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Accounting for detectability in reef-fish biodiversity estimates

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ABSTRACT: Assessments of the biodiversity and structure of coral reef fish communities are often plagued by inadequate sampling and biases inherent in commonly used Underwater Visual Census (UVC) methods. Of these biases, heterogeneity in the detectability of reef-fish species is often ignored, even though it may have substantial effects on biodiversity estimates. Using highly replicated UVC sampling of all fish species at 4 sites in Tanzania, East Africa, we show that detectability varies greatly across species and is affected by traits such as body size and schooling behaviour, and that detectability of reef fishes can be readily accounted for by the application of Capture-Mark-Recapture (CMR) models. Based on our results, we recommend that approximately 24 point counts are necessary to assess full reef-fish species richness at sites in the Western Indian Ocean.

KEY WORDS: Mark-recapture · Underwater Visual Census · Coral reefs · Bayesian · Marine reserve

INTRODUCTION

Coral reef fish communities are exceptional among marine environments for their high levels of diversity and productivity — yet the biodiversity of reef ecosystems is under threat from natural and anthropogenic stress (Bellwood et al. 2004). Disturbance-induced effects on reef fishes have been observed across the Indo-Pacific, with 62% of species declining in abundance within 3 yr of a large-scale bleaching event (Wilson et al. 2006). Accurate measurements of reef-fish species richness and community structure are essential for monitoring progress towards biodiversity targets (Hutchings & Baum 2005) and for prioritising conservation actions. However the ability to accurately measure species richness can be constrained by inherent biases in survey methods and the limited replication commonly used to employ them.

Underwater Visual Census (UVC) is the most widely used method for surveying reef-fish communities. UVCs typically consist of transects or point counts — methods that rely on trained observers recording fish presences, lengths, and abundances observed within a fixed volume of the water column. Although UVC methods have many well known biases, they currently represent the best available method for non-destructive sampling of reef-fish communities. Destructive methods such as rotenone sampling may provide more complete counts, but they have, by definition, an adverse effect on reef fishes (Ackerman & Bellwood 2000), making them an ironic choice for researchers studying declines in biodiversity. Species richness bias is the difference between the actual and predicted number of species present at a given location, and can arise due to heterogeneity among habitats (Edgar & Barrett 1999), observers (Thompson &

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Mapstone 1997), species (Kulbicki & Sarramégna 1999), random instantaneous movement (McClanahan et al. 2007), and the choice of method itself (Watson & Quinn 1997, Kulbicki & Sarramégna 1999, Samoilys & Carlos 2000). Most of these problems are dealt with through technique standardisation and by the assumption that biases are consistent among studies (Ackerman & Bellwood 2000). However, unknown systematic heterogeneity can seriously bias estimates of species richness, directly affecting the ability to make accurate assessments of biodiversity.

Detectability is defined as the probability of observing a particular species during a given sampling occasion conditional on its presence at that location (Boulinier et al. 1998). UVC based studies routinely assume that detectability = 1 across all species but it can vary substantially among reef fishes due to physical, behavioural, or life-history characteristics. For example, lethrinids have been shown to avoid divers (Kulbicki 1998, Kulbicki & Sarramégna 1999), leading to a frequent lack of agreement between UVC and fishing data in tropical fisheries (Jennings & Polunin 1995, Kulbicki 1998). Cryptic morphology or behaviour can also affect detectability, as more than 90% of cryptic species may be undetected by UVC methods (Willis 2001); the recognition of low detectability has led to surveys that target only a subset of the community that excludes the least detectable species. There is also a strong, positive relationship between detectability and abundance (Dorazio & Royle 2005) that can generate substantial heterogeneity among surveys. Compounding this issue is the fact that surveys are routinely conducted using relatively low numbers of replicates. Not accounting for detection, heterogeneity may be acceptable if the bias is small relative to the size of the target community but it is essential to estimate both the magnitude of biases present and the appropriate level of sampling required if UVC data are to be used to study full biodiversity and community dynamics.

Using a UVC data set that does not truncate the species observed into a subset of observable species and includes a uniquely high level of replication, we demonstrate how covariate Capture-Mark-Recapture (CMR) models can be used to account for species-specific detection probabilities of reef fishes and suggest specific sampling guidelines given the target community of interest. Furthermore, we test the assumption that detection probability = 1 across all species and explore how detection probabilities vary with several species-specific traits (family group, functional group, maximum total length, and schooling behaviour). We compare functional groups and family groups to see which are more consistent in their level of detectability. Reef-fish data are conventionally analysed by family because life-history and behaviour are thought to correlate well with taxonomy. However, groupings based on diet (functional groups) are increasingly being used to represent species roles in the environment (Bellwood et al. 2003). We predict that large, schooling fish are more detectable and that detectability will be higher in sites with marine reserve status (fully protected from fishing) compared to sites that were fished, due to an *a priori* assumption of higher abundance in marine reserves.

METHODS

Survey methods and data. Our UVC surveys were conducted near the Tanzanian islands of Unguja and Pemba in the Western Indian Ocean (Fig. 1), a region

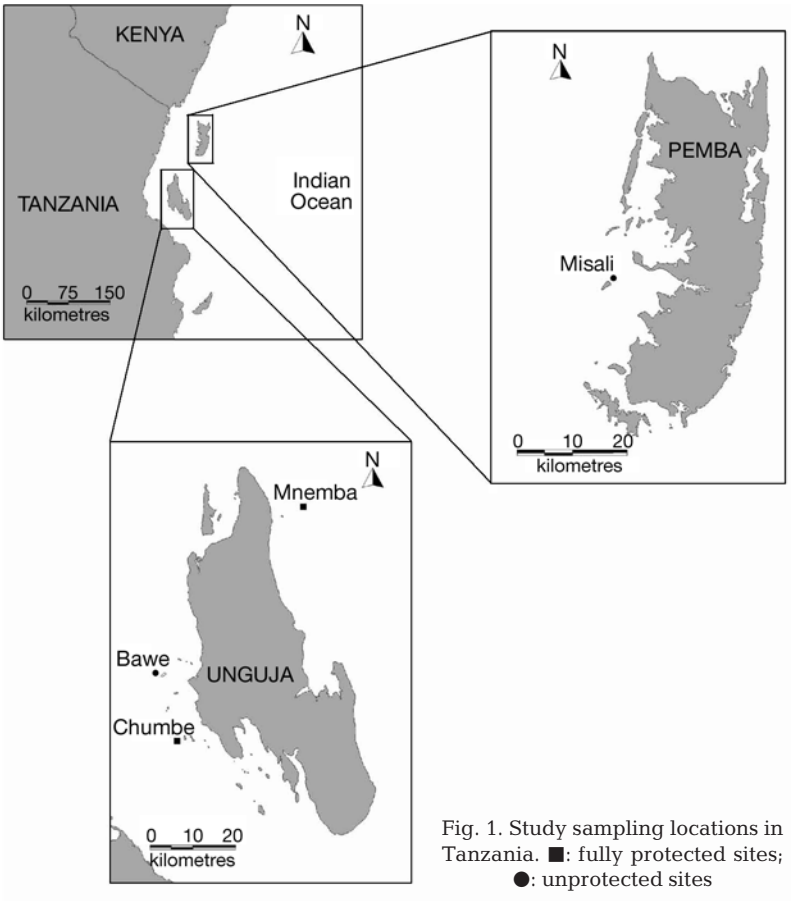

Fig. 1. Study sampling locations in Tanzania. ■: fully protected sites; ●: unprotected sites

of relatively high fish species richness (~1000 spp.), making it ideal for estimating detectability across a range of fish species. We sampled species richness from 2 sites fully protected from fishing (Chumbe, Mnemba) and from 2 unprotected sites (Bawe, Misali) from December 2003 to February 2004. The 4 sites represented a range of habitat and physical characteristics (Table 1), from 18 to 78% live hard coral cover and from 0.06 to 0.88 km^2 of total reef area. Only coral reef habitat was surveyed at each site to minimize variation in habitat between sites. We sampled a large number of replicate point counts (n = 24) at each site, giving a total of 96 counts, allowing us to estimate detection probabilities of cryptic species and to accurately assess species richness among these sites. All available reef zones at a site were sampled (to a maximum of 15 m), with the range of depths at a site varying according to its topography.

We conducted stratified random sampling at each site, with sites divided into approximately equal (1000 m^2) sections and these sections into zones (reef flat, reef crest and reef slope). Sections and zones were paired and sampled in an arbitrary order. Reef slopes were sampled in the first section and reef crest or flat in the second. Two observers entered the water together and swam for 15 fin kicks in opposite directions to allocate the first sample. We allocated a second sample by swimming a further 15 fin kicks in the same direction along the depth contour. Each observer arbitrarily selected a centre point for the sample, estimated the location of the perimeter of the sample area for a 7 m radius from the centre and recorded any large fish that moved out of the area as they approached. A marker was placed at the centre of the sample area as a reference point.

All fish species present or entering a 7 m radius around the centre point during a 15 min period were included, with no limits on size or family. Observers stayed in the centre of the sampling point for the first 5 min, rotating 360°, and recording the most visible species. They then actively searched the entire area for the remaining 10 min. Observers alternately searched for cryptic demersal species by looking behind, under, and into coral colonies, and for pelagic species by looking up and around the water column. A few species inside the structure of the reef were likely to have been missed; however, we believe the majority of fish species were detected in the sample area. Observers were already experienced in Indo-Pacific reef-fish identification, but further training was conducted before sampling began using digital underwater pictures from Lieske & Myers (2001) and Fishbase (Froese & Pauly 2007) as species references.

Table 1. Site characteristics of sampling locations in Tanzania. Live hard coral cover, rugosity (habitat complexity), and depth are average values at each location, calculated from measurements in each sample. Rugosity was measured on an index of 1 to 10, with 1 being the least rugose habitat

Location	Factor			
	% live coral	Rugosity	Depth (m)	Total area (km^2)
Bawe	78	4.5	5.2	0.37
Chumbe[a]	50	5.0	5.0	0.57
Misali	27	4.9	7.3	0.88
Mnemba[a]	18	2.7	2.3	0.06

[a]Protected from fishing

Statistical analysis. CMR models are used to estimate total population size in a given area across a number of capture occasions (Williams et al. 2001) or to estimate total species richness from observations of species present through a given number of sampling occasions (Boulinier et al. 1998, Dorazio & Royle 2005). Although these models are recommended for dealing with detectability in biodiversity studies (Yoccoz et al. 2001, Dorazio et al. 2006) they have not previously been applied to reef-fish communities. The major assumption required for these models is that the population or community is closed across sampling occasions (no immigration or emigration) within a given study area for the duration of sampling (Williams et al. 2001). Although nearly all reef fishes have a planktonic larval stage that makes reef systems at least partially open, an assumption of population closure can frequently be made at appropriately defined scales (Hixon et al. 2002). Reef fishes show considerable site fidelity (Zeller & Russ 1998), with movements that are generally restricted to within discrete patch reefs; few individuals move across reef channels (Chapman & Kramer 2000). Given such individual behaviour, the short time scale of sampling, and the fact that we were modelling the presence of species, we assumed that the sites were closed during the study period.

CMR models have multiple forms that account for specific sources of heterogeneity in population index counts from recaptured animals (Otis et al. 1978, Dorazio et al. 2006). By convention, M_0 is a null model that assumes the probability of animal capture is constant among species and sampling occasions. For consistency with previous CMR literature we retain the M_x model notation to describe the basic models but use community-level terminology throughout. Commonly cited sources of bias in population-level studies include heterogeneity through time (M_t), by individual (M_h), and in response to capture (M_b) (Williams et al. 2002). Previously, CMR modelling frameworks have conditioned potential sources of heterogeneity on covariate information of the captured individuals (Huggins 1989) but we found that implementation of these

models was prohibitively slow, and therefore implemented a standard logistic regression approach for estimating the probability of detection (p_{ik}) as a conditional likelihood:

$$L = \prod_{i=1}^{n}\prod_{k=1}^{t} p_{ik}^{z_{ik}}(1-p_{ik})^{1-z_{ik}} \quad (1)$$

dependent only on the species being observed, $z_{ik} = 1$, or not $z_{ik} = 0$, at each sampling occasion. A logit link was used to account for covariates of interest, with a general form of each model (M_x) for species i during sampling occasion k given by:

$$\ln\left(\frac{p_{ik}}{1-p_{ik}}\right) = \beta_0 + \beta_1 x_{1,ik} + \beta_2 x_{2,ik} + \ldots + \beta_{x_j} x_{j,ik} \quad (2)$$

where detectability varies by $\beta_{x_1}\ldots\beta_{x_j}$ for covariates $x_1\ldots x_j$ for p_{ik} in Eq. (1). We compared the results given by this approach to those given by the special conditional likelihood of Huggins (1989) using results from one site (Bawe) to ensure results were consistent.

Using information gathered from expert opinion, we selected 4 available covariates for detection, including fish family group, functional group, maximum attainable total length (TL_{max}), and presence/absence of schooling behaviour. Functional groups were defined by known feeding behaviour and range of diets while schooling behaviour was defined by fish being consistently aggregated in groups of >5 individuals. The 'scrapevator' category was the combined 'scraper' and 'excavator' groups of Bellwood et al. (2004), both of which remove reef substrate during feeding. Different combinations of these factors comprised 7 candidate models of individual heterogeneity (Table 2). It is important to note however, that, although these covariates are available for the detectable portion of the community, the undetected proportion is non-identifiable, and theoretically may bear no resemblance to the detectable fishes (Link 2003).

Table 2. Candidate model set for estimating reef-fish detectability in Tanzania. Factors included family group, *f* (1), functional group, *g* (2), maximum total length, *l* (3), and schooling behaviour, *s* (4)

Model	Factors	Hypothesis
M_0	{. . . .}	All species have equal detectability
M_f	{1. . .}	Detectability varies by family group
M_g	{. 2 . .}	Detectability varies by functional group
M_l	{. . 3 .}	Detectability is a function of size
M_{fl}	{1 . 3 .}	Detectability varies by family group and size
M_{gl}	{. 2 3 .}	Detectability varies by functional group and size
M_{fls}	{1 . 3 4}	Detectability varies by family group, size, and schooling behaviour

In population-level conditional models, covariate factors for capture are assumed to arise as random draws from an underlying distribution common to the entire group (i.e. random effects) (Huggins 1989); we made this assumption for the effect of TL_{max} and schooling behaviour. However we did not believe this assumption to be appropriate for family and functional group membership: we could not conceive of how a common detectability distribution for all fish family groups would arise, given their distinct life-history characteristics. We therefore estimated unique functional and family-level detection probabilities that were conditioned only on the species observed within each group.

We used the PyMC 1.3 (Fonnesbeck 2006) toolkit for the Python programming language (Python Software Foundation 2006) to conduct our analysis. Most CMR modelling has been implemented in programs CAPTURE (Rexstad & Burnham 1991) or MARK (White & Burnham 1999); however, we developed a Bayesian approach, implemented through Markov-chain Monte Carlo (MCMC) simulation. PyMC gave us a high-level of flexibility for specifying likelihoods in an open-source, object-oriented framework that is particularly applicable to ecological analyses. As we had no prior information available on detection probabilities we used the default uniform priors provided by PyMC. To assess MCMC convergence, we relied on a formal convergence method proposed by Geweke (1992), whereby an MCMC chain is considered to have reached convergence when the majority of z-scores fall within 2 standard deviations of 0 (Geweke 1992). By default, PyMC plots the z-scores of the difference between initial segments along the chain and the last 50% of the chain and convergence can then be assessed by eye. In all of our models we ran an initial 15 000 iterations as a burn-in period and interpreted posterior distributions and convergence from a subsequent 50 000 iterations. Bayesian model fit was assessed using the goodness of fit (GOF) methods provided by PyMC, whereby a discrepancy measure is used to compare the deviance of the observed data from the expected parameter values to the deviance of simulated data from the expected parameter values (Gelman et al. 2004). Ideal model fits yield a GOF value of 0.5, indicating equivalence between the simulated and observed deviance. Once adequate GOF and convergence had been confirmed for each model, we evaluated the relative strength of the candidate models using the Deviance Information Criterion (DIC) (Spiegelhalter et al. 2002). Models with lower DIC scores are considered closer, in an information sense, to the true model and are considered to be more appro-

priate for the data than models with higher values. Although there is ongoing debate regarding the theoretical use of DIC, its use has consistent support on practical evidence (Spiegelhalter & Marshall 2006). For each set of candidate models run at each of the 4 sampling sites we used DIC scores to interpret the relative weight of evidence for each candidate model using DIC-based model weights (sensu Burnham & Anderson 2002).

Finally, to assess the consistency of UVC point counts among levels of replication, we examined the change in mean probability of detection ($\hat{p}$), under a range of replicate sampling occasions using both a complete (183 to 219 spp.) and truncated (53 to 75 spp.) species list from each site. Unlike our data, many surveys count only diurnally active, non-cryptic, reef associated fish; we elicited expert opinion to compose a truncated species list that represented these groups. Maintaining the original order of the data and beginning with the first point count, a truncated set of data was run for each sampling location with model M_0 for $k = \{3, 5, 15, 24\}$ sampling occasions. M_0 was used as models with $k < 5$ sampling occasions are not recommended for inference (MacKenzie et al. 2006) and our interest was specifically in how average values changed through time. The order of counts was retained to reflect normal sampling conditions for k given the point counts already completed, thus maintaining the sampling structure of the data. We compared the rate of change in $\hat{p}$ from k across all sites using the self-starting asymptotic non-linear regression model (SSasymp) in the nlme (linear and nonlinear mixed effects models) library for the statistical programming language R (R Development Core Team 2008). Models with fixed and random effects for each parameter were compared using Akaike's Information Criterion (AIC).

RESULTS

Model GOF was high (0.44 to 0.51) for the top-ranked model at every site, indicating that the models were appropriate for analysis of reef-fish detectability. DIC supported similar models at all sites — model M_{fls} at Bawe, Chumbe, and Misali, and model M_{fl} at Mnemba (Table 3). These models were the top-ranked models for all sites having >99% of the total model weight and providing strong evidence that together, family group and TL_{max} were most informative covariates of detectability. This suggests that the detection properties of point counts and the fish communities were consistent among sites. Our model results were highly consistent with the use of Huggins' (1989) approach for all models at Bawe.

Table 3. Model selection summary for top-ranked covariate models of Tanzanian reef-fish detectability. Data included 24 replicate point counts at each location. Number of parameters in model i (K), deviance goodness of fit (GOF), deviance information criterion (DIC_i), relative DIC (ΔDIC_i), and DIC-based model weights (w_i) are shown. Covariate factors per model (indicated by model subscripts) include family group (f), maximum reported total length (l), functional group (g), and schooling behaviour (s)

$Model_i$	K	GOF	DIC_i	ΔDIC_i	w_i
Bawe					
M_{fls}	35	0.479	5091.43	0.00	0.765
M_{fl}	34	0.470	5093.80	2.37	0.234
M_f	33	0.472	5107.49	16.06	0.01
Chumbe					
M_{fls}	40	0.507	5811.14	0.00	0.898
M_{fl}	39	0.545	5815.50	4.36	0.102
M_f	38	0.389	5861.35	50.21	0.000
Misali					
M_{fls}	46	0.442	5640.58	0.00	0.929
M_{fl}	45	0.343	5645.72	5.14	0.071
M_f	44	0.359	5742.17	101.59	0.000
Mnemba					
M_{fl}	39	0.457	5118.44	0.00	0.932
M_{fls}	40	0.387	5123.69	5.25	0.068
M_f	38	0.315	5190.25	71.81	0.000

Convergence z-scores for model M_{fls} and M_{fl} parameters were consistently within 2 standard deviations of 0 with few exceptions, confirming adequate model convergence among models at all sites; this was reflected in the parameter traces and posterior distributions. However for families where only a single species was observed (e.g. pseudochromids), convergence diagnostics showed occasional departures from this range. We did not consider this to be a major problem as these groups were few and contributed little to the community-level parameter estimates; the results highlighted that, because family (or functional) group parameters are estimated only from the detection histories of species within the group, more than 1 or 2 species must be observed for group parameter estimates to be generally informative.

Community-level parameter estimates showed that models M_{fls} and M_{fl} consistently increased estimated richness by 7 to 17% over simple species counts (Table 4). While Chumbe had the highest initial richness at 219 species it also had the lowest estimated increase, largely due to having a narrower range of detectability estimates than the other sites; Misali had the greatest estimated increase at 34 undetected species. Bayesian 95% credible intervals did not overlap at all sites, indicating process-based differences in species richness among sites. Mean detection probabilities were less than 0.35 at all locations, showing that moderate levels of replication (~7) would be required at any given site to have a 95% chance of seeing a fish

Table 4. Estimates of community parameters from top-ranked models of 24 replicate point counts for Tanzanian Underwater Visual Census surveys in 2003. Given are estimate mean ($\hat{\theta}$), estimate standard deviation ($\hat{SD}(\hat{\theta})$), and 95% Bayesian estimate prediction limits (PL)

Quantity (θ)	Naïve estimate	Estimator	$\hat{\theta}$	$\hat{SD}(\hat{\theta})$	95% PL
Species richness					
Bawe	192	N_B	221.98	25.35	(196.17, 275.78)
Chumbe	219	N_C	236.06	8.67	(225.63, 254.33)
Misali	206	N_{Mf}	240.22	31.91	(214.98, 279.98)
Mnemba	183	N_M	201.94	7.23	(190.33, 216.23)
Mean detection probability					
Bawe	1[a]	p_B	0.28	0.13	(0.08, 0.45)
Chumbe	1[a]	p_C	0.27	0.11	(0.07, 0.41)
Misali	1[a]	p_{Mf}	0.32	0.16	(0.05, 0.52)
Mnemba	1[a]	p_M	0.34	0.16	(0.06, 0.54)
Length parameter					
Bawe	0[a]	$\beta_{l,B}$	−0.007	0.001	(−0.011, −0.0036)
Chumbe	0[a]	$\beta_{l,C}$	−0.014	0.002	(−0.018, −0.010)
Misali	0[a]	$\beta_{l,Mf}$	−0.021	0.002	(−0.026, −0.017)
Mnemba	0[a]	$\beta_{l,M}$	−0.023	0.003	(−0.029, −0.017)
Schooling effect					
Bawe	0[a]	$\beta_{s,B}$	0.22	0.09	(0.03, 0.39)
Chumbe	0[a]	$\beta_{s,C}$	0.18	0.09	(0.00, 0.35)
Misali	0[a]	$\beta_{s,Mf}$	0.23	0.09	(0.06, 0.40)

[a]By assumption

of average detectability at each location. Bawe and Chumbe had more similar average detectability estimates than Mnemba and Misali, despite differences in marine protection. However, live coral cover was ~2× higher in Bawe and Chumbe than Mnemba and Misali, making it a possible driver of higher abundance (and therefore higher detectability) in these western sites.

Length parameter estimates were negative for all sites, with lower probabilities of detection for larger bodied species. These effects were substantive, with detectability reductions of 1 to 3% per 10 cm of TL_{max} (Table 4). Posterior length effect distributions were well estimated and characteristically normal, with z-scores near 0 throughout the MCMC chains. Once again estimates were similar within region, with estimates for Bawe and Chumbe being more similar than those for Misali and Mnemba. Schooling species had higher average detectability (of between 5 and 10%) and this was consistent among sites (Table 5).

Detection probabilities varied substantially among fish family groups and among sites, with posterior detectability distributions having consistent form among sites but showing little overlap in many instances (Table 6, Fig. 2). The exception to this pattern was apogonids in Misali, where only 2 species were detected, resulting in a broad, uninformative posterior distribution. Family group estimates were consistently lower in Bawe and Chumbe than in Misali and Mnemba, further suggesting that similarity in habitat were more important than the presence of fishing in influencing probabilities of detection.

Under model M_0, average probability of detection declined with increasing replication at all sites using both a complete and truncated species list (Fig. 3). Our mixed-effects models strongly supported a constant rate of decline among all sites, with higher rates of decline using the truncated species list (Table 7). Given the estimated per replicate asymptotic rates of decline in average detectability, these results indicated that the number of replicates needed to reach 50 and 95% of the asymptotic site average detectability were 5 and 19 point counts respectively for the full species list, and 1 and 15 point counts for the truncated species list. As expected with greater sample size, the standard deviation of $\hat{p}$ also decreased asymptotically—although these values were <0.031 for all replicate counts.

DISCUSSION

Reef-fish studies have infrequently addressed the issue of detectability in UVC data, often because protocols have been long-established and detection-specific methods such as distance sampling require considerable retraining to implement. Even where distance sampling has been adopted (e.g. Kulbicki & Sarramégna 1999) it is difficult to determine how novel methods compare to those that are widely used. From our CMR modelling approach we have demonstrated that the use of covariate information can accommodate detection biases inherent among fish groups from conventional UVC data.

Table 5. Range of estimated detection probabilities for fish of small (10 cm) and large (60 cm) maximum attainable total lengths among sites given schooling or non-schooling behaviour under Model M_{fls}. Results are relative to the average detection probability at each site

	Schooling		Non-schooling	
	Small	Large	Small	Large
Bawe	0.32	0.14	0.27	0.11
Chumbe	0.31	0.24	0.26	0.20
Misali	0.27	0.16	0.24	0.14
Mnemba	0.32	0.13	0.29	0.11

Table 6. Estimated mean detection probabilities for observed reef-fish families among sites given the top-ranked model at each location. Values include Bayesian 95% prediction limits in parentheses. –: families not observed

Family	Bawe	Chumbe	Misali	Mnemba
Acanthuridae	0.17 (0.11, 0.24)	0.43 (0.35, 0.51)	0.55 (0.48, 0.61)	0.58 (0.51, 0.66)
Apogonidae	0.20 (0.13, 0.21)	0.12 (0.08, 0.16)	0.47 (0.32, 0.62)	0.10 (0.04, 0.16)
Atherinidae	0.04 (0.01, 0.11)	–	0.21 (0.04, 0.40)	–
Aulostomidae	–	0.48 (0.26, 0.72)	0.91 (0.83, 0.98)	0.87 (0.76, 0.96)
Balistidae	0.17 (0.04, 0.34)	0.34 (0.20, 0.49)	0.42 (0.31, 0.52)	0.60 (0.49, 0.71)
Blennidae	0.24 (0.17, 0.30)	0.26 (0.20, 0.33)	0.21 (0.04, 0.40)	0.24 (0.17, 0.31)
Belonidae	–	–	0.20 (0.03, 0.36)	–
Caesionidae	0.12 (0.05, 0.19)	–	0.31 (0.22, 0.41)	0.08 (0.03, 0.14)
Carangidae	0.12 (0.01, 0.29)	0.24 (0.01, 0.55)	0.66 (0.36, 0.89)	–
Chaetodontidae	0.34 (0.28, 0.41)	0.26 (0.21, 0.32)	0.54 (0.49, 0.60)	0.53 (0.45, 0.60)
Cirrhitidae	–	0.12 (0.03, 0.22)	0.35 (0.20, 0.51)	0.42 (0.30, 0.54)
Clupeidae	0.20 (0.05, 0.35)	0.07 (0.01, 0.17)	–	–
Diodontidae	0.06 (0.01, 0.17)	–	0.09 (0.01, 0.27)	–
Dasyatidae	–	0.33 (0.13, 0.52)	–	0.08 (0.01, 0.21)
Ephippidae	–	0.14 (0.01, 0.31)	0.09 (0.01, 0.27)	–
Fistulariidae	–	–	0.70 (0.34, 0.95)	0.57 (0.18, 0.92)
Gobiidae	0.10 (0.05, 0.15)	0.12 (0.07, 0.16)	0.07 (0.02, 0.12)	0.10 (0.02, 0.19)
Haemulidae	0.59 (0.46, 0.72)	0.36 (0.22, 0.50)	0.78 (0.66, 0.89)	0.78 (0.67, 0.89)
Holocentridae	0.08 (0.03, 0.14)	0.26 (0.15, 0.37)	0.73 (0.65, 0.81)	0.63 (0.52, 0.74)
Labridae	0.46 (0.42, 0.51)	0.39 (0.34, 0.43)	0.45 (0.41, 0.49)	0.54 (0.49, 0.60)
Lethrinidae	0.27 (0.15, 0.38)	0.49 (0.38, 0.59)	0.39 (0.28, 0.52)	0.36 (0.22, 0.51)
Lutjanidae	0.18 (0.07, 0.31)	0.53 (0.38, 0.69)	0.57 (0.44, 0.70)	0.55 (0.42, 0.68)
Kyphosidae	–	–	0.46 (0.23, 0.70)	0.50 (0.29, 0.73)
Monacanthidae	0.17 (0.09, 0.27)	0.27 (0.16, 0.38)	0.26 (0.13, 0.40)	0.22 (0.11, 0.32)
Mullidae	0.28 (0.16, 0.39)	0.36 (0.26, 0.45)	0.55 (0.46, 0.64)	0.58 (0.48, 0.67)
Muraenidae	–	0.07 (0.01, 0.18)	–	0.23 (0.01, 0.47)
Nemipteridae	0.48 (0.34, 0.63)	0.51 (0.37, 0.66)	0.86 (0.76, 0.95)	0.84 (0.75, 0.92)
Ophichthidae	–	–	–	0.20 (0.01, 0.52)
Ostraciidae	0.11 (0.03, 0.22)	0.23 (0.05, 0.43)	0.13 (0.02, 0.25)	0.08 (0.01, 0.20)
Pempheridae	0.09 (0.01, 0.21)	–	0.48 (0.28, 0.67)	0.14 (0.03, 0.27)
Pinguipedidae	0.51 (0.31, 0.71)	0.60 (0.41, 0.78)	0.39 (0.17, 0.59)	0.16 (0.02, 0.33)
Platycephalidae	–	–	0.10 (0.01, 0.22)	–
Plotosidae	–	0.11 (0.01, 0.25)	0.07 (0.01, 0.20)	–
Pomacanthidae	0.21 (0.15, 0.28)	0.57 (0.48, 0.67)	0.55 (0.47, 0.63)	0.54 (0.41, 0.66)
Pomacentridae	0.38 (0.34, 0.42)	0.39 (0.35, 0.43)	0.56 (0.51, 0.60)	0.51 (0.46, 0.56)
Priacanthidae	–	–	0.38 (0.11, 0.60)	0.17 (0.01, 0.38)
Pseduochromidae	0.03 (0.01, 0.11)	–	0.04 (0.01, 0.12)	–
Ptereleotridae	–	0.07 (0.01, 0.18)	0.34 (0.20, 0.48)	–
Scaridae	0.37 (0.30, 0.45)	0.53 (0.45, 0.60)	0.59 (0.51, 0.67)	0.69 (0.60, 0.77)
Scombridae	0.06 (0.01, 0.12)	–	–	–
Scorpaenidae	–	0.09 (0.03, 0.16)	0.07 (0.01, 0.15)	0.12 (0.03, 0.23)
Serranidae	0.27 (0.18, 0.35)	0.40 (0.26, 0.57)	0.43 (0.30, 0.57)	0.45 (0.34, 0.56)
Siganidae	0.39 (0.21, 0.60)	0.09 (0.01, 0.18)	0.35 (0.20, 0.53)	0.33 (0.18, 0.46)
Syngnathidae	0.05 (0.01, 0.16)	0.23 (0.07, 0.40)	0.27 (0.13, 0.40)	–
Synodontidae	0.44 (0.29, 0.59)	0.47 (0.32, 0.62)	0.45 (0.28, 0.60)	0.20 (0.04, 0.43)
Tetraodontidae	0.23 (0.14, 0.32)	0.39 (0.29, 0.48)	0.43 (0.34, 0.52)	0.52 (0.41, 0.62)
Zanclidae	0.30 (0.14, 0.48)	0.13 (0.07, 0.19)	0.87 (0.79, 0.96)	0.78 (0.63, 0.91)

Reef-fish detectability

We observed a wide range of individual detectabilities ($\hat{p}$ = {0.05 to 0.54}), highlighting the erroneous assumption conventionally made in UVC surveys that p = 1. The detectability differences we observed among sampling locations suggest that comparing raw counts among sites may be substantially misleading. The failure of this assumption is particularly acute for monitoring of biodiversity, where sampling bias can mask important ecological trends (Yoccoz et al. 2001). The strong relationship between detectability and abundance (Dorazio & Royle 2005) means that species that have been depressed to low levels are likely to go undetected, despite their continued presence at a given reef. While many researchers are aware of this issue and, as a result, conduct surveys on a subset of the fish community, the conservation implications for a species being present but undetected versus being locally extinct are important; areas thought to be

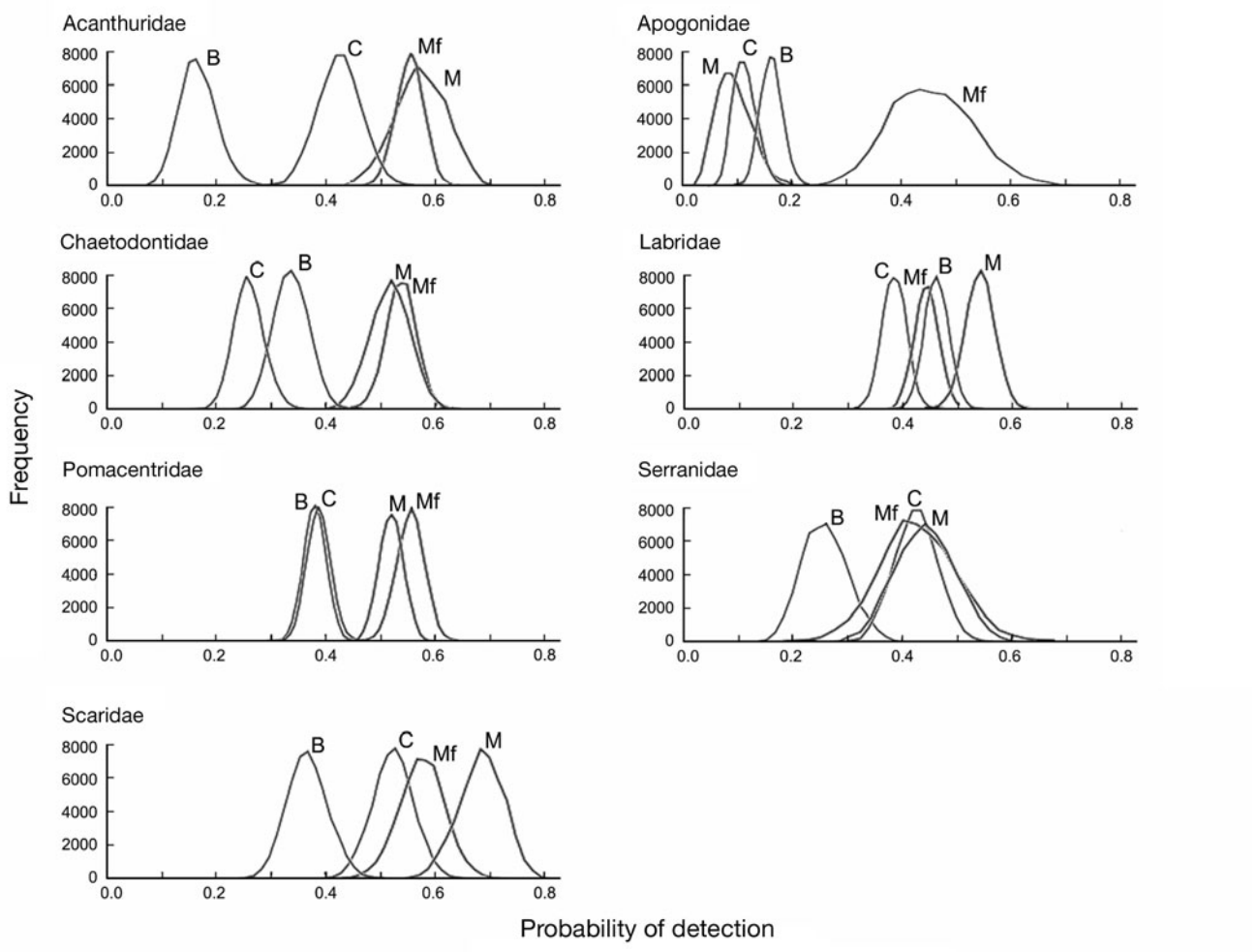

Fig. 2. Posterior detectability estimates by site for common coral reef-fish families in Tanzania. Site labels are Bawe (B), Chumbe (C), Misali (Mf), and Mnemba (M). Except for the Apogonidae in Misali, estimates are based on observations of at least 5 species

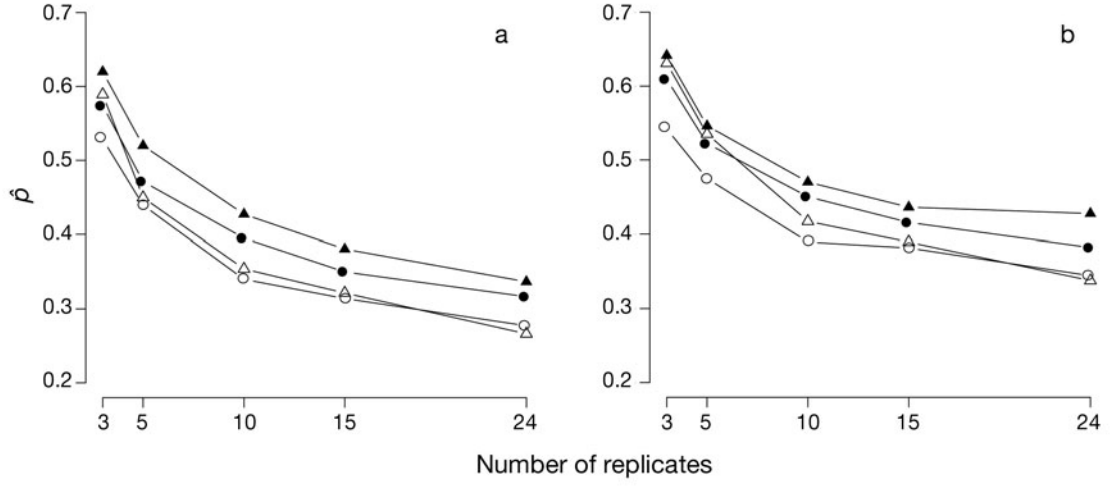

Fig. 3. Posterior mean detectability estimates ($\hat{p}$) by site (○: Bawe; △: Chumbe; ●: Misali; ▲: Mnemba) per number of replicate point counts for (a) entire fish community and (b) truncated species list. Rate of decline is constant among sites within each species list (a, r = –1.57; b, r = –1.61)

Table 7. Summary statistics for asymptotic mixed-effects models of declines in average probability of reef-fish detection across replicate Underwater Visual Census point counts using full and truncated species lists for Tanzanian reef fishes. Model M1 assumes random-effects for all parameters at each site; Model M2 assumes random-effects for only the asymptote term ($\hat{p}_{lim}$); Model M3 assumes random-effects for $\hat{p}_{lim}$ and the initial mean probability of detection ($\hat{p}_0$). Statistics include number of parameters (K), AIC value, likelihood ratio (*L*-ratio), and best-fitting model parameter estimates with 95% frequentist confidence intervals. *L*-ratio tests are for M1 vs. M2, and M2 vs. M3

Model comparison			
Model[a]	K	AIC	*L*-ratio
Full species list			
M1	10	−77.9	
M2	5	−83.4	4.50
M3	3	−83.5	3.95
Truncated species list			
M1	10	−83.55	
M2	5	−81.47	12.08
M3	3	−87.34	9.87

Model summaries			
Estimator	θ	*SE*(θ)	95% CL
Full species list – M2			
$\hat{p}_0$	0.80	0.05	(0.71–0.89)
$\hat{p}_{lim}$[b]	0.31	0.02	(0.27–0.35)
$\hat{r}$	1.57	0.13	(1.30–1.84)
Truncated species list – M3			
$\hat{p}_0$[b]	0.79	0.041	(0.71–0.87)
$\hat{p}_{lim}$[b]	0.38	0.017	(0.34–0.41)
$\hat{r}$	1.61	0.10	(1.42–1.81)

[a] $p_k = p_{lim} + (p_0 - p_{lim})e^{-rk}$
[b] Random effect

irreparably disturbed run the risk of being abandoned while still having some chance for recovery.

The modeling framework we implemented estimated species richness independently for each location, based on the observation history of each species across all point counts. More complex hierarchical models have the potential to estimate detection biases across sites and among locations, where location-specific covariates can be included as part of the probability model. In addition, occupancy models are available (e.g. Dorazio et al. 2006) that can disentangle species presence from detectability and these should prove important in future applications to reef-fish surveys. However occupancy models require a greater number of sampling locations than were available from this study and our results focused on the high level of repeat sampling to understand trends in detection bias across a wide range of sampling effort.

The negative effect of TL_{max} on detectability was somewhat surprising to us (although possibly not for others). However, this effect most likely represents substantial differences in reef-fish behaviour depending on body size and the small survey areas used in conventional UVC estimates. Small reef fish tend to be both more cryptic and more territorial than large fishes (Warner & Hoffman 1980), making them potentially more or less detectable depending on the relative importance of those behaviours within a given assemblage. As larger fishes tend to move in or out of the sampling areas at irregular intervals their overall detectability during any given survey would be likely to be lower than for smaller, more territorial fishes. Our results indicate that the level of territoriality present among small fishes far outweighed any decreases in detectability due to crypsis among smaller fishes and the consistency of these results across all sampling locations was substantial. This suggests that UVC methods are most suitable for surveying many small species of reef fish. Unsurprisingly, schooling fish were more detectable, confirming that higher instantaneous abundance is positively related to detectability.

Our results were remarkably consistent across all sites despite their differences in habitat and reef area. Length had a negative effect on detectability across all sites; schooling behaviour had a positive effect; richness estimates consistently increased species counts; and a constant rate of decline was observed with increasing replication. However site-level differences in detectability were observed among locations, which could have been due to differences in local abundance, possibly related to the availability of live hard coral cover at each location. However the consistencies observed among locations suggest that some factors, such as fish length, universally affect reef-fish detectability; further studies may confirm this in other reef systems.

Sampling results

The asymptotic declines we observed in average detectability with increased replication demonstrated that at low replicate numbers (<5), only the most detectable species tend to be observed by point counts. With increasing levels of replication, greater numbers of low-detection species contribute to the community average, at a decreasing rate, up to about 20 point counts, when most of the low-detection species have been observed. The declines observed in average detectability were not surprising, yet the consistency in the rate of decline among sites demonstrated that point counts are a consistent method of UVC among sampling locations, a finding that has not to our knowledge been reported previously. Point counts have been shown to be consistent with UVC transects under controlled conditions (Watson & Quinn 1997) and to have

higher levels of precision than other UVC methods (Samoilys & Carlos 2000), but our results suggest further that point counts are unbiased among sites, making them a robust methodology for surveying patch reefs at multiple locations.

Determining an appropriate sample size has been an inconsistent aspect of UVC surveys, with replication levels often determined by logistical, as opposed to inferential, considerations (Samoilys & Carlos 2000). Where the statistical properties of UVC methods have been explored, precision and statistical power have been the metrics of greatest interest, as they address the question of how many counts a study will have to make to achieve a consistent and accurate estimate. Point count precision has been shown to stabilize at 10 to 15 replicate counts (Samoilys & Carlos 2000), suggesting that, at those levels, a representative sample of the fish community has been acquired. However, our results emphasize that the number of point counts should be, costing aside, determined by the research question of interest.

If a study aims to sample the dominant, most detectable species at a given location (i.e. using a truncated species list) 70% of these groups are likely to have been observed after 5 or more point counts, when the average probability of detection is beyond 70% of the asymptotic detection probability for the entire target list (Fig. 3b). Similarly, at 12 point counts 90% of the range of species detectabilities have been observed, suggesting an approximate range of between 5 and 12 point counts are appropriate survey levels for highly detectable species. Similar levels of replication have been recommended elsewhere (Samoilys & Carlos 2000). However if the goal is to census the species available at a given location (i.e. observe total biodiversity), many more point counts are required (Fig. 3a). At 24 point counts our surveys sampled 98% of the detectable species present in the community, suggesting that 24 or more point counts would be required to observe the entire range of detectable species. In biodiversity surveys this may be essential for achieving accurate estimates, even when correcting for detection bias.

Although low-detection species represent a substantial proportion of total reef-fish biomass, they are frequently excluded from surveys due to being 'too hard to see.' Low replication (n = 6) UVC data may consistently miss gobies in UVC transects at sites where they are, in fact, the most abundant fish family captured by subsequent rotenone sampling (Ackerman & Bellwood 2000). Monacanthid species frequently show strong, negative biases in UVC transects, primarily due to low detectability (Edgar et al. 2004). Yet cryptic species are important components of reef food webs, contributing substantially to detrital nutrient cycling and representing a large proportion of local biodiversity (Depczynski & Bellwood 2003, Wilson 2004). Ignoring the presence of these species may lead to problems interpreting the competitive interactions, resource allocations, and small-scale processes that drive a large proportion of reef productivity (Ackerman & Bellwood 2000).

In cases where the objective is to survey a representative sample of the range of fishes at a site, including cryptic speces (e.g. blenniids, apogonids etc.), higher replication is essential. Too few replicates will not pick up most cryptic species, making low-replicate surveys (<10 to 15) dubious sources for the presence of low-detection ($p < 0.20$) fishes. Sampling bias may be particularly acute on coral reefs where serious declines in species richness have recently been reported (Graham et al. 2006) and are expected to increase in the future (Bellwood et al. 2005, Wilson et al. 2006). If declines reported to be true losses of species are, in fact, non-detections due to low abundance, study conclusions may be considerably biased. The distinction between extinct and functionally extinct is difficult to define. Accounting for detectability in estimating species losses through time is an important issue that, as a major component of occupancy studies (MacKenzie et al. 2006), CMR models can address directly.

Biases present in UVC data have been documented previously, yet the effect of detectability on biodiversity indices has been largely unaddressed. If we are to effectively address disturbance-induced losses of reef-fish species it is essential that the estimators we use are not generating false negatives that represent sampling errors rather than ecological processes. Areas with low abundance may frequently be diverse but contain many undetected species. When unaccounted for, detection biases may strengthen arguments for marine protection when in reality, differences in diversity observed between fished and unfished locations primarily reflect differences in abundance (Edgar & Barrett 1999). Whether areas of low abundance include functionally extinct or actually extinct species may be important in particular management contexts, whereby recovery from low abundance levels in some areas may not be feasible due to limited conservation resources. Regardless of the management objective however, it is important that decision makers are provided the most accurate information available. Our modelling approach has demonstrated that covariate information can inform the estimation of detection biases inherent among fish groups from standard UVC data and, although non-identifiable, estimate a portion of the unobserved species. Biodiversity inventories with relatively low replication can use such information to improve their estimates of species richness at a site and monitor the probability occupancy for species of conservation concern. The CMR modelling techniques we

used are generally applicable to reef-fish surveys, requiring no additional sampling effort to complete, and can be easily implemented in freely available software. We therefore recommend that CMR models be frequently used to explore detectability patterns in studies using UVC data, even when abundance estimates have been made, in an effort to improve reef-fish biodiversity estimates.

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