Range of View Determines Characterisation of Pelagic Fish and Shark Assemblages

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Contents

Abstract

Understanding patterns in the distribution, diversity, and abundance of marine organisms is key to the conservation and management of ocean biodiversity. Increasingly, ecological studies worldwide employ baited remote underwater video systems (BRUVS) to survey pelagic and demersal fish and shark assemblages. However, numerous factors such as water turbidity, light availability and obstructions can restrict the range of view (RoV) available to the video camera, potentially introducing bias in the characterisation of marine assemblages. Given the influence of sampling unit size on the estimation of ecological attributes such as diversity and abundance, it is crucial to understand how variation in RoV influences the characterisation of fish and shark assemblages using BRUVS. Subsampling locations from a global dataset of mid-water stereo-BRUVS footage from three ocean basins, we calculated species richness, total abundance, and total biomass of pelagic fish and shark assemblages across a range of reconstructed RoVs between 2 and 8 m, and compared these estimates to those of a standard RoV of 10 m. A statistically significant (p<0.05) effect of RoV was observed for species richness, total abundance, and biomass. Approximately 17% of species richness, 23% of total abundance, and 33% of total biomass remained undetected at 6 m relative to 10 m, with this bias exacerbated as RoV was further reduced. This study highlights the importance of knowing and standardising the sampling unit size for midwater BRUVS in the sampling of pelagic fish and shark assemblages. It also argues for why it is so critical that stereo- rather than mono- camera BRUVS are used as the latter do not allow determination of the RoV.

Key words: Sampling unit size • Stereo-BRUVS • Mono-BRUVS • Pelagic fish and shark assemblage • Turbidity • Detection •

1. Introduction

Fundamental to the sustainable use of the world's oceans is an understanding of the status and trends in wildlife populations. Sampling of fish and shark assemblages provides insight on characteristics of marine ecosystems including estimates of species richness, total abundance, and total biomass, important indicators of environmental and biological condition (García & Martinez 2012, Piet et al. 2017). Reconstructed fisheries data have revealed a trend of declining fish stocks since 1996 (Pauly & Zeller 2016), jeopardizing food security (Pauly et al. 2005, Rice & Garcia 2011). Such a decline is largely the result of overexploitation (Pauly et al. 1998, Froese et al. 2016), exacerbated by climate change (Cheung et al. 2009, Cheung et al. 2012, Vergés et al. 2014). Long term monitoring of environmental systems requires a robust and reliable sampling framework to assess the relationship between human activities and ocean health. Fisheries data are problematic in that they involve lethal sampling and only provide information on targeted species. Moreover, such time series data cease upon the enforcement of no-take marine protected areas. As such, researchers have developed non-extractive methods to sample fish populations. The improvement of small, inexpensive action cameras has led to the employment of video-based methods for sampling of fish and shark assemblages (Letessier et al. 2013, Bouchet & Meeuwig 2015, Letessier et al. 2015, Struthers et al. 2015).

Baited remote underwater video systems (BRUVS) are increasingly used to assess fish and shark assemblages in the effort to gather fisheries independent data (Cappo et al. 2003, Whitmarsh et al. 2017). Species richness estimates can be made by presence absence counts of species observed (Cappo et al. 2004). Relative abundance of each observed species is estimated as the maximum number of individuals of a species within the frame at any one time (MaxN), avoiding repeated counts (Willis et al. 2000). Fork-length can be measured via the epipolar geometry available with a two camera, stereo-BRUVS setup (Cappo et al. 2006). This fork-length can be converted into an estimate of the individual's weight via the species' length-weight relationship (Froese 2006) and summed across abundance to derive total biomass. The relatively inexpensive and lightweight design of BRUVS allows for multiple replicates across large areas of ocean collecting comprehensive samples from areas of interest including marine parks (Malcolm et al. 2007, Barley et al. 2017, Harasti et al. 2018. Hill et al. 2018), biodiversity hotspots such as the waters around deep-water canyons, and seamounts, as well as artificial structures (Bond et al. 2018, Bouchet et al. 2018a, Caselle et al. 2018). BRUVS have the advantage of being non-extractive and can therefore be used for the sampling and monitoring of endangered animals (Brooks et al. 2011, Goetze & Fullwood 2013). They are safe as they

obviate the need for personnel in the water, simultaneously addressing the evasive behavioural bias that fish display with human presence in diver transects (Colton & Swearer 2010, Langlois et al. 2010, Watson et al. 2010). While bait is an attractant, research shows that cameras attract a wide range of trophic levels (Harvey et al. 2007) and that baited systems generate more precise estimates of abundance than unbaited systems (Bernard & Götz 2012), despite variability in bait plumes (Heagney et al. 2007). Advancements to the BRUVS include a midwater rig that is capable of sampling the open ocean environment, necessary for monitoring of pelagic fish and shark populations (Bouchet et al. 2017, Letessier et al. 2017). Footage produced via BRUVS can be archived for future studies and data collected can be collated for larger spatial and temporal scale analysis (Oh et al. 2017). An important gap in the standardisation of these systems is rig design - a single camera in mono-BRUVS vs two in stereo-BRUVS. The former have been predominant in past studies owing to the common perceptions that they incur lower short-term costs, require less physical space for storage in the field, and have reduced processing times during video analysis (Whitmarsh et al. 2017).

BRUVS imagery can vary in its range of view (RoV) which in turn determines the sampling unit size. Sampling unit size influences observer perception of ecological patterns (Levin 1992). For instance, with increasing sampling unit size, patterns of species richness, abundance and biomass reflect mechanistic overlaps (Williams 1943). Depending on the scale of this effect, variation in sampling unit size can lead to erroneous conclusions about ecological structure and function (Stout & Vandermeer 1975, Kwiatkowska & Symonides 1986, Melo et al. 2003) and make it difficult to compare outcomes of studies that use different sampling unit sizes. For BRUVS, the sampling unit size is a cone that encloses a volume of water dictated by rig configuration (camera field of view settings and distance between cameras in a stereo-rig) and RoV. RoV is a function of changing light availability (e.g. due to water turbidity or camera depth), physical obstructions by reefs or pylon structures, and fish saturation. Stereo-BRUVS have the capability of measuring a 3-dimensional space in front of the camera via epipolar geometry; this includes an accurate measurement of maximum distance an animal can be detected in front of the camera (Harvey et al. 2002, Harvey et al. 2010). Two-thirds of studies fail to mention the visibility of their BRUVS footage (Harvey et al. 2013). A small number of studies mention negligible effects of RoV on assemblage metrics however these studies used mono-BRUVS where RoV estimates are based upon unreliable visual guesses (Cappo et al. 2011, Gilby et al. 2017). Other studies suggest RoV might influence assemblage assessments only in very high turbidity waters where maximum RoV can be less than a metre (Unsworth et

al. 2014). The only evidence of increasing the sampling unit size yielding a decrease in assemblage metric estimates is from underwater visual census methods where increasing the sample radius caused the observer to miss cryptic species, where only close inspection would have recorded them (Samoilys & Carlos 2000). The true relationship behind sampling unit size of BRUVS and the resulting characterisation of the assemblage is thus indeterminate and warrants exploration, particularly given the rise in use of mono-BRUVS.

Variability in RoV will influence the number fish likely to be detected by pelagic BRUVS, changing estimates of species richness, total abundance, and total biomass. To determine the degree to which RoV heterogeneity influences, as well as the range at which it no longer significantly affects these assemblage characteristics, we analysed stereo-BRUVS footage under a range of simulated RoV conditions. I test the hypotheses that increasing ROV leads to higher estimates of species richness, total abundance and total biomass. The rate of increase is estimated and breakpoints at which the rate of increase in these estimates slows are determined. Substantial variation between these ranges would support the requirement of a known sampling unit size and the adoption of a stereo-BRUVS standard.

2. Materials and Methods

2.1. Stereo-BRUVS Sampling

To test the hypothesis that RoV influences fish and shark assemblage metrics, videos were subsampled from four locations out of a global database of midwater stereo-BRUVS deployments undertaken between 2015 and 2018 by the Marine Futures Lab, University of Western Australia (Fig. 1). The advantage of selection from such an archive is that consistent methods were applied to the collection of all footage (Bouchet et al. 2018b). All sampling was done in a long-line configuration with each of five midwater stereo-BRUVS rigs separated by 200 metres (Fig. 2). The long-line soaks for a minimum of 120 minutes (with video analysis later truncated at 120 minutes) and each rig is baited with 1.5 kg of mashed pilchards (*Sardinops* spp.*)

The locations chosen for this analysis were Ascension Island in the central Atlantic, the British Indian Ocean Territory (BIOT) and Cocos (Keeling) Islands, both in the Indian Ocean basin, and Revillagigedo Archipelago from the Eastern Pacific ocean, based on their generally high water clarity. At each of the four locations, a subsample of 20 deployments was selected for the RoV analysis. Deployments were chosen on the basis that there was a RoV of at least 10 metres to allow for a comparison of standardised sampling units up to and including 10 metres from the camera. Additionally, as BRUVS were deployed in a long-line configuration of 5 rigs separated each by 200 m, samples were taken from different longlines to avoid dependence between samples.
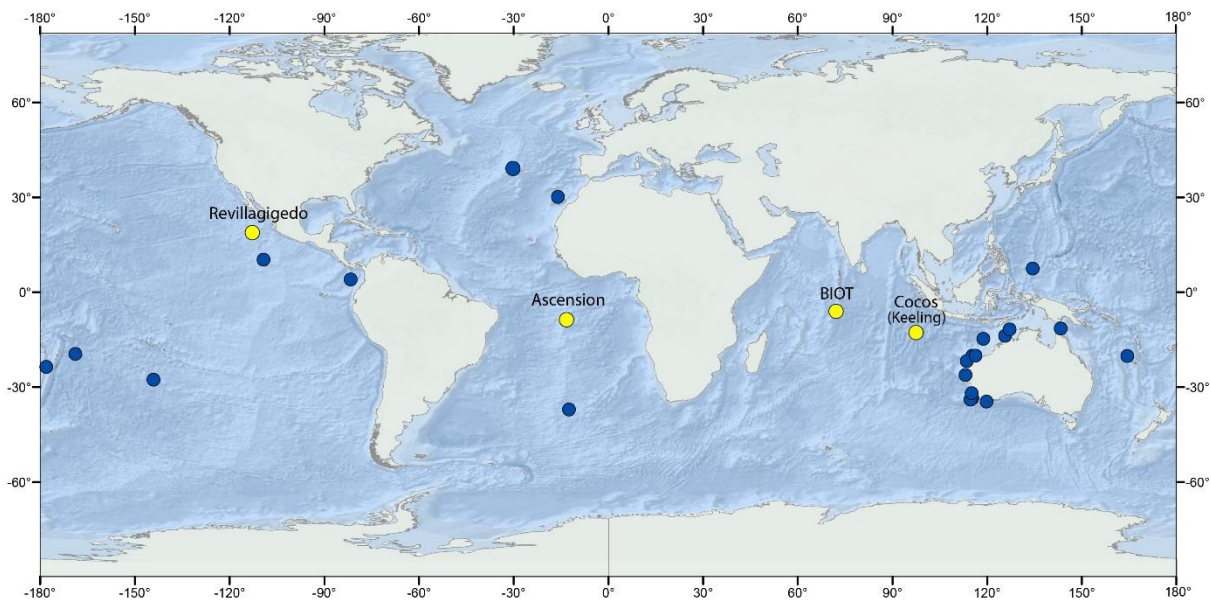

Fig. 1. Locations of midwater stereo-BRUVS sampling conducted by the Marine Futures Lab 2015-2018. Focus locations highlighted in yellow are Ascension Island, British Indian Ocean Territories (BIOT), Cocos (Keeling) Islands, and Revillagigedo Archipelago.
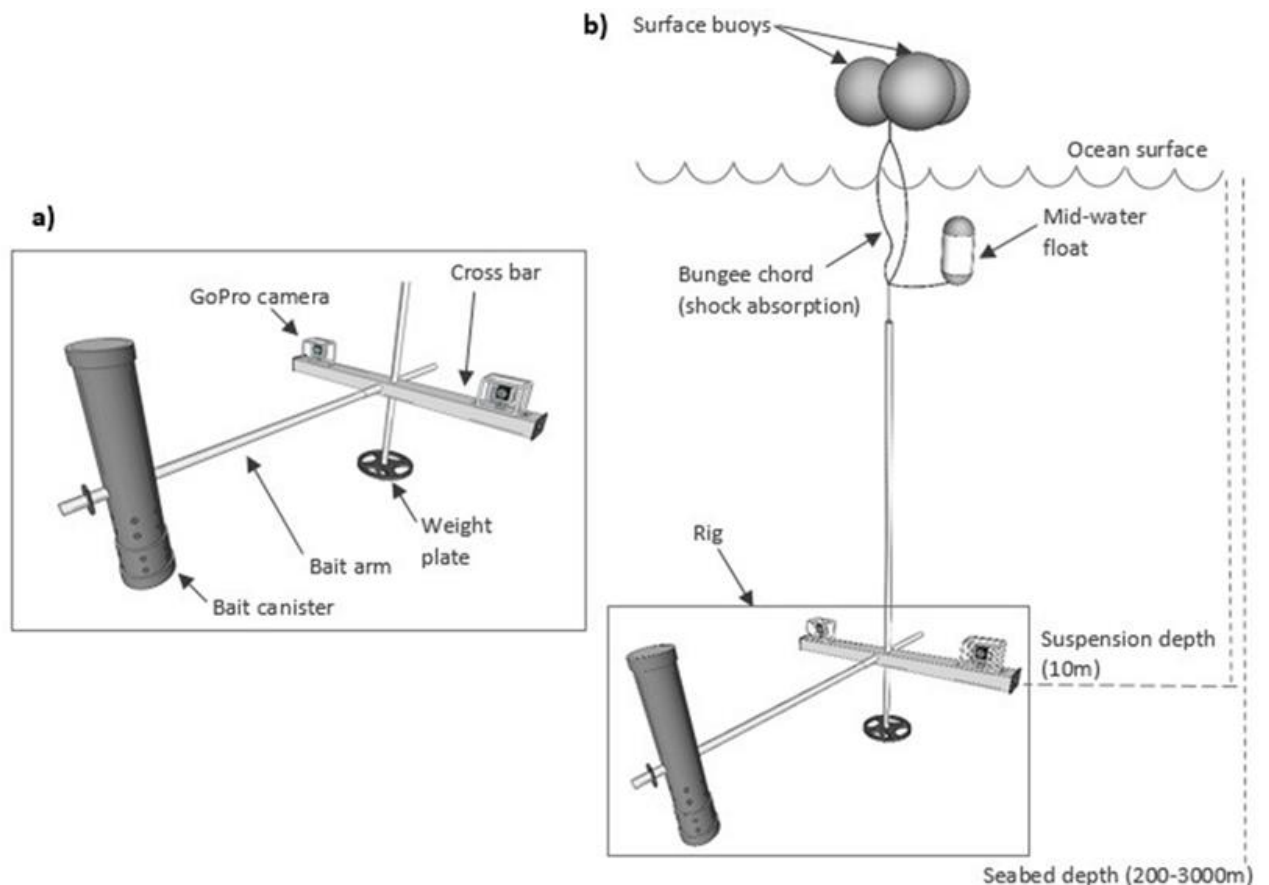
Fig. 2. Drifting midwater stereo-BRUVS used to sample pelagic fish and shark assemblages (a) annotated schematic of midwater stereo-BRUVS unit and (b) instruments as arranged underwater (Bouchet & Meeuwing 2015).

2.2. Image analysis

Fish and shark assemblages are typically characterised by the species richness, total abundance, and total biomass. I estimated values for each of these metrics based on records generated from the image analysis software Event Measure (www.seagis.com.au). Event Measure permits the simultaneous analysis of footage from both stereo cameras and the corresponding 3-dimensional calibration providing length and range measurements for animals observed. Measurements were taken every 30 seconds throughout the 120-minute deployment, this process resulted in a representative selection of 240 frames subsampled for each metric. Only animals that appeared within the volume of water sampled by the stereo configuration (i.e. the overlapping fields of view of both cameras) were sampled to ensure accurate range measurements. Species observed over the subsampled frames were aggregated for a species richness for each deployment. Relative abundance was estimated as the maximum number of individuals in a frame to avoid repeated counts, and total abundance was measured by the sum of each species' maximum value of MaxN over the 240 frames sampled. Fork-length

measurements were recorded and converted to individual weights based on the length-weight equation ($W = aL^b$), where W is weight, L is length and the 'a' and 'b' are parameters available on Fishbase.org (Froese & Pauly 2009). Individual weights corresponding to the MaxN counts across all species were then summed to estimate total biomass.

To simulate a series of reduced RoV's, the range recorded with observations on individual animals were binned with respect to 2 m RoV intervals up to 10 metres. Each bin is accumulative of the bin closer, as animals observed within 2 m will still be visible at 4 m and so forth. This allowed the estimate of species richness, total abundance, and total biomass to be categorised for each RoV bin within a deployment. The RoV, a linear measurement, was converted into a sampling volume for each 2 m bin. Based on the vertical and horizontal extent of the cameras, given the GoPro's field of view and 21 mm focal point, 0.8 m separation and 4° convergence angle, the volumes were calculated by James Seager via the Event Measure software (www.seagis.com.au) (Table 1).

Table 1. Horizontal extent (Ext_h) and vertical extent (Ext_v) and the volume of water measured (Vol) at different ranges (RoV) from the stereo-BRUV setup given a 21 mm focal point, 0.8 m separation and 4° convergence angle of the two GoPro Hero 4's.

RoV (m)	Ext_h (m)	Ext_v (m)	Vol (m^3)
2.0	2.2	1.4	1.8
4.0	5.1	2.9	18.4
6.0	7.3	4.3	63.9
8.0	9.5	5.8	149.4
10.0	11.7	7.2	287.4

2.3. Effect of RoV on species richness, total abundance, and total biomass

The key hypothesis to be tested was whether the RoV influenced estimates of species richness, total abundance and total biomass within a pelagic fish and shark assemblage. Univariate analyses of variance were performed using PRIMER-E v7 statistical package with the PERMANOVA+ add on (Anderson et al. 2005, Clarke & Gorley 2015). To address the non-independence of RoV bins, as each is accumulative of lower RoV bins, repeated measures permutational analyses of variance (rmPERMANOVA) were performed (Quinn & Keough 2002, Figurski et al. 2016). The rmPERMANOVAs tested Euclidean distance similarity matrices, log transformed for total abundance and total biomass to reduce the influence of overly abundant and heavy species, that were calculated for each of the three continuous

dependent variables (species richness, $\log_{10}$ of total abundance, and $\log_{10}$ of total biomass), with RoV bin as the repeated measure (Haugo et al. 2011, Scyphers et al. 2011, Salo et al. 2015). A PERMANOVA was chosen because it allows for three-factor designs, considers an interaction term and does not assume a normal distribution of errors (Anderson 2014). A three-factor, partially nested design was used (Anderson 2001), where the factor 'RoV' was analysed as a fixed factor with five levels (2, 4, 6, 8, and 10 m), the factor 'location' was a fixed factor with four levels (Ascension Island, BIOT, Cocos (Keeling) Islands, and Revillagigedo Archipelago), and the factor 'deployment' was a random factor with 20 levels nested within 'location'. If no significant interaction ($P > 0.05$) occurred between RoV and location, the interaction was removed and the rmPERMANOVA rerun. If RoV resulted in a significant main effect permutational pairwise t-tests were performed on the RoV to determine the significance of each two-metre loss of view and determine if a breakpoint exists whereby an increase in RoV will no longer significantly influence the metric. I also tested for differences between locations where location was significant as a main effect. All pairwise t-tests were run with 9999 permutations.

If estimates of species richness, total abundance, or total biomass are direct functions of increasing sampling unit size, in this case volume of water sampled, it may be possible to predict fish and shark assemblage characteristics given a projected range. To build such predictive models and to visualise the results of the rmPERMANOVA tests, regressions were plotted for the mean species richness, $\log_{10}$ of mean total abundance and $\log_{10}$ of mean total biomass against the $\log_{10}$ of volume sampled within each RoV bin. In order to compare all locations on the same scale, regardless of productivity and relative abundance of the region, percentages of each metric per RoV bin were calculated relative to the 10 m bin. The mean percentage at each reduced RoV bin for species richness, total abundance, and total biomass across all locations were plotted to visualise the accumulation of each metric and the extent of underestimating at reduced RoV.

Some species are likely to interact with the bait canister to a greater degree than others given behavioural heterogeneity (Heagney et al. 2007, Hardinge et al. 2013). This compounds with the chance of detecting larger, rarer species that only a large sampling unit size offers (Kobe & Vriesendorp 2009). Both factors suggest the detectability of species will be a function of RoV. The mean minimum approach distance of each species was calculated to understand which species were likely to remain undetected at a reduced RoV due to behavioural or size attributes (Santana-Garcon et al. 2014). Representative species were plotted relative to RoV bin to visualise and compare the species composition of an assemblage at increasing ranges.

3. Results

The analyses generally showed a strong effect of RoV and location on species richness, total abundance and total biomass. There were no significant interactions (P>0.05) between factors within the rmPERMANOVA indicating that RoV and location acted independently on assemblage metrics (Appendix 1). The interaction term was thus removed for subsequent analyses. A significant effect (P<0.05) was observed for RoV in all three metrics and a significant effect of location was observed for species richness and $\log_{10}$ of total biomass but not for $\log_{10}$ of total abundance (Table 2).

Table 2. Results of rmPERMANOVA assessing the effects of location and RoV, with deployment as a nested factor within location, on a Euclidean distance similarity matrix calculated for species richness, $\log_{10}$ of total abundance, and $\log_{10}$ of total biomass with interaction removed (perm=9999). Significant effects (P<0.05) highlighted in bold.

	df	MS	Pseudo-F	P
Species richness				
Location	3	43.4	8.1	**0.001**
RoV	4	26.0	67.4	**0.001**
Deployment (location)	76	5.3	13.8	**0.001**
Residual	316	0.4		
$\log_{10}$ total abundance				
Location	3	1.0	1.6	0.201
RoV	4	2.3	82.7	**0.001**
Deployment (location)	76	0.6	23.2	**0.001**
Residual	316	2.8E-2		
$\log_{10}$ total biomass				
Location	3	11.3	4.3	**0.008**
RoV	4	15.1	72.0	**0.001**
Deployment (location)	76	2.6	12.6	**0.001**
Residual	316	0.2		

As there was a significant effect of RoV detected for all three metrics, permutational pairwise t-tests were conducted to determine between which bins there was a significant difference in estimates and whether a breakpoint could be distinguished. The species richness estimates differed between most RoV simulations, with significant increases in estimates still being observed out to 10 m. The same trend was observed for total abundance estimates, with no breakpoint observed thus a significantly different estimate was observed for each RoV bin. A breakpoint was observed in the estimation of biomass, whereby a biomass detected at a 10 m RoV does not significantly differ from that in the 6 m RoV.

Table 3. Results of permutational pairwise t-tests between RoV bins on a Euclidean distance similarity matrix calculated for each of species richness, $\log_{10}$ total abundance and $\log_{10}$ total biomass of a pelagic fish and shark assemblage across four locations (perm=9999). Significant effects ($P<0.05$) highlighted in bold.

		10 m	8 m	6 m	4 m
Species richness					
	8 m	**0.033**			
	6 m	**0.035**	**0.031**		
	4 m	**0.036**	0.053	0.128	
	2 m	**0.030**	**0.029**	**0.030**	**0.027**
$\log_{10}$ total abundance					
	8 m	**0.023**			
	6 m	**0.003**	**0.004**		
	4 m	**0.001**	**0.001**	**0.002**	
	2 m	**0.001**	**0.001**	**0.001**	**0.001**
$\log_{10}$ total biomass					
	8 m	0.122			
	6 m	0.065	0.122		
	4 m	**0.03**	**0.028**	**0.027**	
	2 m	**0.028**	**0.029**	**0.03**	**0.03**

The permutational pairwise t-tests between locations were only performed for species richness and total biomass as there was no significant effect of location observed for total abundance (Table 4). There was a distinction between BIOT and the other three locations in terms of their species richness estimates. For the $\log_{10}$ of total biomass, Ascension Island was significantly different to both BIOT and Cocos (Keeling) Islands but not Revillagigedo Archipelago.

Table 1. Results of permutational pairwise t-tests between locations on a Euclidean distance similarity matrix calculated for each of species richness and $\log_{10}$ total biomass (perm=9999). Significant effects ($P<0.05$) highlighted in bold.

		Ascension	BIOT	Cocos
Species richness				
	BIOT	0.213		
	Cocos	**0.030**	0.128	
	Revillagigedo	**0.029**	0.053	**0.031**
$\log_{10 b}$ total biomass				
	BIOT	**0.029**		
	Cocos	**0.002**	0.921	
	Revillagigedo	0.053	0.711	0.145

Regression models indicated a common pattern of increasing estimates of species richness, total abundance, and total biomass with increasing sampling unit size, (ie. the $\log_{10}$ of the volume of water calculated and presented in Table 1). The four locations can be divided into two clear groups of specie richness estimates as the regression lines for BIOT and, to a lesser degree, Ascension Island, have visually higher elevations than those of the two relatively depauperate locations, Cocos (Keeling) Islands and Revillagigedo Archipelago (Fig. 3a). A closer relationship across all three sites was the cause for a non-significant effect of location on the $\log_{10}$ of total abundance (Fig. 3b). The accumulation rate of abundance estimates with increasing RoV is consistent across all locations. The regression plot for $\log_{10}$ total biomass over $\log_{10}$ volume displays an even distribution of elevation across locations with the significance between Ascension Island having the greatest estimates for total biomass and both BIOT and Cocos (Keeling) Islands having lower estimates of total biomass (Fig. 3c).The proportional accumulation of each metric across increasing RoV bins suggested severe underestimates at lower RoV bins. Reducing the RoV to 6 m, on average, species richness, total abundance, and total biomass were underestimated by 17%, 23%, and 33% respectively (Fig. 3d-f). This underestimate worsens with further reduced RoV with 2 m only accounting for 48% of species, 39% of total abundance, and 26% of total biomass.
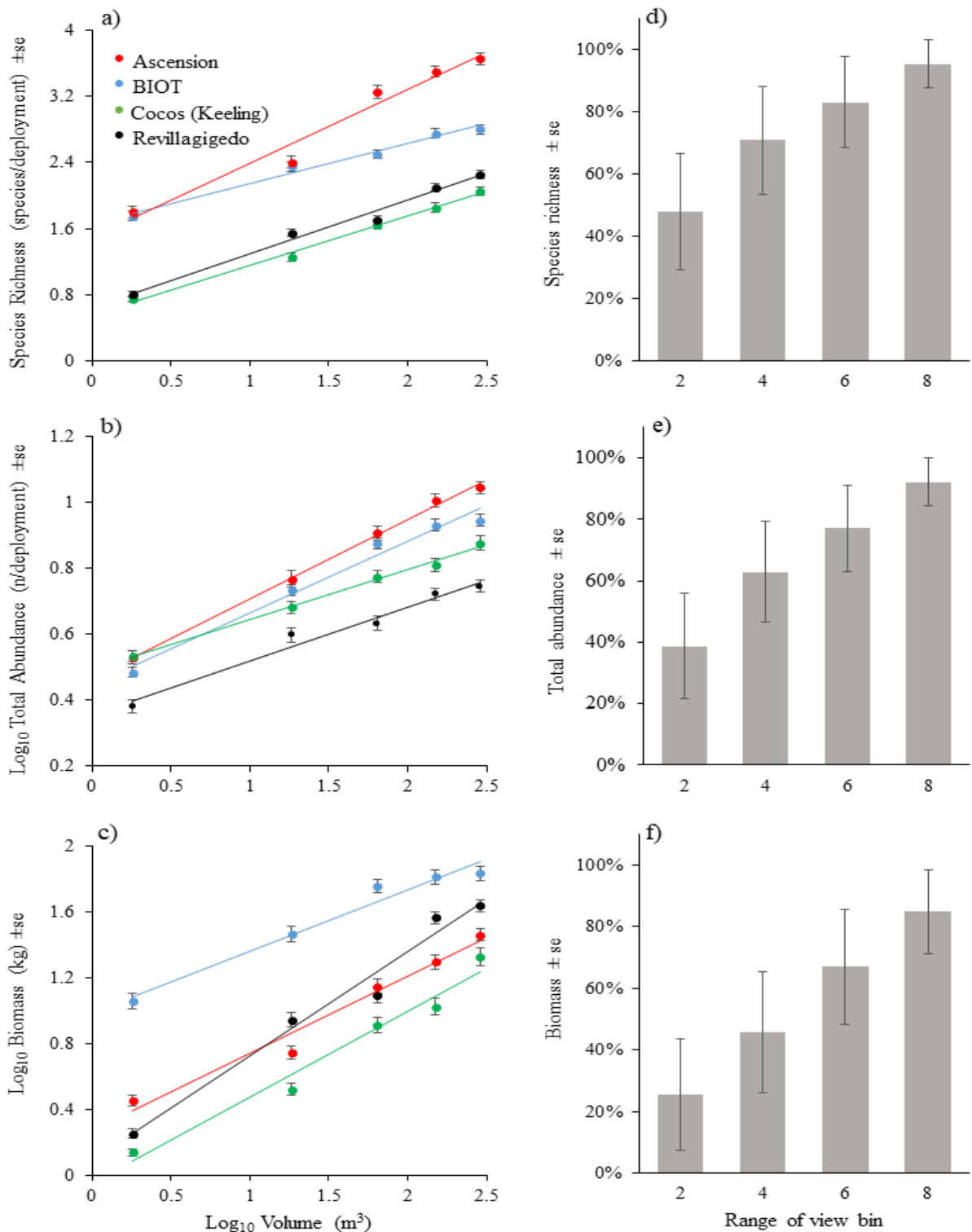
Fig. 3. Regression plots of (a) mean species richness (species/deployment), (b) mean $\log_{10}$ total abundance (n/deployment), (c) mean $\log_{10}$ total biomass (kg) with ± standard error bars against the $\log_{10}$ of volume (m^3) as sampled at reduced ranges of view of a pelagic fish and shark assemblage for four locations: Ascension Island (blue), British Indian Ocean Territories (BIOT) (red), Cocos (Keeling) Islands (green), and Revillagigedo Archipelago (black). Mean percentage accumulation of (d) species richness, (e) total abundance, and (f) total biomass for every video at each increasing range of view bin relative to 10 m. Values are averaged across all four locations ± standard error bars.

Considering the mean minimum range species are detected on the stereo-BRUVS suggests smaller bodied, structurally associated individuals such as driftfish (*Psenes* sp.*) and juvenile big-eye trevally (*Caranx sexfasciatus*) were observed closer to the camera than larger bodied individuals like yellow fin tuna (*Thunnus albacares*) and great barracuda (*Sphyraena barracuda*) (Fig. 4). Other smaller bodied (<50 mm) animals such as scad (*Decapterus sp.*) were rarely detected outside the 4 m range. The five species of shark represented in this figure have a range of mean minimum distances. Galapagos sharks (*Carcharhinus galapagensis*) were often observed interacting directly with the bait canister at a close proximity to the stereo-BRUVS whilst blue sharks (*Prionace glauca*) were detected at a mean minimum range of 8 m, suggesting a warier behaviour towards the stereo-BRUVS. Large bodied, rare species such as beaked whales (*Ziphiidae* sp.) and black marlin (*Istiompax indica*) were not observed within 10 m of the stereo-BRUV.
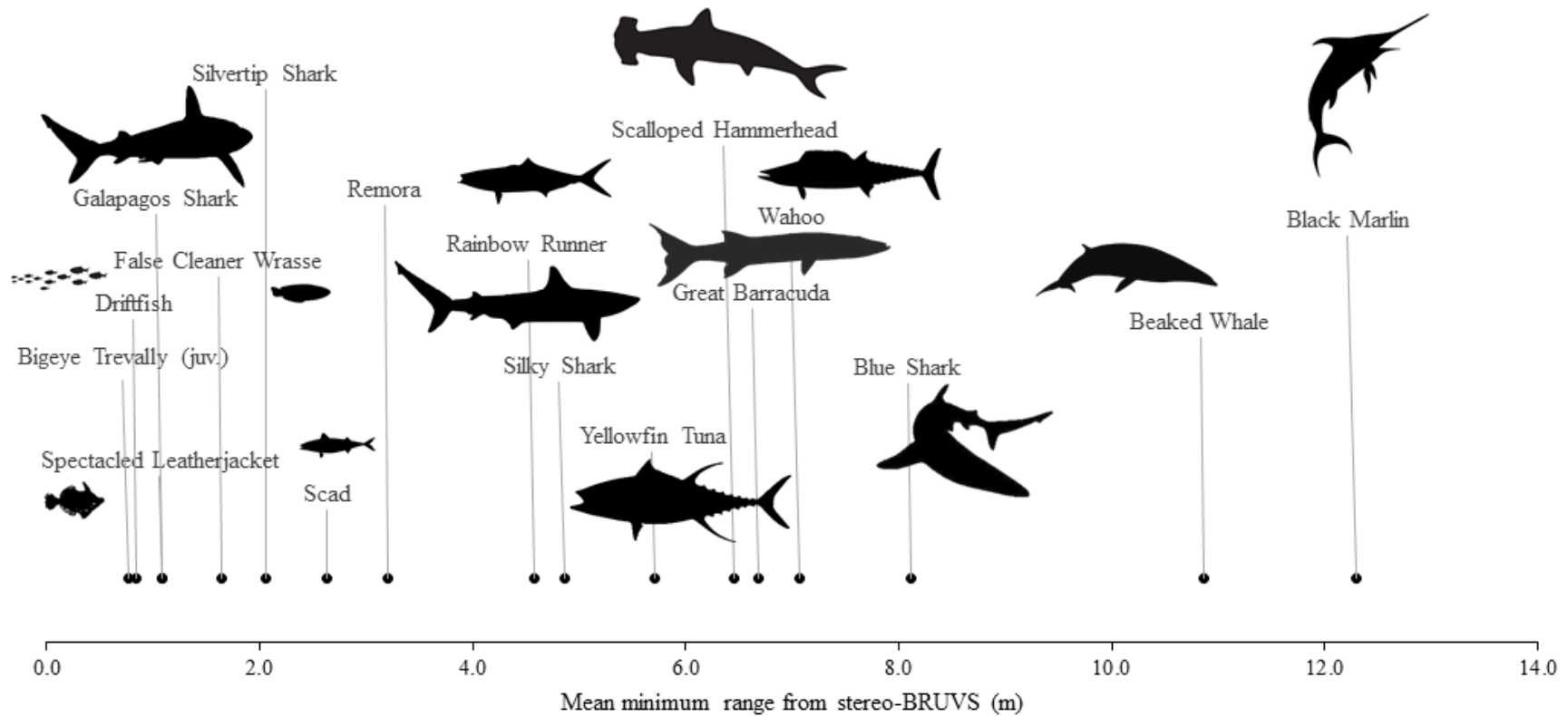
Fig. 4. Mean minimum range selected species were detected from the stereo-BRUVS within pelagic assemblages combined across four locations: Ascension Island, British Indian Ocean Territories, Cocos (Keeling) Islands, and Revillagigedo Archipelago.

4. Discussion

Estimates of species richness, total abundance, and biomass of fish and shark assemblages sampling were strongly affected by the RoV. Even at a considerable RoV of 6 m, 17% of species richness, 23% of total abundance, and 33% of total biomass remained undetected. This is consistent with previous studies on effects of sampling unit size on population metrics (Stout & Vandermeer 1975, Levin 1992, Melo et al. 2003). The linear increases in species richness, total abundance, and total biomass with increasing RoV contrasts with that of previous studies of fish and shark assemblage sampling using alternative techniques (Samoilys & Carlos 2000, Cappo et al. 2011, Gilby et al. 2017). However, it is consistent with other stereo-BRUVS studies (Unsworth et al. 2014). The taxa composition of an assemblage will reflect the RoV sampled, with behavioural and size variability potentially biasing trophic structure analyses. Thus, it is essential to distinguish sampling unit size between deployments for valid comparisons (Williams 1943, Willis 2000).

Fish and shark assemblage characteristics are generally a function of their location, with mechanisms behind the population patterns attributed to latitudinal position, productivity, connectivity, and human impact (Tittensor et al. 2010, Belmaker et al. 2011, Jetz & Fine 2012). The variance in estimates across the four focal locations of the present study is consistent with this idea and promotes location specific understanding of fish and shark assemblages (Hobbs et al. 2014, Wirtz et al. 2014, Fourriere et al. 2016, Samoilys et al. 2018). The relatively high species richness estimates for BIOT is consistent with the theory of tropical locations providing greater estimates of species richness compared to higher latitudes (Stevens 1989). Biomass estimates observed at each location coincide with primary productivity estimates available from www.seaaroundus.org with the greatest biomass estimates observed at Ascension Island that is estimated to have a primary productivity of 314.239^{-2}day^{-1}. Cocos (Keeling) Islands is estimated to have a primary production of 257.45^{-2}day^{-1}, the lowest of the four focal locations, this is supported by the biomass estimates. Despite the differences between each location's assemblage metrics, there is no interaction of location and RoV, thus the accumulation rate over increasing RoV is homogenous.

Logistical constraints will often affect a way we sample a population, in the present case, RoV is a variable that is unable to be controlled for and thus those sampling via stereo-BRUVS face three options to control for sampling unit size. The first option is to standardise a RoV to be sampled. This option is recommended when some videos have a much greater RoV than the

others and has been previously used to ensure length measurements are accurate and animals are within proximity where they are identifiable (Harvey et al. 2010). The second option is to remove videos recorded that are low-visibility. Such an option is possible where large numbers of samples are collected but difficult if sample sizes are small. The third option is to make predictions via rarefaction curves and predictive modelling. Rarefaction for the comparison of non-like sampling unit sizes is a statistical approach to meet some of the challenges faced in ecological studies (Colwell et al. 2012). Regression models presented in this paper explain between 97% and 99 % of variance for each metric at that specific location and can be used to interpolate data for footage with low RoV (Appendix 2). The compilation of data from more locations will help in the construction of a more robust model that is able to predict for RoV in all pelagic environments.

The implications of this study should translate to demersal surveys using video technology. Benthic BRUVS for sampling demersal fish and shark assemblages present further challenges in terms of standardising for sampling unit size as there can be multiple levels of RoV within a single frame. Reef structures at various proximities to the camera can obstruct the RoV, calculating the sampling unit size in this situation is difficult, as such the standardisation of volume sampled is sometimes unachievable. The structural association of many demersal species will bias the results of creating models based on non-obstructed videos (Willis & Anderson 2003). Previous benthic rig designs that control for a sampling unit size were cameras facing downwards into a known volume (Willis et al. 2000), this design has since been outdated due to behavioural bias such a camera arrangement incurs (Langlois et al. 2006). Further research is required to determine if demersal assemblages are influenced by RoV to the extent pelagic assemblages are.

Single camera, mono-BRUVS saturate the fish and shark assemblage literature (Whitmarsh 2017). In addition to the advantages the BRUVS technique provides, short term costs and simplistic image analysis of single camera designs has seen contemporary sampling favour mono-BRUVS. However, mono-BRUVS do not have an accurate measure of volume sampled, thus sampling unit size is unknown. Owing to the significant effect of RoV on species richness, total abundance, and total biomass, the data collected via mono-BRUVS are not only incomparable but assumptions of population patterns based on these data are uncertain. Ensuring appropriate comparison is only possible with the stereo-BRUVS design as it has the capacity to calculate and standardise for sampling unit size.

The present study suggests a strong effect of sampling unit size on pelagic fish and shark assemblage characterisation, with RoV having a significant influence over metrics such as species richness, total abundance, and biomass. It is thus necessary to know the RoV of the BRUVS used for sampling. Stereo-BRUVS are capable of range estimates and are recommended as the standard in pelagic fish and shark assemblage surveys. Their capability to distinguish between sampling unit sizes is invaluable when generating comparable data as well as having the potential for constructing predictive models to allow rarefaction of data from previously unusable footage. This study reinforces the requirement of a standardised RoV in future analyses of fish and shark assemblages via stereo-BRUVS.

Acknowledgements

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Appendices

Appendix 1. Results of rmPERMANOVA assessing the effects of location and RoV including interaction, with deployment as a nested factor within location, on a Euclidean distance similarity matrix calculated for species richness, $\log_{10}$ of total abundance, and $\log_{10}$ of biomass (perm=9999). Significant effects ($P<0.05$) highlighted in bold.

	df	MS	Pseudo-F	P
Species richness				
Location	3	43.4	8.1	**0.001**
RoV	4	26.0	40.0	**0.001**
Deployment (location)	76	5.3	14.2	**0.001**
Location x RoV	12	0.6	1.7	0.057
Residual	304	0.4		
$\log_{10}$ total abundance				
Location	3	1.0	1.6	0.211
RoV	4	2.3	66.1	**0.001**
Deployment (location)	76	0.6	23.2	**0.001**
Location x RoV	12	3.5e-2	1.3	0.234
Residual	304	2.7e-2		
$\log_{10}$ total biomass				
Location	3	11.3	4.3	**0.007**
RoV	4	15.1	48.0	**0.001**
Deployment (location)	76	2.6	12.8	**0.001**
Location x RoV	12	0.3	1.5	0.111
Residual	304	0.2		

Appendix 2. Equations and R^2 of trend lines for each location per species richness, $\log_{10}$ total abundance, and $\log_{10}$ total biomass over the $\log_{10}$ of volume in Fig. 2a-c.

Metric	Location	Equation	R^2
Species richness	Ascension Island	$y = 0.48x+1.66$	0.97
	BIOT	$y = 0.89x+1.50$	0.97
	Cocos (Keeling) Islands	$y = 0.59x+0.56$	0.99
	Revillagigedo	$y = 0.65x+0.65$	0.98
$\log_{10}$ total abundance	Ascension Island	$y = 0.23x+0.45$	0.98
	BIOT	$y = 0.24x+0.47$	0.99
	Cocos (Keeling) Islands	$y = 0.15x+0.49$	0.99
	Revillagigedo	$y = 0.16x+0.35$	0.98
$\log_{10}$ total biomass	Ascension Island	$y = 0.37x+0.99$	0.97
	BIOT	$y = 0.47x+0.28$	0.97
	Cocos (Keeling) Islands	$y = 0.52x-0.05$	0.97
	Revillagigedo	$y = 0.63x+0.09$	0.97