

Habitat complexity and fish size affect the detection of Indo-Pacific lionfish on invaded coral reefs

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Abstract A standard approach to improving the accuracy of reef fish population estimates derived from underwater visual censuses (UVCs) is the application of species-specific correction factors, which assumes that a species' detectability is constant under all conditions. To test this assumption, we quantified detection rates for invasive Indo-Pacific lionfish (*Pterois volitans* and *P. miles*), which are now a primary threat to coral reef conservation throughout the Caribbean. Estimates of lionfish population density and distribution, which are essential for managing the invasion, are currently obtained through standard UVCs. Using two conventional UVC methods, the belt transect and stationary visual census (SVC), we assessed how lionfish detection rates vary with lionfish body size and habitat complexity (measured as rugosity) on invaded continuous and patch reefs off Cape Eleuthera, the Bahamas. Belt transect and SVC surveys performed equally poorly, with both methods failing to detect the presence of lionfish in >50 % of surveys where thorough, lionfish-focussed searches yielded one or more individuals.

Conventional methods underestimated lionfish biomass by ~200 %. Crucially, detection rate varied significantly with both lionfish size and reef rugosity, indicating that the application of a single correction factor across habitats and stages of invasion is unlikely to accurately characterize local populations. Applying variable correction factors that account for site-specific lionfish size and rugosity to conventional survey data increased estimates of lionfish biomass, but these remained significantly lower than actual biomass. To increase the accuracy and reliability of estimates of lionfish density and distribution, monitoring programs should use detailed area searches rather than standard visual survey methods. Our study highlights the importance of accounting for sources of spatial and temporal variation in detection to increase the accuracy of survey data from coral reef systems.

Keywords Underwater survey methods · Strip transect · Point count · Detection probability · Correction factor · *Pterois volitans/miles*

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Introduction

Underwater visual census (UVC) is the most widely used approach for assessing the density and biomass of coral reef fishes (Edgar et al. 2004; Kulbicki et al. 2012). UVCs are primarily conducted using SCUBA and encompass a range of methods, the most common of which are belt transects and stationary visual census (Murphy and Jenkins 2010). While UVCs are generally quick, inexpensive, non-destructive, and adaptable, a growing body of literature documents the limitations of their use (e.g., Samoilys and Carlos 2000; Gilbert et al. 2005; Colvocoresses and Acosta 2007; Murphy and Jenkins 2010). In particular, UVC protocols, which are generally designed to survey communities, can greatly underestimate the

abundance of individual species (Harvey et al. 2004; Gilbert et al. 2005). Moreover, this bias is not constant across taxa; detectability varies significantly with a number of species traits (MacNeil et al. 2008a, b; Kulbicki et al. 2010). As a result, small, cryptic, and hole-dwelling species have been shown to be particularly underrepresented in UVCs (Ackerman and Bellwood 2000; Willis 2001; Gilbert et al. 2005).

To correct for variable detection among species, several studies have employed species-specific correction factors to account for bias in detectability by a given survey method (e.g., Sale and Sharp 1983; Gilbert et al. 2005). To avoid erroneous conclusions when comparing survey data collected at different times and places, such correction factors should only be applied to surveys conducted under the range of conditions for which the factors were estimated, (McCallum 2005; Colvocoresses and Acosta 2007; Thomson et al. 2012). However, to date, few studies have explicitly investigated spatial and temporal covariates of fish detection probability.

Bias in detection across time and space could prove especially problematic for species for which accurate estimates of density and biomass are needed to inform management decisions. Invasive Indo-Pacific lionfish (*Pterois volitans* and *P. miles*) are a prime example, as they are now a primary threat to coral reef conservation throughout the Caribbean region (Sutherland et al. 2010; Albins and Hixon 2011). Through their predation on native species, lionfish are predicted to have long-term effects on the structure and function of reef ecosystems (Albins and Hixon 2011; Green et al. 2012). Effective survey techniques are crucial for estimating abundance, distribution, and the effectiveness of control efforts for this invasive predator. Currently, several agencies monitoring the lionfish invasion rely upon data collected from UVCs of fish communities to obtain lionfish density and biomass data (e.g., Brandt et al. 2009; NOAA 2012; NPS 2012; Ruttenburg et al. 2012). However, conducting accurate surveys for lionfish can be difficult due to their cryptic nature and crepuscular activity patterns (Fishelson 1975; Green et al. 2011). Kulbicki et al. (2012) provided an estimate of detection probability of approximately one lionfish detected for every eight lionfish present on reefs in their native Indo-Pacific range, based on comparisons between UVC and rotenone surveys. However, this estimate was derived from pooling samples conducted in different locations using different methods, and there have been no attempts thus far to estimate detection probability for this species in the invaded range or to evaluate potential sources of systematic variation in detection.

In this study, we estimate the probability of detecting lionfish on invaded continuous and patch reefs using a modified double sampling method (McCallum 2005), in which we evaluate the likelihood that each lionfish found in

an area by detailed lionfish-focussed searches will also be found by two conventional UVC methods, the belt transect and stationary visual census (SVC). We then determine whether detection probability varies systematically with two factors: habitat complexity and lionfish body size. Given that the goal of monitoring for lionfish is often to obtain accurate estimates of biomass over space and time, we also estimate whether correction factors derived from site-specific detection probabilities improve the accuracy of lionfish biomass estimates obtained by conventional UVC methods. Rigorously quantifying sources of bias in detection probability has important implications for the use of visual survey data in the estimation and comparison of density and biomass not only of invasive lionfish but also of all fishes for which these methods are the primary way in which population status is characterized.

Methods

Study sites

To measure the detection rates of lionfish using conventional underwater visual survey methods, as well as sources of detection variability, we conducted surveys of lionfish and habitat structure on coral reefs off Cape Eleuthera, The Bahamas (371812.77E, 2747170.62N), between June 2011 and February 2012. Two types of coral reef habitats occur in the study area: a continuous reef wall bordering Exuma Sound, with a crest at 10–20 m depth, and shallow inshore patch reefs, each 200–300 m² in area, at 3–4 m depth. The continuous reef has lower live coral cover (~5–10 %) and higher microalgae cover (~30–70 %) than the patch reefs (coral: ~20–40 %; macroalgae: ~5–30 %). Lionfish were first reported off Cape Eleuthera in 2005 and are now commonly sighted on all reefs. The location of visual surveys was selected randomly from a map of sites monitored by the Cape Eleuthera Institute. Sampling was conducted on days with similar environmental conditions to reduce the number of variables which may influence lionfish detection. All surveys were conducted by the authors using SCUBA on clear days during daylight hours between 0900 and 1500 h, when underwater visibility was greater than 30 m. The authors conducted a number of training surveys prior to data collection to ensure that search methods and detection levels were consistent across observers.

Survey methods

We used two conventional underwater visual survey methods: the belt transect survey (Sale and Sharp 1983) and the stationary visual census (SVC; Bohnsack and

Bannerot 1986), in addition to detailed lionfish-focussed searches (LFS). At each survey site, we used one of the two conventional methods, immediately followed by a LFS over precisely the same area. A site therefore denotes an area surveyed twice.

Prior to each survey, 24–30 m of transect line (depending on reef size) was laid across the reef. During SVC surveys, a stationary diver, positioned at the 7.5 m mark along the transect line, recorded the number and body size (TL to the nearest 1 cm) of all reef fishes, including lionfish, observed within a cylinder of 7.5 m radius (estimated by referencing the distance along the transect line) for 12 min, followed by a 2-min roving diver search of the habitat within the cylinder area to locate lionfish (B. Ruttenburg, pers. comm.). To perform belt transect surveys, we swam along the transect line at a constant speed of 5 m min⁻¹ while recording the number and size of all reef fishes, including lionfish, sighted with 2 m of either side of the transect tape. We also recorded the position of each lionfish sighted in relation to location along the transect line, as well as the perpendicular distance from the transect line.

Immediately following each conventional survey, a second surveyor conducted a detailed lionfish-focussed search (LFS) of the same survey site to record the size and location of all lionfish (Green 2012). During these searches, the observer swam the site in an S-shaped pattern, searching all crevices and overhangs for lionfish, using a dive light as needed (survey time was approximately 15 min per 120 m²). Given that lionfish are often inactive during the day (Green et al. 2011) and do not usually flee from the proximity of divers (personal observations), it is unlikely that lionfish moved in the interval between the conventional UVC and the LFS. However, we noted the behavior of each lionfish encountered as either active or inactive, following Green et al. (2011). Data from LFS were used to approximate the actual abundance and size distribution of lionfish at each site, against which data from belt transect and SVC surveys were compared. However, because LFS still relies on visual detection, a few lionfish may still have escaped detection at each site; hence, our approach may slightly overestimate detection success of the two conventional visual survey methods.

Finally, to quantify small-scale habitat complexity, we took six measures of rugosity along the belt transect line at each site. Rugosity was measured by fitting a fine-linked 3-m-long chain to the substrate perpendicular to the transect line at 4- to 5-m intervals (depending on transect length) and measuring the straight-line distance between the start and end of the chain (Wilson et al. 2007). Rugosity was expressed as the ratio of the total chain length to the straight-line distance, with larger numbers representing more rugose substrates. The six measurements were averaged to obtain a single value per site.

Data analysis

We calculated two probabilities of lionfish detection. The first—individual detection probability—pertains to the detection of individual lionfish, which we use to identify the mechanisms driving variable detection of individual lionfish. The second—site-specific detection probability—represents a site-level measure pertaining to the proportion of lionfish biomass detected at a given site, which we use to calculate and compare lionfish biomass values obtained from standard UVC versus LFS methods implemented at the same sites.

To calculate individual detection probability, we compared the size and location of each lionfish sighted during the SVC or transect survey with those of lionfish sighted during the LFS of the same site, which enabled us to score each individual lionfish as ‘detected’ (1) or ‘not detected’ (0). To examine the effect of lionfish body size and habitat complexity on individual detection probability, we created a generalized linear mixed-effects model (GLMM) where the probability of each lionfish being sighted (binary response; 0 or 1) was nested within the site at which it was located (a random effect) and predicted by body size (TL in cm), average rugosity of the site, survey type (SVC or transect), and reef type (continuous or patch reef). We included interactions between lionfish size and rugosity because we hypothesized that the effect of lionfish size on detectability might vary at different levels of rugosity (e.g., detectability of small lionfish might be disproportionately greater in less complex habitats). We started with the full model, carried out backward model selection, progressively removing non-significant interactions and terms, and conducted analysis of deviance tests between reduced models to assess improvement in fit (Zuur et al. 2009). Plotting residuals against fitted values for the final model revealed homogeneous errors, indicating adequate model fit.

To calculate site-specific detection probability, we first converted lionfish lengths to weights using the allometric scaling relationship $W = aL^b$ (where W is body mass in g, L is total length in cm, and a and b are scaling constants with values of 0.00497 and 3.291, respectively; Green et al. 2011). For each site, we estimated ‘total’ lionfish biomass as the sum of weights of lionfish located during the LFS and ‘detected’ lionfish biomass as the sum of weights of lionfish sighted during the belt transect or SVC at the same site. We standardized both total and detected biomass by survey area to obtain grams of lionfish 100 m⁻². Next, we calculated detection probability for each site as the ratio of detected lionfish biomass to total lionfish biomass. To examine the effect of lionfish body size and habitat complexity on site-specific detection probability, we created a generalized linear model (GLM) where the proportion of lionfish biomass detected was predicted by average lionfish

body weight (of all individuals locate during LFS, in g) and average rugosity for each site, as well as the type of conventional survey used (belt transect or SVC), and reef type (continuous or patch reef). We accounted for overdispersion in our model by correcting the standard errors using a quasi-GLM (Zuur et al. 2009). Again, we included interactions between lionfish size and rugosity, and starting with the full model, carried out backward model selection and validation as described above.

The actual abundance of an organism at a site can be estimated by dividing detected abundance by detection probability at that site (e.g., Thomson et al. 2012). Thus, we used the inverse of the site-specific detection probability to correct biomass estimates from belt transects and SVC, using habitat rugosity and mean lionfish weight obtained from each site. To measure the improvement in biomass estimates obtained by using site-specific correction factors, we compared lionfish biomass estimates for each site obtained using three methods: (1) uncorrected sightings from LFS (considered to be the best estimates), (2) uncorrected sightings data from conventional surveys, and (3) sightings data from conventional surveys corrected for variation in detectability owing to habitat complexity (i.e., rugosity) and lionfish size (i.e., mass in g). To compare the estimation methods, we used a linear mixed-effects model (LMM) where lionfish biomass density (g lionfish 100 m⁻²) was predicted by estimation method and grouped by site (i.e., one estimate from each of three methods at each site). We evaluated differences between pairs of estimation methods using Bonferroni-corrected pair-wise comparisons.

Bias in the average size of lionfish estimated by conventional UVC surveys will affect the correction factor applied to lionfish sightings data. To determine whether bias exists, we created a linear model in which mean lionfish weight (in g) from LFS was predicted by mean lionfish weight (in g) from conventional UVCs of the same sites. Only surveys on which at least one lionfish was detected using the conventional method could be included in the analyses.

Results

We conducted a total of 60 visual surveys on Cape Eleuthera reefs: 33 sites were surveyed with a belt transect (21 on continuous and 12 on patch reefs) and 27 sites with a SVC (15 on continuous and 12 on patch reefs). Lionfish-focussed searches (LFSs) of these sites yielded a total of 142 lionfish ranging in size from 2 to 41 cm TL (mean \pm SD; 20 \pm 8 cm). Lionfish density per site, as documented by LFS, ranged from 0 to 31 individuals 100 m⁻² (mean \pm SD; 3 \pm 6 individuals 100 m⁻²). The LFSs indicated that lionfish were present within the boundaries of 22 transect sites and 18 SVC sites (66 and 67 % of each survey type,

respectively). All lionfish observed were stationary and in contact with the substrate. Only sites where at least one lionfish was present (as detected by LFS) were included in our analyses of detection probability.

Only 28 % of lionfish within transect sites and 22 % of lionfish within SVC sites were detected using the conventional survey protocols. Moreover, 64 % of belt transects and 53 % of SVCs failed to detect the presence of any lionfish when one or more lionfish were observed with a LFS of the same site. Both individual lionfish body size and habitat complexity, as measured by average rugosity, significantly predicted whether an individual was detected with conventional survey methods, with the likelihood of detection being highest for large lionfish in low rugosity habitat (Table 1A; Fig. 1). There was no significant interaction between individual lionfish size and rugosity, indicating that the effects of both on lionfish detectability are additive. This effect was the same for both conventional survey methods: lionfish detection probability did not differ significantly between belt transect and SVC surveys (Table 1A). Detection probability did vary significantly between reef types (Table 1A; Fig. 1), with higher detection on patch reefs.

Both mean lionfish body size and habitat complexity (i.e., rugosity) also significantly influenced the proportion of lionfish biomass detected using conventional methods, with the proportion of biomass detected being highest for sites with large lionfish (on average) and low rugosity (Table 1B; Fig. 2). Again, we did not find a significant interaction between lionfish size and rugosity, and site-level detection probability did not differ significantly between belt transects and SVC surveys but was significantly higher on patch reefs (Table 1B; Fig. 2). Using the inverse of these detection probabilities as biomass correction factors, we estimate that lionfish biomass detected using belt transect and SVC surveys must be multiplied by 1.2–200, on average, depending on site-specific mean lionfish size and habitat rugosity (Fig. 2). Site-specific correction factors varied greatly between reef types, with correction factors being 8–33 times greater for continuous reefs than for patch reefs (Fig. 2).

Estimates of lionfish biomass (g lionfish 100 m⁻²) generated from conventional UVC were significantly lower than those generated from LFS of the same site, with mean total biomass exceeding detected biomass by \sim 200 % (Table 1; Fig. 3). There was a significant relationship between the site-specific mean weight of lionfish (in g) estimated by LFS and by a conventional UVC for the 18 sites where UVCs detected lionfish, with a slope not significantly different from 1 (Table 1D), but the negative intercept of this relationship indicates that the average size estimated from UVCs is consistently larger than that from LFS at the same sites. We thus subtracted this intercept

Table 1 Results from A) the final generalized linear mixed-effects model (GLMM) of probability of individual lionfish detection, B) the final generalized linear model (GLM) of site-specific probability of lionfish biomass detection, C) Bonferroni-corrected pair-wise comparisons from the linear mixed model (LMM) of lionfish biomass per site ($\text{g } 100 \text{ m}^{-2}$), and D) linear model (LM) of mean lionfish size (mass in g)

Models	Responses	Variables	Estimate	SE	P
A. GLMM	Individual lionfish detection (0/1)	Intercept	-2.74	3.87	0.478
		Lionfish length	0.33	0.07	<0.0001
		Rugosity	-6.48	3.01	0.031
		Reef type (patch reef)	5.60	1.91	0.003
B. GLM	Site-specific lionfish detection (proportion)	Intercept	5.92	3.23	0.076
		Lionfish length	0.003	0.001	0.035
		Rugosity	-6.13	2.69	0.028
		Reef type (patch reef)	3.93	1.62	0.020
C. LMM	Lionfish biomass	UVC: LFS	-213.36	37.48	<0.0001
		UVC: cUVC	-87.95	37.48	0.021
		cUVC:LFS	-125.95	37.48	0.001
D. LM	Mean lionfish size from LFS	Intercept	-35.94	24.74	0.166
		Mean lionfish size from conventional surveys	0.94	0.05	<0.0001

Lionfish total length was measured in cm. Individual lionfish detection response could be 0 (not detected by conventional survey methods) or 1 (detected). Site-specific lionfish biomass detection responses were proportions, calculated as the ratio of lionfish biomass detected during conventional surveys to total lionfish biomass obtained from a lionfish-focussed search of the same site. Reef type is a two-level factor, with 'continuous reef' as the baseline against which 'patch reef' (in parentheses) was compared. For C), lionfish biomass was estimated in three ways: lionfish-focussed searches (LFS), conventional visual underwater visual surveys (UVC), and with application of site-specific correction factors to conventional visual survey data (cUVC)

value to adjust UVC-derived mean lionfish size and used the resulting size to identify the relevant correction factor for each site (Fig. 2). Applying site-specific correction factors to UVC data, to account for variation in detection with lionfish body size and habitat rugosity, increased mean detected lionfish biomass significantly (Table 1; Fig. 3). However, the large proportion of UVCs (>50 %) yielding no detections—which thus could not be adjusted via a detectability correction factor—resulted in biomass estimates that were still significantly lower than those obtained by LFS (Table 1; Fig. 3).

Discussion

Our study reveals that two commonly used underwater visual survey methods, the belt transect survey and the stationary visual census (SVC), detect fewer than 30 % of lionfish present in an area and, in more than 50 % of cases, fail to detect any lionfish when one or more individuals are actually present. The likelihood of detecting lionfish in belt transects and SVC surveys varies markedly in relation to at least two factors: lionfish body size and habitat complexity (here, measured as rugosity), with the effect of habitat complexity being much greater than that of lionfish body size alone (Table 1). Importantly, because these factors can vary widely across space and time, accounting for this

variation is far from straightforward and cannot be accomplished using a single correction factor. The distribution of lionfish body sizes in the Caribbean varies with the stage of invasion and habitat type (Claydon et al. 2012). Moreover, our study was conducted on reefs within a modest range of rugosity values (1.2–1.8), whereas some reefs can be far more complex (i.e., rugosity values 2–3; Alvarez-Filip et al. 2009). Our results suggest that, when using conventional survey methods, lionfish detectability will be lowest on reefs that have small lionfish and high rugosity and will approach zero on the most rugose reefs.

A potential solution to the issue of variable detectability of lionfish could be to apply correction factors to conventional survey data which reflect various combinations of site conditions. Bias in detectability associated with variable habitat complexity can be estimated, and survey data retroactively corrected, if rugosity measures are available for an invaded site. Our study shows that when lionfish are detected during conventional surveys, the average size estimated can be adjusted to approximate that generated from more thorough, lionfish-focussed surveys by using the relationship between the two measures (Table 1D). Moreover, the effect of reef rugosity on detection was ~6 times that of lionfish size, indicating that correction factors are not affected greatly by small errors in estimates of average lionfish size. However, correction factors cannot be applied to conventional surveys that fail to detect lionfish when

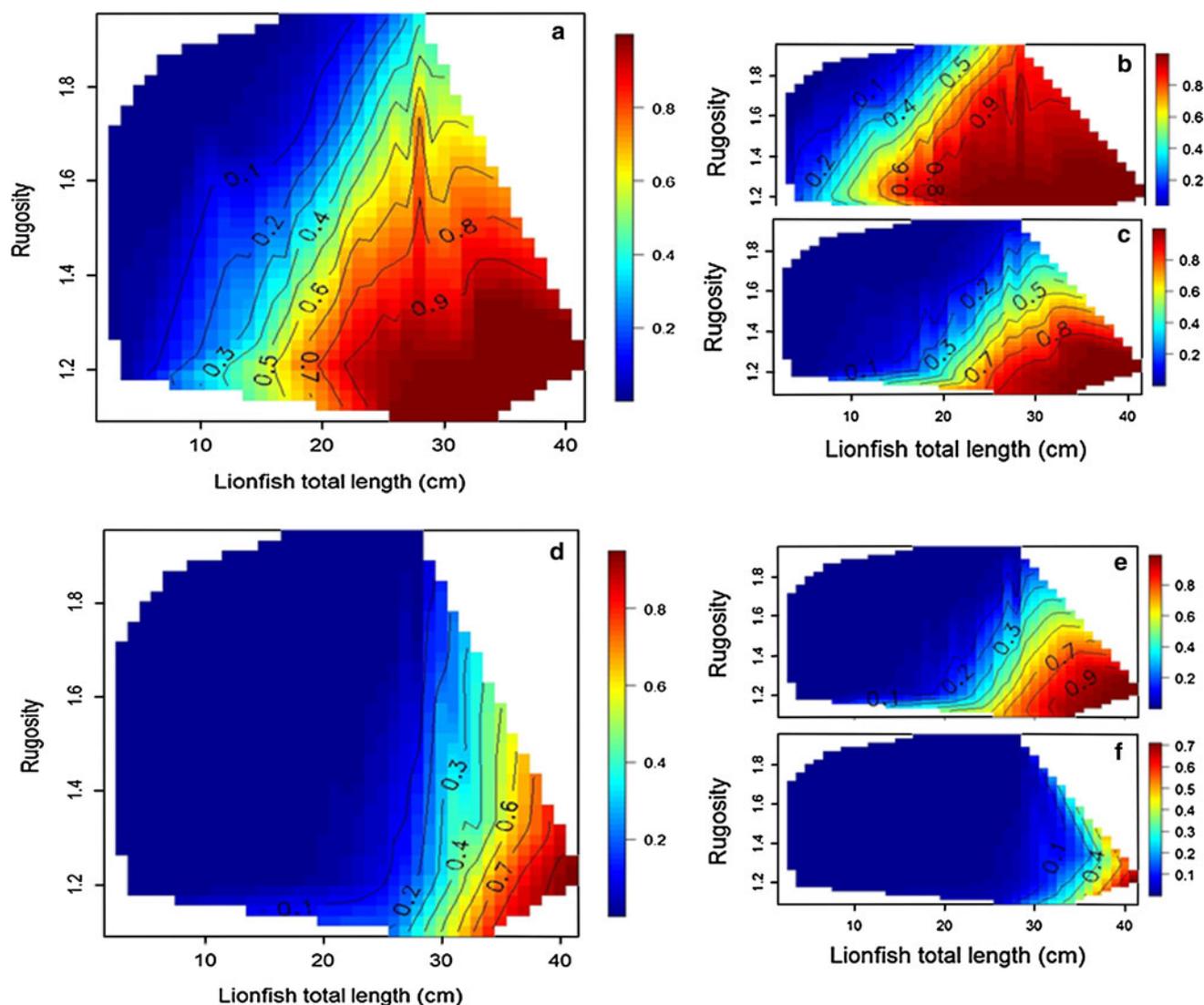


Fig. 1 Contour plots of predicted mean probability of detecting individual lionfish on **a** patch reefs and **d** continuous coral reefs in the Bahamas for various combinations of lionfish total length (cm) and mean site rugosity, and corresponding upper and lower 95 % confidence limits for patch reefs (**b** and **c**, respectively) and

continuous reefs (**e** and **f**, respectively). *Black bands* denote a change in detection probability of 0.1. *Cooler colors* denote the combinations of lionfish body size and reef rugosity yielding low detection probabilities, while warmer colors denote scenarios in which detection probability is higher

lionfish are present, as was the case for more than 50 % of the surveys we conducted with conventional methods. As a result, even though lionfish biomass from surveys on which at least one individual was detected could be adjusted to approximate more closely actual lionfish biomass on those particular surveys, the overall estimate of lionfish biomass across all conventional surveys remained significantly lower than that generated from lionfish-focussed searches of the same sites.

The low lionfish detection rates reported here, which vary in relation to habitat complexity and fish body size, suggest that conventional survey methods are of limited use for accurately tracking invasion status over time and space.

To increase the accuracy and reliability of lionfish population density and biomass data, monitoring programs should incorporate detailed lionfish-focussed searches (e.g., Green 2012). Although the degree to which lionfish-focussed searches reflect actual abundance cannot be known without verification through destructive sampling of reef habitats, our study clearly demonstrates that LFSs yield significantly higher, and presumably more accurate, estimates of lionfish biomass than conventional methods (Fig. 3). However, this more accurate characterization of lionfish populations comes at a cost. For example, adding a LFS to each SVC would double the time required to survey a given area, while adding a LFS to each transect survey

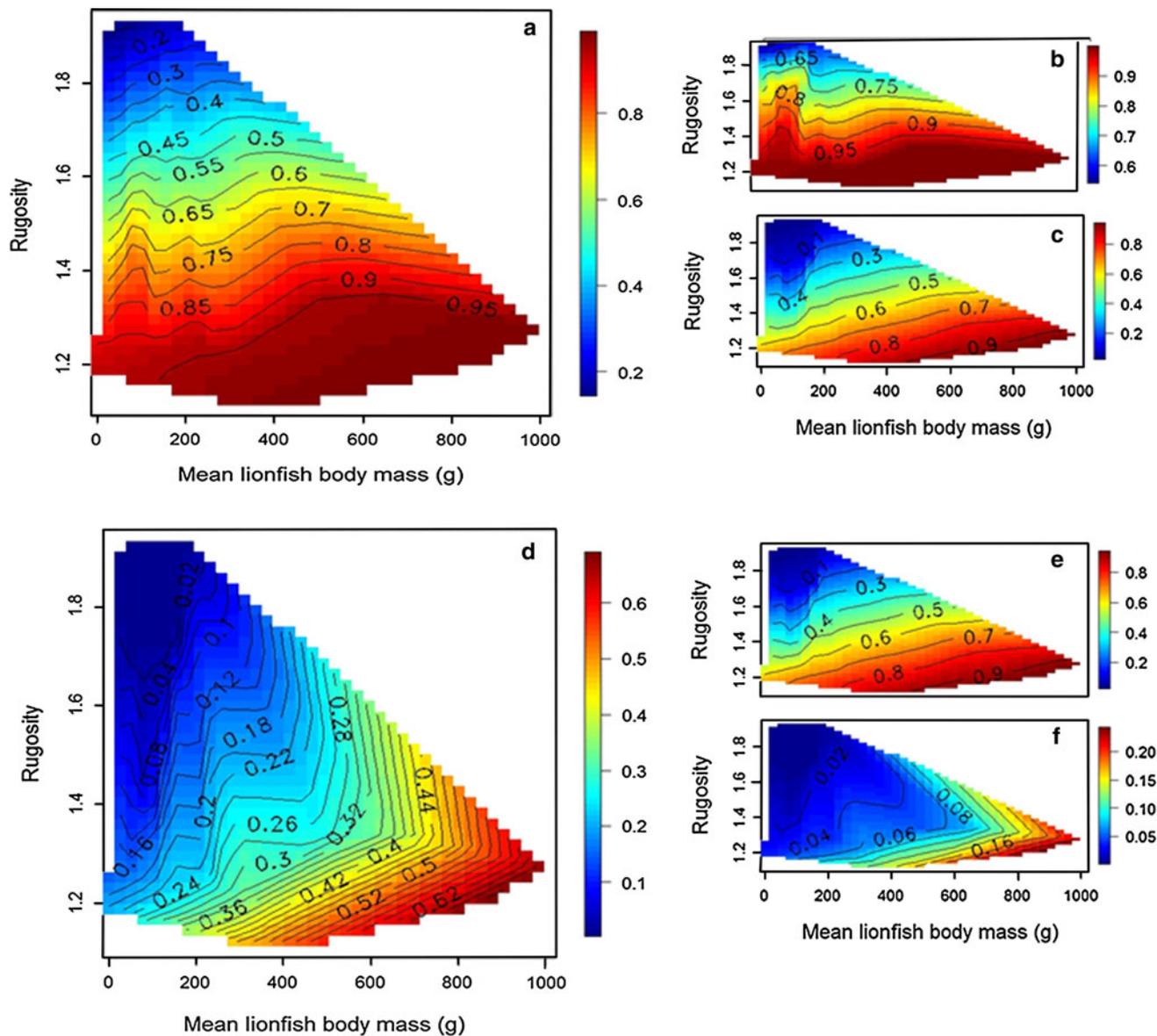


Fig. 2 Contour plots of predicted mean site-specific lionfish biomass detection probability for **a** patch reefs and **d** continuous coral reefs in the Bahamas for various combinations of mean lionfish body mass (g) and mean site rugosity, and corresponding upper and lower 95 % confidence limits for patch reefs (**b** and **c**, respectively) and continuous reefs (**e** and **f**, respectively). Site-specific detection

probability was estimated from the ratio of lionfish biomass detected during a conventional underwater visual survey to total biomass from a lionfish-focussed search of the same site. *Black bands* denote a change in detection probability of 0.1. Color scheme is as described in Fig. 1

would more than triple the time needed. Managers will need to balance trade-offs between lionfish data quality and the number of sites surveyed, and more generally, resources devoted to lionfish monitoring and to other essential conservation activities. However, the decision to employ robust lionfish monitoring strategies may yield significant benefits. For example, the extent to which lionfish reduce the biomass of native reef fish depends on both lionfish density and body size (Côté and Green 2012). Accurate estimates of biomass can thus help to predict the overall impact of

lionfish. Moreover, site-specific targets for lionfish removal to curb native fish declines can be identified but can only be successfully implemented with accurate measures of lionfish biomass (Côté and Green 2012).

Although we have focussed on two systematic sources of bias in the detection of lionfish, others may exist. For example, lionfish detectability varied significantly between patch reefs and continuous reefs in our study. While lionfish sizes and average rugosity varied markedly between the two habitats (mean lionfish length was 18 ± 6 cm (SD)

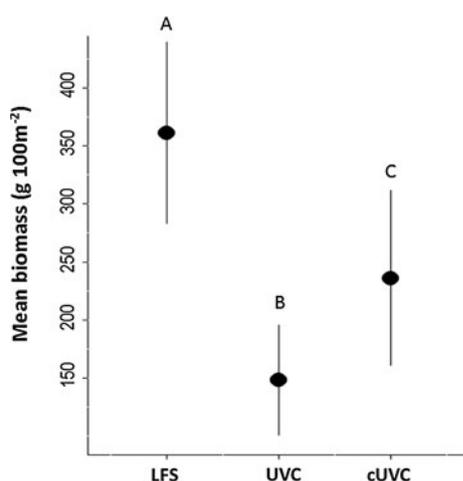


Fig. 3 Estimates of lionfish biomass ($\text{g } 100 \text{ m}^{-2}$) on Bahamian coral reef sites, obtained by three methods: lionfish-focussed searches (LFS), conventional underwater visual surveys (UVC), and conventional surveys adjusted with site-specific detectability correction factors (inverse of detection probabilities shown in Fig. 2) (cUVC). Different letters denote significant differences between estimation methods (Table 1C). All estimation methods were calculated for each site ($n = 60$). Points represent means bounded by 95 % confidence intervals

and 27 ± 8 cm, while mean rugosity was 1.83 ± 0.32 and 1.21 ± 0.06 , for patch and continuous reefs, respectively), these factors were both incorporated into the model, thus there is likely some other fundamental difference between these habitats which affects lionfish detection rates. Possibilities include reef height [e.g., vertical relief sensu Luckhurst and Luckhurst (1978)] and/or the number and size of holes within the reef matrix (e.g., Hixon and Beets 1987). Although we did not measure reef height systematically, it appeared to differ between continuous and patch reefs, with the deeper continuous reefs extending ~ 3 m above the sand, whereas shallower patch reefs were only ~ 1.5 m high. Other studies have found that vertical relief is one of the only habitat metrics that correlates with the number of small holes (<10 cm diameter) in a reef (Wilson et al. 2007). Thus, it is possible that more holes within continuous reefs may have offered more shelters for resident fish, and thus decreased our ability to detect lionfish in these habitats compared with lower-relief patch reefs. In addition, detectability could vary with time of day or weather conditions. To deal with these potential sources of variability, surveys are usually consistently conducted at the same time, typically limited to daylight hours for logistical reasons. While the diurnal nature of most reef fish (Hobson 1973) makes such timing appropriate, this is not necessarily the case for lionfish and other crepuscular or nocturnal species (e.g., Gilbert et al. 2005). It is well known that activity—and thus visibility—of lionfish increases with diminishing light levels, such as occur

during crepuscular periods and on overcast days (Fishelson 1975; Côté and Maljković 2010; Green et al. 2011). While conducting lionfish surveys at dawn or dusk may improve estimates of population status, the logistical difficulties of conducting crepuscular surveys may outweigh the benefits.

Numerous studies have emphasized the shortcomings of common underwater visual survey methods for the detection of cryptic fishes and advocate instead the use of modified methods that account for species characteristics and behavior (Kulbicki 1998; Ackerman and Bellwood 2000; Samoilys and Carlos 2000; Willis 2001; Gilbert et al. 2005). The application of a standard correction factor may yield estimates of abundance and biomass which approximate reality, but only if survey conditions are similar to those under which the factor was estimated (e.g., Christensen and Winterbottom 1981; Sale and Sharp 1983; Whitfield et al. 2007; Kulbicki et al. 2012). Here, using invasive lionfish as an example, we have demonstrated that accounting for systematic sources of bias in detection probability across seascapes improves the accuracy of estimates obtained by visual census but that even with bias correction, conventional census methods underestimate lionfish abundance and biomass. Our study is one of the first attempts to quantify within-species sources of variation in detection probabilities for marine fishes and highlights the importance of tailoring survey methodologies to account not only for the unique characteristics of the species under scrutiny but the conditions under which it is being scrutinized.

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References

- Ackerman JL, Bellwood DR (2000) Reef fish assemblages: a re-evaluation using enclosed rotenone stations. *Mar Ecol Prog Ser* 206:227–237
- 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. *Environ Biol Fish*:1–7. doi:10.1007/s10641-011-9795-1
- Alvarez-Filip L, Dulvy NK, Gill JA, Côté IM, Watkinson AR (2009) Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. *Proc R Soc Lond B Biol Sci* 276:3019–3025
- Bohnsack JA, Bannerot SP (1986) A stationary visual census technique for quantitatively assessing community structure of coral reef fishes. NOAA Technical Report NMFS 41, NOAA
- Brandt ME, Zurcher N, Acosta A, Ault JS, Bohnsack JA, Feeley MW, Harper DE, Hunt JH, Kellison T, McClellan DB, Patterson ME, Smith SG (2009) A cooperative multi-agency reef fish monitoring protocol for the Florida Keys coral reef ecosystem. Natural Resource Report NPS/SFCN/NRR—2009/150. National Park Service, Fort Collins, CO

- Christensen MS, Winterbottom R (1981) A correction factor for, and its application to, visual censuses of littoral fish. *S Afr J Zool* 16:73–79
- Claydon J, Calosso M, Traiger S (2012) Progression of invasive lionfish in seagrass, mangrove and reef habitats. *Mar Ecol Prog Ser* 448:119–129
- Colvocoresses J, Acosta A (2007) A large-scale field comparison of strip transect and stationary point count methods for conducting length-based underwater visual surveys of reef fish populations. *Fish Res* 85:130–141
- Côté IM, Green SJ (2012) Potential effects of climate change on a marine invasion: the importance of current context. *Curr Zool* 58:1–8
- Côté IM, Maljković A (2010) Predation rates of Indo-Pacific lionfish on Bahamian coral reefs. *Mar Ecol Prog Ser* 404:219–225
- Edgar GJ, Barrett NS, Morton AJ (2004) Biases associated with the use of underwater visual census techniques to quantify the density and size-structure of fish populations. *J Exp Mar Biol Ecol* 308:269–290
- Fishelson L (1975) Ethology and reproduction of pteroid fishes found in the Gulf of Aqaba (Red Sea), especially *Dendrochirus brachypterus* (Cuvier), (Pteroidae, Teleostei). *PSZNI Mar Ecol* 39:635–656
- Gilbert M, Rasmussen JB, Kramer DL (2005) Estimating the density and biomass of moray eels (Muraenidae) using a modified visual census method for hole-dwelling reef fauna. *Environ Biol Fish* 73:415–426
- Green SJ, Akins JL, Maljković A, Côté IM (2012) Invasive lionfish drive Atlantic coral reef fish declines. *PLoS ONE* e32596
- Green SJ (2012) Monitoring: an essential action. In: Morris JAJ (ed) *Invasive lionfish: a guide to control and management*. Gulf and Caribbean Fisheries Institute Special Publications Series Number 1. Marathón, Florida, 113p
- 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
- Harvey E, Fletcher D, Shortis MR, Kendrick GA (2004) A comparison of underwater visual distance estimates made by scuba divers and a stereo-video system: implications for underwater visual census of reef fish abundance. *Mar Freshw Res* 55:573–580
- Hixon MA, Beets JP (1987) Shelter characteristics and Caribbean fish assemblages: experiments with artificial reefs. *Bull Mar Sci* 44:666–680
- Hobson ES (1973) Diel feeding migrations in tropical reef fishes. *Helgol Wiss Meeresunters* 24:361–370
- Kulbicki M (1998) How the acquired behaviour of commercial reef fishes may influence the results obtained from visual censuses. *J Exp Mar Biol Ecol* 222:11–30
- Kulbicki M, Cornuet N, Vigliola L, Wantiez L, Moutham G, Chabanet P (2010) Counting coral reef fishes: interaction between fish life-history traits and transect design. *J Exp Mar Biol Ecol* 387:15–23
- Kulbicki M, Beets J, Chabanet P, Cure K, Darling E, Floeter S, Galzin R, Green A, Harmelin-Vivien M, Hixon M, Letrouneur Y, Lison de Loma T, McClanahan T, McIlwain J, MouTham G, Myers R, O’Leary JK, Planes S, Vigliola L, Wanties L (2012) Distributions of Indo-Pacific lionfishes (*Pterois* spp.) in their native ranges: implications for the Atlantic invasion. *Mar Ecol Prog Ser* 466:189–205
- Luckhurst BE, Luckhurst K (1978) Analysis of the influence of substrate variables on coral reef fish communities. *Mar Biol* 49:317–323
- MacNeil MA, Tyler EHM, Fannesbeck CJ, Rushton SP, Polunin VC, Conroy MJ (2008a) Accounting for detectability in reef-fish biodiversity estimates. *Mar Ecol Prog Ser* 367:249–260
- MacNeil MA, Graham NAJ, Conroys MJ, Fannesbeck CJ, Polunin NVC, Rushton SP, Chabanet P, McClanahan TR (2008b) Detection heterogeneity in underwater visual-census data. *J Fish Biol* 73:1748–1763
- McCallum DA (2005) A conceptual guide to detection probability for point counts and other count-based survey methods. USDA Forest Service General Technical Report PSW-GTR-191. USDA Forest Service, Albany, CA
- Murphy HM, Jenkins GP (2010) Observational methods used in marine spatial monitoring of fishes and associated habitats: a review. *Mar Freshw Res* 61:236–252
- NOAA (2012) CoRIS: NOAA’s coral reef information system. NOAA Coral Reef Conservation Program. http://coris.noaa.gov/activities/fish_monitoring_protocol/. Accessed 3 Sept 2012
- NPS (2012) Inventory and monitoring program: marine fish communities. US National Park Service online database. http://science.nature.nps.gov/im/units/sfcn/marine_fish.cfm. Accessed on 3 Sept 2012
- Ruttenburg BI, Schofield PJ, Akins JL, Acosta A, Feeley MW, Blondeau J, Smith SG, Ault JS (2012) Rapid invasion of Indo-Pacific lionfishes (*Pterois volitans* and *Pterois miles*) in the Florida Keys, USA: evidence from multiple pre- and post-invasion data sets. *Bull Mar Sci* 88:1051–1059
- Sale PF, Sharp BJ (1983) Correction for bias in visual transect censuses of coral reef fishes. *Coral Reefs* 2:37–42
- Samoilys MA, Carlos G (2000) Determining methods of underwater visual census for estimating the abundance of coral reef fishes. *Environ Biol Fish* 57:289–304
- Sutherland WJ, Clout M, Côté IM, Daszak P, Depledge MH, Fellman L, Fleishman E, Garthwaite R, Gibbons DW, De Lurio J, Impey AJ, Lickorish F, Lindenmayer D, Madgwick J, Margerison C, Maynard T, Peck LS, Pretty J, Prior S, Redford KH, Scharlemann JPW, Spalding M, Watkinson AR (2010) A horizon scan of global conservation issues for 2010. *Trends Ecol Evol* 25:1–7
- Thomson JA, Cooper AB, Burkholder DA, Heithaus MR, Dill LM (2012) Heterogeneous patterns of availability for detection during visual surveys: spatiotemporal variation in sea turtle dive—surfacing behaviour on a feeding ground. *Methods Ecol Evol* 3:378–387
- Whitfield PE, Hare JA, David AW, Harter SL, Munoz RC, Addison CM (2007) Abundance estimates of the Indo-Pacific lionfish *Pterois volitans/miles* complex in the Western North Atlantic. *Biol Invasions* 9:53–64
- Willis TJ (2001) Visual census methods underestimate density and diversity of cryptic reef fishes. *J Fish Biol* 59:1408–1411
- Wilson SK, Graham NAJ, Polunin NVC (2007) Appraisal of visual assessments of habitat complexity and benthic composition on coral reefs. *Mar Biol* 151:1069–1076
- Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) *Mixed effects models and extensions in ecology with R*. Springer, New York