger, more fecund individuals in deeper waters rapidly repopulating the shallows.

Côté *et al.* (2014) found that culling can change lionfish behaviour, increasing avoidance of divers, leading to suggestions that culling and associated behaviours might actually be exacerbating impacts on prey communities by conditioning lionfish to hide. Distance sampling, with the ability to monitor the detection probability of lionfish, may also provide an important tool in tracking changes in behaviour and provide a more accurate estimate of population if such a behaviour change occurs.

Management plans and recommendations call for accurate evaluations of population density and abundance of lionfish as primary objectives, as well as identifying and prioritizing areas for vigilant control (Morris and Whitfield, 2009). The ability to generate accurate estimates of lionfish density, and as such track population changes and management effectiveness over time using repeat sampling, makes distance sampling an important tool to augment management capacity. In addition to providing generalized density information, distance sampling could be used to look at localized dispersal patterns in order to further focus management efforts on the areas most affected by the lionfish invasion.

The goal of this study was to test distance sampling as an effective tool for estimating lionfish density and abundance and to determine if detection probability might focus mitigation strategies. The use of distance sampling presents new opportunities to streamline management and potentially enhance management efforts against invasive lionfish in the Caribbean, where national environmental management budgets are often severely limited.

The Florida Keys national marine sanctuary (FKNMS) encompasses a combined shoreline of 2990 km, and the proposed management of invasive lionfish in the sanctuary is estimated to cost ~ $US1 million over 5 years (Morris and Whitfield, 2009). The total shoreline of the TCI is 389 km, approximately 13% of that of the FKNMS, indicating that a removal programme of this magnitude in the TCI would require funding in the order of ~$US130 000 over 5 years. These costs would represent a significant investment to the TCI's Department of Environment and Maritime Affairs (DEMA), that has an annual budget of ~$US1.4 million across all programmes. By utilizing distance sampling to prioritize areas, track success, and adapt removal efforts, lionfish management will be more efficient, reducing the long-term strain on environmental budgets in the TCI, as well as providing better adaptive estimates of related costs.

Local initiatives in the TCI should look to strengthen fishers' and tourists' involvement in removal, while a dedicated removal programme with target thresholds should be established by DEMA. We recommend that DEMA utilizes initial data of depth characteristics seen in this study, and augments monitoring using distance sampling to track success of population density threshold targets. The results of monitoring should be used to adapt removal efforts and prioritize management sites, combined with additional (perhaps externally funded) programmes to evaluate biomass of prey communities.

Efforts to encourage purchase and consumption of lionfish are widespread throughout the Caribbean, yet the difficulties involved with securing a reliable supply of large enough lionfish fillets, often inhibits large-scale take-up by restaurants. Given the improbability of complete eradication, research should focus on understanding and reducing the ecological impacts of lionfish, and raising the efficacy of removal efforts. Distance sampling can provide more precise information for managers and fishers to enhance removal and also strengthen incentives for fishermen to target lionfish. Lionfish management in the TCI should focus on actively encouraging spear fishers to include lionfish within their target species, guiding them with depth and habitat recommendations to enhance their encounter rate of large lionfish. Furthermore, research should investigate the trade-off between lionfish size and detection probability over a depth gradient. These initial findings suggest there might be an effective culling depth at ~15–20 m where detection probability and encounter rate are maximized (Figure 4), however, caution is advised as local conditions and invasion history may create wide geographic variability.

Distance sampling is not a method for wholesale replacement of simple survey techniques, but given the need to assess spatial and depth variation in invasive species distributions, it can be a valuable tool to increase accuracy and efficacy of removal strategies (Green *et al.*, 2013). This study illustrates the differences in abundance and detectability related to depth, however, given the limited scale of this study, it is recommended that distance sampling be used to establish a baseline of lionfish density in key conservation sites throughout the Caribbean. These initial studies can evaluate locally relevant depth abundance and detectability; be used to compare subsequent removals and gauge successes, and thereby estimate the frequency and intensity of removal programmes necessary to sustain lionfish populations at suggested thresholds.

ACKNOWLEDGEMENTS

We would like to thank Drew Kilker, Payton Leech, and Leah Shamlian for assistance during fieldwork, and Samantha Strindberg for data analysis comments. This study was carried out with logistical support provided by the School For Field Studies. This is contribution number 976 from the Smithsonian Marine Station at Fort Pierce, Florida.

REFERENCES

Albins MA, Hixon MA. 2008. Invasive Indo-Pacific lionfish *Pterois volitans* reduce recruitment of Atlantic coral-reef fishes. *Marine Ecology Progress Series* **367**: 233–238.

Albins MA, Hixon MA. 2011. Worst case scenario: potential long-term effects of invasive predatory lionfish (*Pterois volitans*) on Atlantic and Caribbean coral-reef communities. *Environmental Biology of Fishes* **96**: 1151–1157.

Barbour AB, Allen MS, Frazer TK, Sherman KD. 2011. Evaluating the potential efficacy of invasive lionfish (*Pterois volitans*) removals. *PLoS ONE* **6**: e19666.

Benkwitt CE. 2013. Density-dependent growth in invasive lionfish (*Pterois volitans*). *PLoS ONE* **8**: e66995.

Bruno JF. 2013. A critique of Mumby *et al*. 2011 'Grouper as a natural biocontrol of invasive lionfish'. *PeerJ PrePrints* **1**: e141v2.

Buckland S, Anderson DR, Burnham KP, Laake J, Borchers D, Thomas L. 2001. *Introduction to Distance Sampling: Estimating Abundance of Biological Populations*. Oxford University Press: Oxford.

Burgiel SW, Muir AA. 2010. *Invasive species, climate change and ecosystem-based adaptation: addressing multiple drivers of global change*. Global Invasive Species Programme (GISP): Washington DC.

Claydon JA, Calosso MC, Traiger SB. 2012. Progression of invasive lionfish in seagrass, mangrove and reef habitats. *Marine Ecology Progress Series* **448**: 119–129.

Côté IM, Maljkovic A. 2010. Predation rates of Indo-Pacific lionfish on Bahamian coral reefs. *Marine Ecology Progress Series* **404**: 219–225.

Côté IM, Green SJ, Morris JA Jr, Akins JL, Steinke D. 2013. Diet richness of invasive Indo-Pacific lionfish revealed by DNA barcoding. *Marine Ecology Progress Series* **472**: 249–256.

Côté IM, Darling ES, Malpica-Cruz L, Smith NS, Green SJ, Curtis-Quick J, Layman C. 2014. What doesn't kill you makes you wary? Effect of repeated culling on the behaviour of an invasive predator. *PLoS ONE* **9**: e94248.

Darling ES, Green SJ, O'Leary JK, Côté IM. 2011. Indo-Pacific lionfish are larger and more abundant on invaded reefs: a comparison of Kenyan and Bahamian lionfish populations. *Biological Invasions* **13**: 2045–2051.

Ensign WE, Angermeier PL, Dolloff CA. 1995. Use of line transect methods to estimate abundance of benthic stream fishes. *Canadian Journal of Fisheries and Aquatic Sciences* **52**: 213–222.

Green SJ, Côté IM. 2008. Record densities of Indo-Pacific lionfish on Bahamian coral reefs. *Coral Reefs* **28**: 107–107.

Green SJ, Akins JL, Côté IM. 2011. Foraging behaviour and prey consumption in the Indo-Pacific lionfish on Bahamian coral reefs. *Marine Ecology Progress Series* **433**: 159–167.

Green SJ, Akins JL, Maljkovic A, Côté IM. 2012. Invasive lionfish drive Atlantic coral reef fish declines. *PLoS ONE* **7**: e32596.

Green SJ, Tamburello N, Miller SE, Akins JL, Côté IM. 2013. Habitat complexity and fish size affect the detection of Indo-Pacific lionfish on invaded coral reefs. *Coral Reefs* **32**: 413–421.

Green SJ, Dulvy NK, Brooks A, Akins JL, Cooper AB, Miller S, Côté IM. 2014. Linking removal targets to the ecological effects of invaders: a predictive model and field test. *Ecological Applications* **24**: 1311–1322.

Hackerott S, Valdivia A, Green SJ, Côté IM, Cox CE, Akins L, Layman CA, Precht WF, Bruno JF. 2013. Native predators do not influence invasion success of pacific lionfish on Caribbean reefs. *PLoS ONE* **8**: e68259.

Hall GB, Close CH. 2007. Local knowledge assessment for a small-scale fishery using geographic information systems. *Fisheries Research* **83**: 11–22.

Jud ZR, Layman CA. 2012. Site fidelity and movement patterns of invasive lionfish, *Pterois* spp., in a Florida estuary. *Journal of Experimental Marine Biology and Ecology* **414–415**: 69–74.

Kulbicki M, Sarramégna S. 1999. Comparison of density estimates derived from strip transect and distance sampling for underwater visual censuses: a case study of Chaetodontidae and Pomacanthidae. *Aquatic Living Resources* **12**: 315–325.

Kulbicki M, Beets J, Chabanet P, Cure K, Darling E, Floeter SR, Galzin R, Green A, Harmelin-Vivien M, Hixon M, *et al*. 2012. Distributions of Indo-Pacific lionfishes *Pterois* spp. in their native ranges: implications for the Atlantic invasion. *Marine Ecology Progress Series* **446**: 189–205.

Landsman S, Jadot C, Ashley M, Claydon JA. 2009. Investigation of the Nassau grouper (*Epinephelus striatus)* fishery in the Turks and Caicos Islands: implications for conservation and management. *Proceedings of the Gulf and Caribbean Fisheries Institute*.

Layman CA, Allgeier JE. 2012. Characterizing trophic ecology of generalist consumers: a case study of the invasive lionfish in The Bahamas. *Marine Ecology Progress Series* **448**: 131–141.

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

Morris JA, Akins JL. 2009. Feeding ecology of invasive lionfish (*Pterois volitans*) in the Bahamian archipelago. *Environmental Biology of Fishes* **86**: 389–398.

Morris JA Jr, Whitfield PE. 2009. Biology, ecology, control and management of the invasive Indo-Pacific lionfish: an updated integrated assessment. NOAA Technical Memorandum NOS NCCOS 99.

Morris JA Jr, Akins JL, Barse A, Cerino D. 2009. Biology and ecology of the invasive lionfishes, *Pterois miles* and *Pterois volitans*. *Proceedings of the Gulf and Caribbean Fisheries Institute* **61**: 1–6.

Mumby PJ, Harborne AR, Brumbaugh DR. 2011. Grouper as a natural biocontrol of invasive lionfish. *PLoS ONE* **6**: e21510.

Newey S, Bell M, Enthoven S, Thirgood S. 2003. Can distance sampling and dung plots be used to assess the density of mountain hares *Lepus timidus*? *Wildlife Biology* **9**: 185–192.

Parker IM, Simberloff D, Lonsdale WM, Goodell K, Wonham M, Kareiva PM, Williamson MH, Holle Von B, Moyle PB, Byers JE, *et al*. 1999. Impact: toward a framework for understanding the ecological effects of invaders. *Biological Invasions* **1**: 3–19.

Priyadharsini S, Manoharan J. 2013. Reproductive biology and histological study of red lionfish *Pterois volitans* from Cuddalore, south east coast of India. *Journal of Aquaculture Research and Development* **4**: 1–9.

Ruiz-Carus R, Matheson RE Jr., Roberts DE Jr., Whitfield PE. 2006. The western Pacific red lionfish, *Pterois volitans* (Scorpaenidae), in Florida: evidence for reproduction and parasitism in the first exotic marine fish established in state waters. *Biological Conservation* **128**: 384–390.

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

Tewfik A, Béné C. 2004. 'The Big Grab': non-compliance with regulations, skewed fishing effort allocation and implications for a spiny lobster fishery. *Fisheries Research* **69**: 21–33.

Thomas L, Buckland ST, Burnham KP, Anderson DR, Laake JL, Borchers DL, Strindberg S. 2002. Distance sampling. In *Encyclopedia of Environmetrics.* John Wiley & Sons. Chichester, UK. pp. 544–552

Thomas L, Buckland ST, Rexstad EA, Laake JL, Strindberg S, Hedley SL, Bishop JRB, Marques TA, Burnham KP. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. *Journal of Applied Ecology* **47**: 5–14.

Tilley A, Strindberg S. 2013. Population density estimation of southern stingrays Dasyatis americana on a Caribbean atoll using distance sampling. *Aquatic Conservation: Marine and Freshwater Ecosystems* **23**: 202–209.

Valdivia A, Bruno JF, Cox CE, Hackerott S, Green SJ. 2014. Re-examining the relationship between invasive lionfish and native grouper in the Caribbean. *PeerJ* **2**: e348.

Whitfield PE, Hare JA, David AW, Harter SL, Muñoz RC, Addison CM. 2007. Abundance estimates of the Indo-Pacific lionfish *Pterois volitans/miles* complex in the western north Atlantic. *Biological Invasions* **9**: 53–64.

