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Comprehensive assessment of shallow surf zone fish biodiversity requires a combination of sampling methods

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ABSTRACT: Surf zones of sandy beaches are crucial environments for numerous fishes but one of the most challenging habitats when it comes to sampling, due to high-energy currents and waves. In this study, we compared the efficiency of 2 methods currently used to sample the biodiversity of shallow surf zone fish communities: the traditional method of beach seine nets and the more recently introduced surf zone Baited Remote Underwater Video Stations (surf-BRUVS). We applied both sampling strategies at 67 sites along 27 sandy beaches with different environmental characteristics in southeastern Brazil. We compared overall abundance, species richness, and beta (turnover) and functional trait diversity recorded from both methods. Our results showed that seine nets captured a higher species richness, greater abundance, greater functional richness and more functionally singular species than surf-BRUVS, particularly in areas with low wave energy. Beta diversity analyses, however, showed a clear difference in assemblage composition detected by each method regardless of environmental conditions, mainly driven by species turnover and variations in abundance. Only seine nets captured small species (<10 cm total length), while surf-BRUVS were more effective in recording larger species. Our results suggest that shallow surf zone assemblages sampled with surf-BRUVS and beach seine nets are almost totally taxonomically and highly functionally divergent, and the application of both methods provides complementary results. Additionally, the non-extractive nature of surf-BRUVS presents an opportunity for sampling vulnerable areas or species. However, when using a single method, researchers should take into consideration each method's biases and be aware that biodiversity may be underestimated for certain groups.

KEY WORDS: Baited remote underwater video stations · Ichthyofauna · Integrated coastal management · Sandy beaches · Seine nets · Surf-BRUVS

1. INTRODUCTION

Sandy beaches make up approximately one-third of the world's coastline (Luijendijk et al. 2018) and sustain coastal economies around the world (Schlacher et al. 2007, Amaral et al. 2016). They also support a diverse and endemic biota and provide key ecosystem goods and services such as capture fisheries (Defeo et al. 2009). Yet, they are trapped between the impacts of urbanization and climate change from both the terres-

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trial side and the aquatic side (Schlacher et al. 2007, Nel et al. 2014). As a consequence, virtually all beaches in the world are now threatened (Defeo et al. 2009, Vousdoukas et al. 2020), and an understanding of sandy beach biodiversity and how this ecosystem will respond to these unprecedented environmental changes is critical to developing effective conservation and management plans (Defeo et al. 2009, Cardoso et al. 2016).

Despite their ecological and societal importance and the high degree of exposure to human impacts, sandy beaches are by far the least studied coastal ecosystem (Nel et al. 2014), particularly the surf zones of sand beaches — the nearshore areas where waves break along the interface of land and sea. To date, fish biodiversity in these nearshore breaking areas has been investigated in approximately 150 studies, the majority of which focus mainly on describing the composition of fish assemblages (reviewed in Olds et al. 2018). Shallow marine waters are crucial environments for a variety of fish species (Valesini et al. 2004), functioning as potential nursery (Lombardi et al. 2014), foraging (Tatematsu et al. 2014) and spawning grounds for fishes (Hirose & Kawaguchi 1998) and as safe zones for juvenile fishes (Inoue et al. 2008). Nevertheless, surf zones are often considered the most challenging area of sandy beaches when it comes to sampling due to hazardous environmental conditions such as currents and waves, and previous studies have pointed out that methodological constraints have compromised a full understanding of surf zone functioning and biodiversity (Olds et al. 2018).

Beach seine nets have historically been the dominant sampling method used in surf zone studies (ca. 75% of papers on surf zone fish, Olds et al. 2018) and are not only popular among scientists across a range of systems but also a common practice in artisanal fisheries around the world (Begossi 2006, Bender et al. 2014). Although this method might be effective in sampling fish from some shallow surf zone habitats, researchers have been arguing that it may introduce biases by underestimating the abundance of benthic species, large predators and highly mobile taxa that are capable of evading the net (Baker & Sheaves 2006, Dorenbosch et al. 2009). Additionally, beach seine nets are extractive methods that result in the removal of not only the target organisms but also bycatch fauna, and there is a growing need for the development of a non-intrusive technology to quantify and monitor fish in marine habitats, especially in protected or vulnerable areas (Murphy & Jenkins 2010).

These issues could be reduced or even overcome when using visual methods such as Baited Remote Underwater Video Stations (BRUVS). BRUVS consist of high-resolution cameras, tied to weights heavy enough to maintain stability on the soft bottom or while floating in the water column with bags of selected bait attached to attract fishes. They are increasingly used for underwater monitoring, as they offer several advantages in decreasing the occurrence of zero counts, increasing the similarity and repeatability between surveys, and providing complementary data on fish behaviour (Cappo et al. 2007). Additionally, BRUVS can be deployed in deeper or heavily structured areas that are not amenable to other sampling methods (such as seines and trawls), are known to record rarer and larger predatory fish species that evade the traditional beach seine net (e.g. Watson et al. 2005), and are a non-invasive method that causes no direct damage to the fauna. However, this technique also has shortcomings: visual methods require good visibility, they produce conservative relative density measures based on the duration of the footage and biases in the types of species attracted to the bait, and they can be difficult to standardize across varied applications due to the aforementioned constraints (Priede & Merrett 1996, 1998, Bailey & Priede 2002, Langlois et al. 2020).

The use of these baited video systems to assess fish biodiversity in surf zones (surf-BRUVS) is a rather new development (Vargas-Fonseca et al. 2016). However, this technology has shown promising results, revealing otherwise undetectable larger fish species and thereby expanding general knowledge on surf zone fish composition (Olds et al. 2018). Nevertheless, surf-BRUVS have so far only been deployed in 5 sandy beach studies in eastern Australia (i.e. Vargas-Fonseca et al. 2016, Borland et al. 2017, Ortodossi et al. 2019 and Mosman et al. 2020 within the surf zone and Schultz et al. 2019 beyond the surf zone). Therefore, their use needs to be tested in different bioregions and under different conditions, especially considering the range of hydrodynamic regimes to which beaches are subjected and which could theoretically compromise the effectiveness of the method. Importantly, BRUVS must be compared with other traditional sampling methods to determine the degree of overlap and comparability generally.

Comparative studies between the use of extractive methods, such as nets, trawls and longlines, and BRUVS have been conducted in vulnerable habitats such as the deep sea (McIntyre et al. 2015, McLean et al. 2015), mangroves (Enchelmaier et al. 2018), reefs (Parker et al. 2016) and seagrass (Unsworth et al. 2014, Schultz et al. 2017) and even in impacted areas such as windfarm plants (Griffin et al. 2016). Knowledge of the biases and advantages of various methods is essential in creating more efficient sampling of either whole fish assemblages or targeted species (Logan et al. 2017), since in some cases, data from BRUVS and seine sampling were not considered comparable (Enchelmaier et al. 2018) but might be complementary (Unsworth et al. 2014). Despite the importance of adequate sampling designs to understand the processes that govern coastal ecosystems and improve conservation strategies and fisheries management (Olds et al. 2018, Reis-Filho et al. 2020), to the best of our knowledge, no study has tested the relative efficiency of surf-BRUVS in sampling shallow surf zone habitats.

This study aims to perform the first evaluation of 2 different methods for assessing the fish biodiversity of shallow surf zones of sandy beaches by comparing the more recently used surf-BRUVS and the traditional beach seine net. We assessed and compared aspects of community composition and diversity recovered by both methods, including species richness, abundance, regional variation in species composition (i.e. beta diversity) and functional trait diversity at 67 sites along 27 sandy beaches across southeastern Brazil with different degrees of wave exposure to test the efficacy of each method under different environmental conditions, since we expected waves to impact sampling efficiency. We expect that the results of this study will help researchers to determine the most appropriate method for sampling the shallow surf zone depending on local conditions and the particular objective of the study, thereby providing more information to guide ecological research as well as conservation and monitoring programs.

2. MATERIALS AND METHODS

2.1. Study area

This study was performed along 27 sandy beaches in the municipalities of São Sebastião, Caraguatatuba and Ubatuba, located on the north coast of the state of São Paulo, southeastern Brazil. This area has a large diversity of sandy beaches due to its physiographic features, and our sampling sites covered a spatial range of 150 km from the northernmost to the southernmost beach. Sandy beaches (Fig. 1) were selected along a gradient, from wave-dominated reflective beaches to tide-modified ultradissipative beaches (McLachlan et al. 2018). All beaches were sampled over 3 mo during the late summer and early autumn of 2018 to avoid drastic changes in the fish assemblage caused by seasonal changes and the entry of cold fronts, which are more common in winter (Pianca et al. 2010).

2.2. Sampling

Each beach was divided into 3 sites parallel to the shore: 2 sites close to each beach edge and 1 in the middle of the beach. These sites were established to account for spatial variation in biotic and abiotic features within a single beach such as differences in exposure to waves and proximity to river mouths, which directly affect fishes and alter other variables known to affect species composition, such as turbidity, primary production and salinity (Araujo et al. 2002, Pessanha & Araújo 2003, Nakane et al. 2013, Borland et al. 2017). Thus, sites were considered and evaluated as separate sampling areas for data analysis. From the 81 sites established, 14 were excluded from the analyses because we could not employ both sampling methods due to safety concerns and/or problems with the BRUVS recording, leaving 67 sites with available data.

Surf-BRUVS consist of a GoPro Hero6+© camera attached to a 10 kg weight and equipped with a bag containing 500 g of selected bait approximately 0.5 m in front of the camera, in this case, the pilchard *Sardinella brasiliensis*, since pilchard are expected to produce more consistent outcomes across feeding guilds compared to other bait types (Wraith et al. 2013). Fish sampling took place during high tide, between 11:00 and 14:00 h, of spring tide periods to standardize for any daily or tidal fluctuation. At each site, 2 surf-BRUVS were deployed 100 m apart, totalling 6 surf-BRUVS at each beach, with sites being a minimum of 200 m apart (Fig. 2). Each surf-BRUVS was deployed at a depth between 1.5 and 2 m, mimicking depths at which the seine nets are towed. We recorded fish for 1 h.

To estimate the efficiency and validity of the deployment of surf-BRUVS and reduce confounding factors in the comparisons, beach seine sampling was conducted at least 1 h after the video recording finished, to avoid any possible aggregation caused by the bait. Fishes were collected using a beach seine net 20 m wide and 2.6 m high with 5 mm mesh and a 2 m high and 4 m long funnel. Two hauls were performed per site by extending the net perpendicular

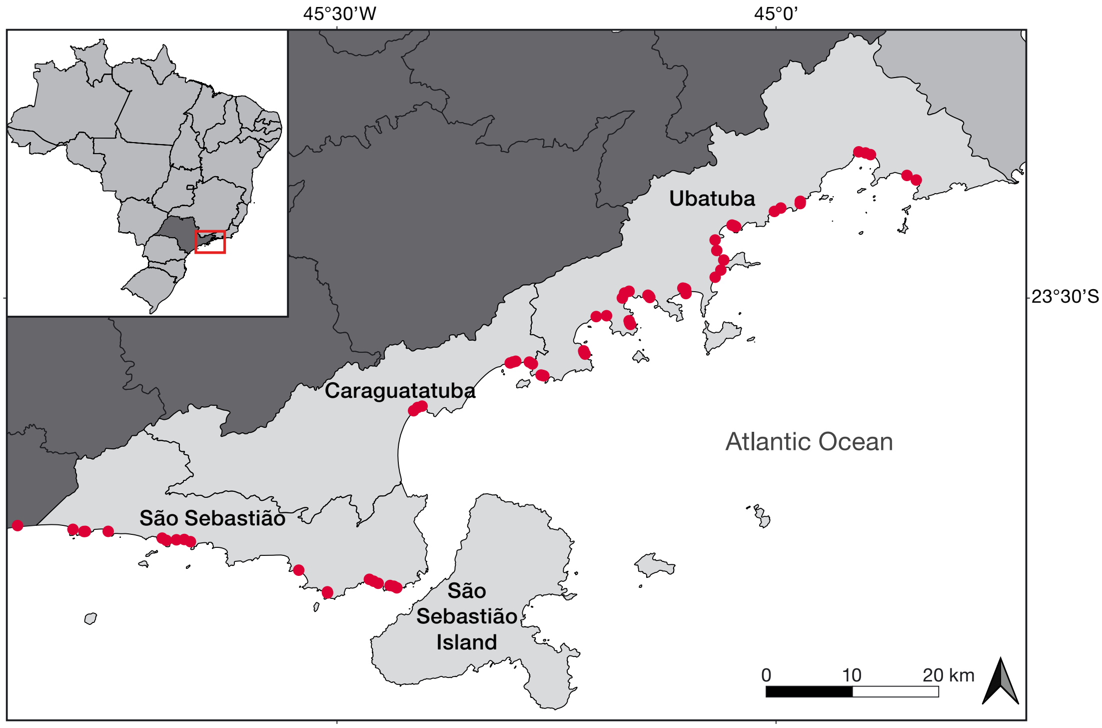

Fig. 1. Study area on the north coast of São Paulo, Brazil, showing 67 sites (red dots) along 27 sandy beaches in the municipalities of São Sebastião, Caraguatatuba and Ubatuba

Fig. 2. Sampling design deployed for a sandy beach, in this case Fazenda Beach, showing 3 survey sites with a distance of >200 m between them with 2 cameras per site separated by 100 m

At each site, to verify the influence of hydrodynamics (i.e. wave height) on the species assemblage captured by each of the methods, significant breaker wave height was measured as the average breaking height of one-third of the highest waves registered of 20 consecutive waves (McLachlan et al. 2018). Besides the hydrodynamic aspect of wave height, this variable may also be used as an estimate of visibility, since the resuspension caused by the dissipation of wave energy along the surf zone influences the turbidity of the water (Manning et al. 2013), which is an important factor that might compromise fish identification through images.

to the shoreline (water depth ≈ 1.5 m) and then pulling for approximately 20 m parallel to the shore; the area swept was approximately 400 m^2 for each haul, following the methodology commonly used in ecological studies. Fishes were immediately frozen and stored in glass containers for further processing. At the laboratory, fishes were counted and identified to species level.

2.3. Data analysis

The 2 samples of each method collected at each site were pooled to form a single count, i.e. 2 seines and 2 BRUVS. The videos collected by the GoPro cameras were processed (we analysed images from minute 5 to minute 65 of every video to minimize the initial observer effect and standardize sampling time) and fish identified and counted using the standard Max N statistic, where abundance is determined as the maximum number of individuals belonging to each species in the field of view at one time (Priede et al. 1994, Willis & Babcock 2000, Murphy & Jenkins 2010). This method avoids repeated counts of the same individuals and gives a conservative estimate of relative density.

To fairly compare total fish richness using each method, we generated rarefaction/extrapolation curves for both the number of individuals as well as the number of samples for each method following Chao & Jost (2012). This procedure allowed us to determine the amount of effort (i.e. how many seines or hours of video) necessary to acquire the same level of biodiversity. Additionally, to determine differences in the relative density of common species, we conducted 2 supplementary tests: (1) a *t*-test on the proportional abundance of the 10 most abundant species across all sites in the assemblages captured by each method and (2) a proportional test on the total number of samples containing each of the top 10 species for each method. We further adjusted our threshold for significance for multiple testing by applying the Bonferroni correction (α/n).

To examine the variation in species composition detected by each method in each sampling site, we calculated the beta diversity between methods using pairwise dissimilarity measures. We first used the framework developed by Baselga (2010) which uses presence–absence data and separates total dissimilarity between assemblages into 2 components accounting for the dissimilarity derived solely from turnover (i.e. total replacement of species, β_{SIM}) and the dissimilarity derived from nestedness (i.e. species-poor sites are subsets of more speciose ones, β_{SNE}). To account for the influence of abundance on beta diversity, we used a later method proposed by Baselga (2013) in which total beta diversity is divided into balanced variation in abundance (β_{BAL}, analogous to turnover) and abundance gradients in which one assemblage is a subset of another (β_{GRA}, nestedness component). Presence–absence beta diversity used the Sørensen index, while abundance-based beta diversity was based on the Bray-Curtis dissimilarity index. Additionally, a non-metric MultiDimensional Scaling (nMDS) (Kenkel & Orlóci 1986) on the presence–absence community matrix was used to visualize differences in community composition sampled by the different techniques.

To evaluate whether functional diversity differed between methods, we collected data on species functional traits from FishBase and compiled a species-by-traits matrix that comprised 4 traits with 17 modalities, which were chosen to verify if methods were more efficient in sampling solitary or school-forming species (association), whether they targeted specific trophic groups (diet) or certain regions of the water column (water column feeding position), or if they had a bias towards species of certain length classes (median length). Then, we calculated 5 metrics of functional diversity: number of singular species, functional richness (FRic), functional dispersion (FDis), functional evenness (FEve) and community-weighted mean (CWM) trait value.

The number of singular species describes the number of functionally unique species in each community if each species had completely orthogonal trait combinations. If all species are completely functionally different (i.e. occupy totally different modalities), the number of singular species will be identical to the total number of species (Laliberté et al. 2014). FRic estimates the total volume of multivariate functional space occupied by a given species assemblage and can be used as a proxy of the range of functional traits represented in an assemblage (Mouchet et al. 2010). FDis refers to the mean distance of all species in a given assemblage from the center of the functional space weighted by their abundances, with low FDis suggesting a convergence of individuals and/or functional traits in multivariate trait space. FEve represents the regularity of the distribution of species abundances in the functional space, with low FEve indicating that some niches have a reduced number of individuals performing those functions (Mason et al. 2005, Mouchet et al. 2010). CWMs summarize the average value of single traits within a community (Garnier et al. 2004) and were used here to determine if the predominant trait sampled by each method differed within the sites. For indices weighted by relative abundances (e.g. FEve or FDis), individual abundances are standardized by the total abundance within each sample (Laliberté et al. 2014), so these metrics can be directly compared among samples where the total abundance differs (for example, due to the survey method).

To investigate whether differences in sampling method or beach environmental characteristics influenced surf fish abundance, species richness and functional diversity (number of singular species, FRic, FDis, FEve), we fit generalized linear mixed models (GLMMs) with method, wave height and their interaction as fixed effects and beach as a varying-intercept random effect, assuming a Poisson distribution for count data (Bolker et al. 2009). Afterwards, a Wald chi-squared test was used to evaluate the significance of each variable. To evaluate the sensitivity of our analysis to repeated samples at the same beach, we collapsed the data into a single mean for each beach and repeated the analysis using a general linear model with the same fixed effects as above and used an F-test to gauge the significance of each predictor. For the CWMs, we fit individual generalized linear models (Nelder & Wedderburn 1972) for each trait and applied the Bonferroni correction for multiple testing, which is α/n, where n is the number of tests. Thus, to achieve statistical significance, the significance level for each predictor in the model had to be less than $\alpha = 0.002$. For all other tests, we held $\alpha = 0.05$.

All analyses were performed in the R statistical environment (version R-3.6.2, R Development Core Team 2019) using the packages iNEXT (Hsieh et al. 2016), betapart (Baselga et al. 2018), FD (Laliberté et al. 2014), vegan (Oksanen et al. 2017) and MASS (Venables & Ripley 2002).

3. RESULTS

3.1. Differences in richness, abundance and beta diversity

A total of 9019 individuals were recorded, comprising 63 species belonging to 25 families (Table S1 in the Supplement at www.int-res.com/articles/suppl/m667p131_supp.pdf). A total of 6999 individuals of 58 species in 23 families were captured using seine nets, while cameras observed 1972 individuals of 21 species in 14 families. Overall, the average numbers of individuals and species were 3 times higher in samples collected using the beach seine net than in those using BRUVS (mean abundance: net = 111 ± 290 SD; camera = 32 ± 72 SD; mean species richness: net = 6.1 ± 4.2 SD; camera = 2.1 ± 1.4 SD). Additionally, based on the results of our GLMMs, the ability of the 2 methods to characterize abundance and richness of the fish assemblage generally depended on the site conditions: in areas with low waves, the seine nets registered higher richness and abundance, while in areas with higher waves, both methods achieved similar results (Fig. 3).

Species accumulation curves demonstrate that the 2 methods yield different measures of total biodiversity: BRUVS yielded 3 times lower richness than seines, even after thousands of individuals or hundreds of samples counted (Fig. 4). Also interesting is that the total diversity observed in a BRUVS saturated after approximately 1500 individuals observed or 50 h of video, whereas richness was expected to continue to increase in beach seine nets even after doubling the number of samples taken. This result implies that more seine nets might need to be deployed to capture the full diversity of species implied by the existing data, while repeated deployment of BRUVS is less likely to reveal any additional species for the subset of the community captured by this method.

Besides the major differences in total richness recovered between the 2 methods, we also found that 7 of the 10 most abundant species across the entire survey differed significantly in their relative abundances between seines and BRUVS, and 5 of the top

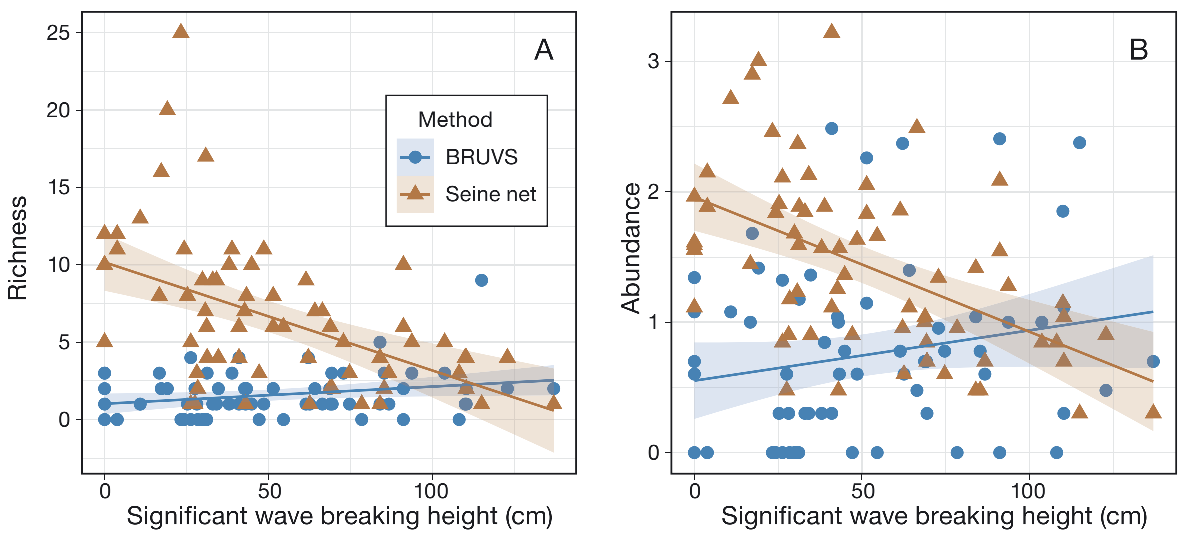

Fig. 3. (A) Species richness and (B) $\log_{10}$+1-transformed abundance as a function of significant wave breaking height (cm) and sampling method. Fitted lines are predictions from generalized linear mixed effects models ± 1 SE

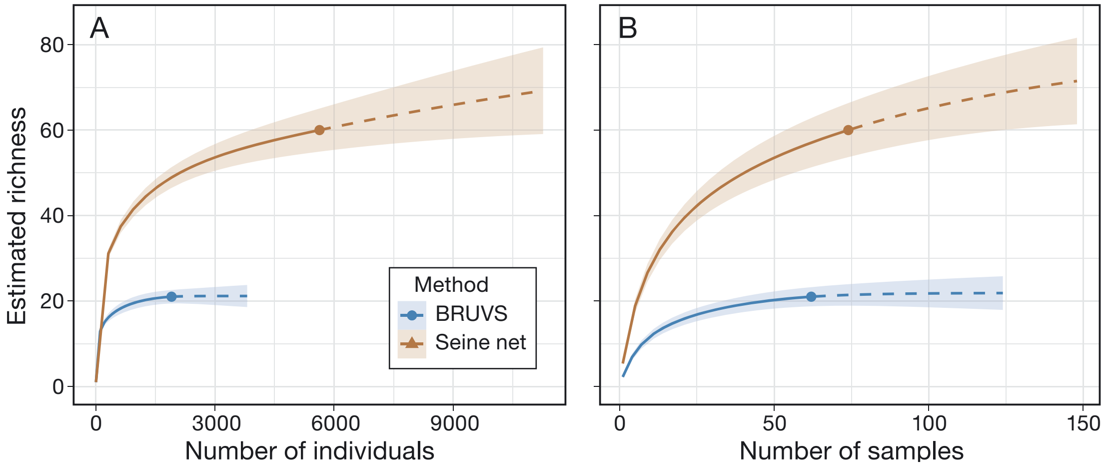

Fig. 4. Coverage-based rarefaction curves based on the (A) number of individuals and (B) number of samples for each method. Solid lines are interpolated, while dotted lines are extrapolated based on the data. Observed richness is given by the dot at the intersection of the solid and dotted lines. Shaded areas represent 95 % CIs

10 species differed significantly in the total number of samples they appeared in between the 2 methods (Table 1). Although the species *Genidens* sp. (camera: 360 individuals; net: 2955 individuals) and *Harengula clupeola* (camera: 986 individuals; net: 967 individuals) were the most abundant for both methods, the nMDS showed that the 2 methods yielded very different community structures, since there is virtually no overlap in the species composition between the 2 methods (Fig. 5).

In line with the nMDS results, beta diversity analyses showed an average difference of >90 % in abundance-weighted assemblage composition detected by each method in each site, and the same pattern was observed for presence–absence data (β_{SOR} = 0.9 ± 0.14; β_{BRAY} = 0.93 ± 0.14). Most of this dissimilarity (ca. 90 %) was driven by species turnover (β_{SIM} = 0.79 ± 0.31; $\beta_{Bray.BAL}$ = 0.83 ± 0.3), while the nestedness component accounted for only 10 % of total beta diversity (β_{SNE} = 0.11 ± 0.2; $\beta_{Bray.GRA}$ = 0.09 ± 0.2). Seine net data represented 43 unique species, belonging to 12 unique families, while cameras recorded only 5 unique species, including 2 elasmobranchs (*Dasyatidae* sp. and *Carcharhinus limbatus*) and the green sea turtle *Chelonia mydas*.

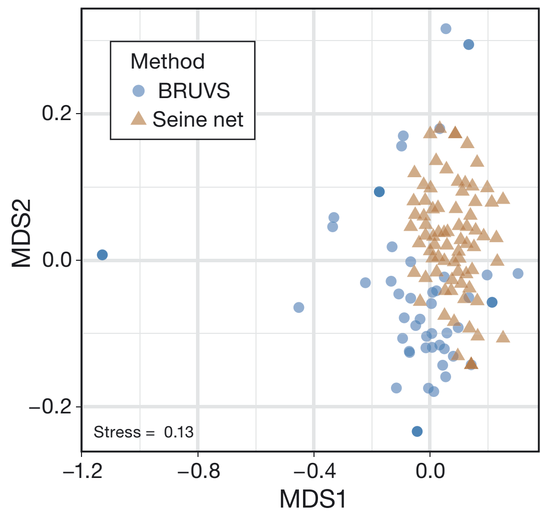

Fig. 5. Non-metric multidimensional scaling (nMDS) analysis of community composition based on the Bray-Curtis dissimilarity matrix of fishes captured by the 2 survey methods

Table 1. Top 10 most abundant species across the survey and whether they differ significantly in terms of their relative density in each sample or in the proportion of samples in which they appeared between the 2 methods. Asterisk (*) indicates significant difference ($p < 0.05$; p-values adjusted for multiple testing)

Species	Relative density (p)	Proportion of samples (p)
Harengula clupeola	4e-05*	0.00016*
Eucinostomus melanopterus	5e-05*	0.11567
Conodon nobilis	0.00052*	0.82708
Trachinotus goodei	3e-04*	0.00413*
Trachinotus carolinus	0.00017*	0.00133*
Lagocephalus laevigatus	0.00674	0.00576
Genidens sp.	0.00832	0.49004
Albula vulpes	0.00275*	0.34185
Menticirrhus littoralis	0.00114*	0*
Umbrina coroides	0.0065	2.00e-05*

Table 2. Relationships between taxonomic and functional metrics, and methods and waves. **Bold** indicates significance ($\alpha = 0.05$)

	Abundance		Species richness		Singular species	
	$\chi^2_{(df=1)}$	p	$\chi^2_{(df=1)}$	p	$\chi^2_{(df=1)}$	p
(Intercept)	32.536	**<0.001**	5.545	**<0.05**	6.8242	**<0.05**
Method	2288.418	**<0.001**	69.551	**<0.001**	55.771	**<0.001**
Waves	91.483	**<0.001**	1.604	0.205	1.405	0.236
Met:Wav	1406.156	**<0.001**	18.544	**<0.001**	16.831	**<0.001**
	Functional richness		**Functional dispersion**		**Functional evenness**	
	$\chi^2_{(df=1)}$	p	$\chi^2_{(df=1)}$	p	$\chi^2_{(df=1)}$	p
(Intercept)	0.6795	0.410	6.350	**<0.05**	46.678	**<0.001**
Method	14.751	**<0.001**	10.120	**<0.01**	0.1455	0.703
Waves	0.0102	0.920	0.195	0.27	3.240	0.072
Met:Wav	3.9907	**<0.05**	0.773	0.11	0.952	0.329

3.2. Functional diversity

Functional diversity analyses also highlighted differences in the characteristics of fish assemblages recorded by each method. The number of functionally singular species was approximately 3 times higher in seine net samples than in the BRUVS, but this difference was reduced with increasing wave action (Table 2). This was also the case for FRic. Wave height, however, did not influence differences in other functional diversity metrics (i.e. FDis and FEve) registered by each method (Table 1). FRic and FDis were higher in samples collected with seine nets, but no difference in FEve was registered between methods (Table 1 and Fig. 6). It is important to mention, however, that FRic and FEve estimates are calculated only for communities with >3 species (Laliberté et al. 2014). Given that assemblages with a low number (<3) of functionally singular species comprised approximately 71% of samples from BRUVS and 23% of samples from seine nets, values of functional diversity metrics are biased towards high-diversity samples, which were more likely in the seines, and differences between methods should be higher.

When we repeated these analyses but instead summarized the data for each of 27 beaches, we found qualitatively identical results to the full dataset for all response variables with a single exception: the interaction between method and wave activity was no longer significant for FRic, although the main effect

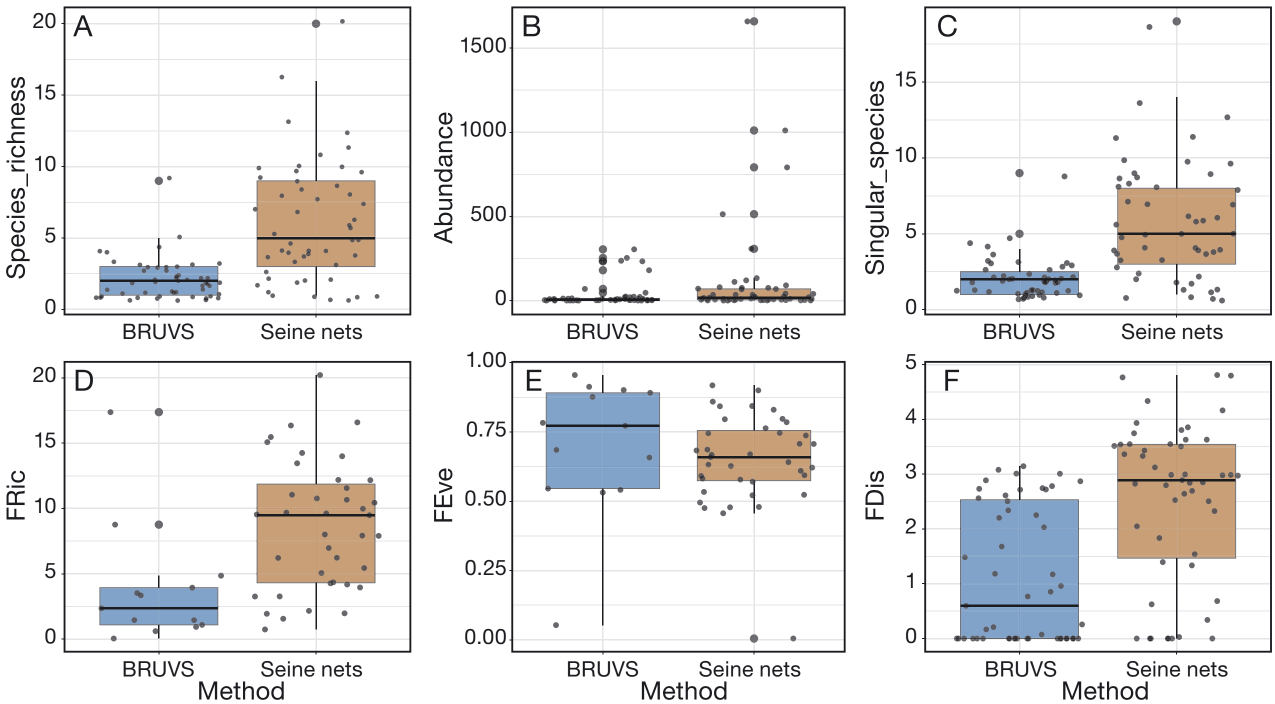

Fig. 6. Differences in the taxonomic and functional metrics (A) species richness, (B) abundance, (C) singular species, (D) functional richness (FRic), (E) functional evenness (FEve) and (F) functional dispersion (FDis) between baited remote underwater video system (BRUVS) (blue) and beach seine net (brown). Small dots represent raw data points (jittered for clarity), and larger dots correspond to outliers

Table 3. Differences in single-trait community-weighted mean (CWM, ±SD) trait values between sampling methods considering 4 traits and 17 modalities. **Bold**: significantly different at $p < 0.001$

Functional trait and modality	CWM BRUVS	CWM Net	p
Association			
School forming	2.47 ± 0.14	2.88 ± 0.03	**<0.001**
Solitary	0.54 ± 0.14	0.12 ± 0.14	**<0.001**
Diet			
Detritus	0.11 ± 0.03	0.03 ± 0.01	<0.05
Phytoplanktivorous	0.11 ± 0.03	0.13 ± 0.03	0.69
Piscivorous	0.45 ± 0.10	0.34 ± 0.10	0.28
Zoobenthivorous	1.98 ± 0.14	1.83 ± 0.10	0.42
Zooplanktivorous	0.35 ± 0.08	0.67 ± 0.06	<0.05
Water column feeding position			
Benthic	1.39 ± 0.10	1.45 ± 0.11	0.66
Demersal	1.16 ± 0.09	0.68 ± 0.07	**<0.001**
Midwater	0.33 ± 0.12	0.71 ± 0.14	<0.05
Surface	0.13 ± 0.08	0.16 ± 0.05	0.77
Median length (cm)			
<10	0	0.25 ± 0.09	**<0.001**
10–20	0.36 ± 0.13	0.49 ± 0.11	0.46
20–30	0.88 ± 0.16	0.81 ± 0.13	0.72
30–40	0.36 ± 0.12	0.54 ± 0.09	0.24
40–60	0.72 ± 0.16	0.71 ± 0.12	0.98
>60	0.67 ± 0.15	0.19 ± 0.09	**<0.001**

of method was still significant, implying differences in this quantity between seines and BRUVS ($p < 0.001$, Table S2). Thus, from this exercise, our results appear robust to the level of aggregation, whether at the site or beach level.

CWM analyses showed that both cameras and seine nets sampled communities that were dominated by school-forming zoobenthivorous fish with a benthic feeding position. However, the seine net was more efficient in sampling school-forming species. Moreover, only seine nets captured species with a median total length of <10 cm. On the other hand, BRUVS were more efficient in sampling solitary species and demersal species (Table 3). Additionally, surf-BRUVS were more efficient in registering species with a median total length of >60 cm.

4. DISCUSSION

A key challenge to improve the effectiveness of conservation planning and fisheries management for coastal waters is to obtain empirical data that provide a reliable representation of ecosystem properties (Olds et al. 2018, Reis-Filho et al. 2020). Our results showed that shallow surf zone samplings with beach seine nets recovered higher species richness and a greater abundance of individuals and functional diversity than those recorded with surf-BRUVS. Importantly, we found that assemblages sampled with BRUVS and beach seine nets are almost taxonomically dissimilar (i.e. high beta diversity between methods mainly driven by species turnover based on both abundance and presence–absence) and strongly functionally dissimilar, and that the application of both methods provides complementary results. Therefore, we propose that the most comprehensive census of regional biodiversity in the shallow surf zone would come from integrating the individual values obtained from both methods conducted simultaneously. In the case of abundance-weighted indices, such as Shannon or Simpson diversity, we also recommend computing rarefied estimates and reporting them in effective numbers of species (or Hill numbers) to account for differences in total abundances due to differences in the amount of effort associated with each method (Chao & Jost 2012).

The lower values in taxonomic and functional metrics detected by surf-BRUVS indicate that this method may underestimate surf fish biodiversity, especially in sites with low wave height that are expected to have higher biodiversity than those with harsher swash climates. This disparity becomes even clearer when looking at the rarefaction curves, which indicate that even if the number of individuals or samples were to be doubled, the gap between estimated fish richness for both methods persists. Limitation of the BRUVS includes bait-dependence bias (Murphy & Jenkins 2010, Lowry et al. 2012, Hardinge et al. 2013, Udyawer et al. 2014) and changes in species interactions caused by baits (i.e. antagonisms: Harvey et al. 2007, Malcolm et al. 2007, McLean et al. 2016). The bait plume attracts fish through olfactory, auditory and behavioural cues which may result in stronger selectivity towards species with accurate sensory systems (Armstrong et al. 1992). Also, the use of bait has been shown to increase the presence of predator species, which can influence species interactions (Armstrong et al. 1992, Jones et al. 2003, Cappo et al. 2004, 2007, Farnsworth et al. 2007, Harvey et al. 2007, Stoner et al. 2008, Watson et al. 2010) and discourage some species from approaching the cameras (Jones et al. 2003) to avoid competition (Willis et al. 2003) or predation (Willis & Babcock 2000, Cappo et al. 2004, 2007, Harvey et al. 2007). This would result in underrepresentation of non-aggressive or lower trophic level species in BRUVS samples (Stoner & Ottmar 2003, Harvey et al. 2007, Malcolm et al. 2007, Stoner et al. 2008). An interesting future avenue of study would be to compare baited and unbaited cameras, which may alleviate some of these issues.

Here, although not statistically significant due to high variation in functional groups within methods and among sites, the presence of piscivorous species in BRUVS data was generally higher than that in samples from seine nets, while the nets in turn captured more zooplanktivorous species in sites where these groups dominated. Additionally, there was a clear bias in the detection of very small species which were found only in seine nets and very large fishes which were found more frequently using BRUVS. These findings underscore that large piscivorous species are generally rarer in this habitat and capable of outswimming the seine net, while cryptic demersal fishes are generally smaller and shier and therefore less prone to showing up on video. These behavioural characteristics would lead to the systematic underestimates of diversity similar to results found in seagrasses (Unsworth et al. 2014).

Studies have also suggested that samples from BRUVS may also present bias due to limitations in species identification. Single-camera BRUVS provide only one perspective, with no possibility to adjust focus or follow particular individuals. Small and cryptic species can on the other hand be retained from the beach seine, which allows for identification in the laboratory (Cappo et al. 2004, Ebner & Morgan 2013, Unsworth et al. 2014, McLean et al. 2016). Water visibility is another issue that may compromise species identification through images (McLean et al. 2016) given that turbidity makes detecting species using underwater cameras only possible when organisms are very close to the bait. In fact, turbidity may explain the strong difference in sampling efficiency between nets and BRUVS in sites with lower wave height. In these habitats, a combination of fine sediments and waves dissipating their energy along a wide surf zone resuspended and mixed sediments into the water column, thereby increasing turbidity (Manning et al. 2014) and compromising the identification of individuals through images, which may lead to further underestimation of the species richness by BRUVS. Therefore, future studies deploying surf-BRUVS should consider the visibility of their specific regions when comparing fish communities between beaches with different environmental characteristics.

Data analysis issues may also reduce the biodiversity estimation in BRUVS samples given that the Max N statistic, the most commonly used technique in deriving abundance data from video images, provides a single non-integrated measure of relative abundance rather than an absolute value. Max N is known to be a conservative measure of relative abundance and may underestimate the abundance of a population of fish (Cappo et al. 2004). An alternative approach to the Max N method is the newly developed Max IND, which counts distinct individuals. This new method of analysis led to an increase in the abundance values observed but should be used with caution since correction factors need to be applied on a species-by-species basis, which is time consuming and therefore only appropriate for rare and/or endangered species (Sherman et al. 2018). Additionally, for the seine net, we have a clear idea of the area coverage of each haul (≈400 m^2) which permits easy standardization of effort (along with seine dimensions and mesh size), while for the cameras, it is difficult to estimate the actual area that is being surveyed due to differences among sites in both the arrangement of the camera and the potential depth of field based on local conditions (e.g. turbidity, refraction). Further exploration of adjusting for visibility and field of view could lead to more robust corrections and permit valid comparisons across widely varying conditions. Nevertheless, within a region, BRUVS are a useful comparative tool, especially when coupled with rarefaction-based estimators, as we have done here.

If one must choose between the 2 methods, beach seine nets alone likely provide more reliable representations of taxonomic and functional biodiversity of surf zone fishes. Moreover, beach seine net surveys also allow measuring and weighing of individuals, thereby yielding reliable estimates of true biomass, which forms an essential part of the stock assessment for several fisheries (Clark 1996). It also allows for a better identification of the life stage of individuals, avoiding errors in measuring spawning stocks or on the appearance of stock–recruitment relationships. Finally, in most countries, the cost of a beach seine net is lower than the cost of a single surf-BRUVS set. Therefore, surf fish studies with seine nets can be performed by research groups working on a restricted budget, although the cost and accessibility of high-definition cameras is likely to decrease with technological developments.

Nevertheless, BRUVS present some advantages over seine nets. For example, seine nets may fail to capture bigger and more mobile fishes (top predators), which are able to escape nets (Lamberth et al. 1995, Pereira et al. 2016). Organisms like skates and rays can also easily escape the nets due to their body shapes and swimming position close to the bottom (McIntyre et al. 2015). In this regard, BRUVS might reveal species that, by virtue of being large and mobile, are of greater economic or conservation interest and could be monitored using BRUVS. They can also be deployed at surf zones with greater depths, where seines are impossible to deploy and which are expected to harbor a higher diversity of fishes (Borland et al. 2017). Also, it takes far less time and fewer people to deploy and retrieve surf-BRUVS in the field, as opposed to seines, which require at least 2 to 3 well-trained people and 20 to 30 min to deploy, sweep the bottom and identify and enumerate the fish assemblage. The videos from BRUVS can be analysed at leisure and also constitute a permanent record for use in future investigations and purposes.

Furthermore, seine netting becomes impossible in heavy surf, uneven surfaces (e.g. rocky bottoms) or the deeper sections of sandy beaches (McLachlan & Brown 2006, Olds et al. 2018). The harsher swash climates also create instability, which do not always guarantee that the net to stays close to the bottom, facilitating fish escape and reducing capture (Lamberth et al. 1995). As the numbers of species and individuals sampled with beach seine nets and BRUVS were similar in areas with higher waves, the use of BRUVS may be advantageous and less dangerous when such conditions are present, such as on exposed beaches. However, both methods were found to be impracticable in areas with very high wave energy (breaking wave height >1.2 m), where even the heavy weights were not able to keep cameras in place and netting was not a viable option due to the very steep slope and absence of a true surf zone.

In a time–effort context, BRUVS present several undeniable benefits. Multiple cameras can be deployed during a fixed period (e.g. 60 min), allowing for a high number of replicates to reduce variability (assuming cameras are placed sufficiently far apart to ensure independence, e.g. at least 100–200 m) (Ellis & DeMartini 1995, Cappo et al. 2004). Finally, it is important to emphasize that the use of visual methods is non-extractive and in a conservation context might be ideal in areas where extractive activities are limited, such as in marine protected areas, or in long-term studies that could impact threatened or endangered populations.

Lastly, it is important to emphasize the need to replicate this study in other bioregions to be able to further confirm the biases found between methods under different conditions or at different scales of resolution (across an entire region, as we have done here, or within particular beaches). This is a fundamental first step in proposing which method (or a combination of both) is most suitable for the objectives of a particular study.

5. CONCLUSIONS

By performing the first comprehensive test on the sampling methods most commonly used to investigate fish biodiversity of sandy beaches, we found that significant differences in taxonomic and functional trait diversity may result from the technique applied. While both underestimated coastal biodiversity, the higher diversity of species and number of individuals sampled using seine nets suggest that this method is more appropriate to investigate shallow surf fish biodiversity, especially in sites with low wave energy. Yet, both methods were shown to sample different aspects of the fish community and provide complementary information that, together, allows for the most accurate assessment of coastal biodiversity to date. Given the distinct bias in detecting species by each particular method, the recommendation for a particular method depends on the objectives of the study. For instance, researchers interested in the monitoring of large predators could safely rely on the sole use of BRUVS. On the other hand, researchers interested in species with small body size or in a more complete estimation of local biodiversity should use seine nets or a combination of both methods.

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