# Short Period Baited Remote Underwater Video as a costbenefit tool to evaluate effectiveness of Marine No-take Zones 

Marcos F. Tomasi ${ }^{\top}$ ©, Linda G. Waters ${ }^{1 \oplus}$, Igor C. S. Cruz ${ }^{1,2}{ }^{\oplus}$, Arthur Z. Güth ${ }^{1}{ }^{\oplus}$, Alexander Turra ${ }^{\top}{ }^{\oplus}$<br>${ }^{1}$ Universidade de São Paulo - Instituto Oceanográfico (Praça do Oceanográfico, 191-Butantã - 05508-120 - SP - Brazil)<br>${ }^{2}$ Universidade Federal da Bahia - Instituto de Geociências - Departamento de Oceanografia (Av. Adhemar de Barros, s/n Campus Universitário de Ondina - Salvador - 40.170-110 - Bahia - Brazil)<br>* Corresponding author: lindagwen@gmail.com


#### Abstract

Evaluating effectiveness of marine No-take Zones (NTZ) can be cost or labor prohibitive, thus comparisons to nearby unprotected areas are typically lacking. Two NTZs were evaluated, the waters surrounding llha Anchieta State Park and Palmas Island in Ubatuba, São Paulo, Brazil, for species richness, diversity, and abundance of ichthyofauna, comparing them with two nearby unprotected "Take" Zones. From 23 deployments using Baited Remote Underwater Video (BRUV), 737 individuals from 51 species of fish were recorded. The NTZ community composition was significantly different from Take Zones, with higher average species richness, abundance, and diversity but similar evenness. Seven species, accounting for more than $72 \%$ of the composition differences between Take and NTZs, were more abundant in NTZs. Comparisons of individual sites within each zone showed high variability for the Mar Virado Take Zone, with one site grouped with NTZs at $30 \%$ similarity. In parallel, BRUV deployed over a short period was assessed as a potential rapid, low-cost method for analyzing the effectiveness of a marine protected area, important for management of sites in low- and middle-income countries with patchy resource availability. BRUV distinguished significant community structure differences between Take and NTZs, with no difference between sites within each classification. Comparing with BRUV conducted for a longer period at two of the four study sites (MV and PA), our rapid study recorded $44.3 \%$ of total species using $28 \%$ of the survey effort. Compared with a multi-method survey as a proxy for a record of all potential species present at a third site (AI), BRUV recorded $30 \%$ of total species using $4.2 \%$ of the survey effort. BRUV showed bias towards size classes $>15 \mathrm{~cm}$ and certain feeding strategies, important to note if assessing a single target species. Overall, this rapid implementation of BRUV showed a clear difference between sites that differed in fishing protection level.


Descriptors: BRUV, Fishing management, Low-cost assessment, Marine protected area, NTZ management.

## INTRODUCTION

As human populations increase, fish stocks and biodiversity are undergoing severe degradation in coastal regions from anthropogenic effects on the environment. Degradation has resulted from the

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exploitation of marine resources, pollution, habitat destruction, climate change, and the related biogeochemical alterations to the ocean (Jackson et al., 2001; Dulvy et al., 2003; Pandolfi et al., 2003; Worm et al., 2005, 2006; Hughes et al., 2013; Barange et al., 2016; Visbeck, 2018; Link and Watson, 2019). New fishery technologies and an increase in fishing effort in the late 20th century collapsed several fish stocks; as of 1997, almost half ( $44 \%$ ) of global stocks were categorized as
fully exploited, $16 \%$ as overfished and $6 \%$ as depleted (Botsford et al., 1997). The rapid decline of these stocks is of concern to governmental and environmental managers, environmental scientists and the scientific community at large (Halpern et al., 2008; Turra et al., 2013). If no action is taken, the most pessimistic of the forecasts suggest that commercial fishing may collapse before 2050 (Worm et al., 2006). No-take Zones (NTZs), a class of Marine Protected Areas (MPAs) where fishing is banned, have been established as a management response to these pressures on fish stocks. They are now frequently implemented globally, and listed as urgent actions in the Aichi Target 11 from the Convention on Biological Diversity (CBD, 2020) and in the UN Sustainable Development Goal 14.5 Life Below Water (SDSN, 2015).

Effective No-take Zones can restore natural age distributions and population densities for species, allow recovery for fish assemblages, and increase abundance of overexploited fish stocks within the NTZ boundaries (Roberts, 1997; Bohnsack, 1998; Halpern and Warner, 2002). NTZs should have sufficient a rea and connectivity w ith other protected areas suitable to effectively preserve fish assemblages; these characteristics are particularly important if the target species is highly mobile (Halpern and Warner, 2003; Moffitt et al., 2011; Breen et al., 2015). A highly effective No-take Zone can achieve a spillover effect, amplifying fish biomass in surrounding areas where fishing is permitted (Roberts, 1997; Bohnsack, 1998). The efficiency of NTZs in achieving these goals should be periodically assessed to then adapt measures to improve future management (Halpern and Warner, 2002; Gell and Roberts, 2003; Halpern, 2003; Micheli et al., 2004; Lester et al., 2009; Palumbi, 2013).

To determine if protected areas show evidence of these positive effects to fish populations, all evaluation techniques require identification of the fish species present. This is typically performed using an Underwater Visual Census (UVC) (Bohnsack and Bannerot, 1986; Cappo et al., 2003), but that requires fish-specialist researchers and extensive time in the field to overcome the inherent bias in sampling accuracy
from differences in diver training and variations in visibility between samples (Thresher and Gunn, 1986; Thompson and Mapstone, 1997; Colton and Swearer, 2010).

The assessment of NTZ effects has been infrequent in low- and middle-income countries (LMIC). While several notable NTZ evaluation studies have been conducted in Brazil (Floeter et al., 2006; Francini-Filho and Moura, 2008; Souza et al., 2018; Anderson et al., 2019; Rolim et al., 2019), long-term monitoring and routine evaluation for management are still lacking in many regions. Methods requiring high costs for manpower or specialized equipment are often a serious concern for management in LMIC regions. Because of advances in quality and cost reduction for underwater cameras, one recent alternative is Baited Remote Underwater Video (BRUV), which attracts fish to the sampling site; the bait increases sample similarity and statistical power of the method without requiring a large number of samples (Cappo et al., 2006) and can be deployed rapidly when visibility conditions are sufficient to see the bait in front of the camera. Both UVC and BRUVmethodsarenon-destructivetechniques, thus well suited to work in MPAs, but BRUV has added advantages of increased cost-effectiveness over UVC (Cappo et al., 2007; Langlois et al., 2010), low manpower requirements, and that samples can be revisited repeatedly by other observers to allow better standardization of data collection (Cappo et al., 2003; Stobart et al., 2007).

This study assessed the effects of two No-take Zones on ichthyofauna community structure versus thoseat found in two comparable nearby tTake zzones. In the process, the results were compared to pre-existing intensive larger scale studies at two of the same study sites, to evaluate the use of short period BRUV as a recommended lowcost technique for monitoring and assessment in this and similar regions in which technical, logistical, or financial support for NTZ assessment is difficult to obtain.

Differences in community composition, species richness, abundance, diversity, and evenness were evaluated using a low number of BRUV deployments in relatively low visibility conditions, within the Anchieta and Palmas Island NTZs and
two proximal Take Zones with similar bottom habitat structures, where fishing was permitted. Samples from sites classified as NTZs are expected to be different than those from Take Zones, while samples within each of the two types of zones are expected to be more similar. The richness of the fish assemblage and the abundance of species of commercial interest in NTZs were expected to be higher than the surrounding fished areas. The trophic structure of fishes is also expected to be different if the NTZs are effective, because targeted fished species are typically from the upper trophic levels.

This low cost implementation of BRUV was simultaneously evaluated for suitability as future standard practice for evaluating NTZ success in regions or conditions where technical, financial, or logistical support resources were not necessarily obtainable. Samples from Anchieta Island are expected to be similar in their detection of at least the larger, bait-attracted fish species to those from a previously existing, long-term, multi-method survey (Souza et al., 2018), with the assumption that it created a comprehensive list of all possible species present. Details regarding number of samples and projections of detection rates via rarefaction curves are provided for both datasets (UVC and BRUV) to aid future management of marine protected areas. Samples from PI and MV were compared to a previously published longduration stereo-BRUV implementation at the same sites (Rolim et al., 2019). The recording time of this short-period implementation was expected to be sufficient to capture most of the characteristic ichthyofaunal species present in the study area.

## METHODS

## Study Area

The study was conducted in the Ubatuba region, in São Paulo state, Brazil, where fishing is an important industry (Diegues, 1974; Tiago et al., 1995; D'Incao et al., 2002; Vianna and Valentini, 2004). The depletion of fisheries stocks in this area, as in the rest of Brazil (Cergole et al., 2002; ReisFilho, 2020), has become concerning to resource managers. Early indications of this prompted the establishment of regions protected from fishing
in Ubatuba, such as the waters surrounding Anchieta Island State Park (hereafter referred to as Anchieta Island, AI) and Palmas Island (PI) within Tupinambás Ecological Station (ESEC Tupinambás). These two NTZs were expected to have achieved some ecological improvement (higher species diversity and richness) because they meet the three of the five objectives proposed for adequate protection of an area (Edgar et al., 2014): (1) no commercial, recreational, sport, and or subsistence fishing allowed; (2) a relatively high enforcement effort; (3) a No-take Zone in place for a long period (30 years).

The marine environment is close to the cliffs of Serra do Mar, where crystalline bedrock is exposed and forms the rocky reef environment. Occurrences of several common fish species have been recorded in both the tropical Western Atlantic and the Brazilian coast (Joyeux et al., 2001; Floeter et al., 2007) despite the soft barrier of Amazon river output (Rocha, 2003). The coastal region of Brazil has been proposed as a single biogeographical province in which many species of common, frequently observed reef fish are distributed along the entire coast of Brazil (Joyeux et al., 2001; Araújo et al., 2020).

The two marine protected sites with Notake rules selected for study were a) the waters surrounding AI, where AI is equivalent to a category II (National Park) from the International Union for Conservation of Nature (IUCN), with the surrounding waters established as a NTZ by a fisheries ordinance (Portaria SUDEPE 56) in 1983, and b) PI, belonging to Tupinambás Ecological Station (ESEC Tupinambás), created in 1987, where human presence is forbidden and equivalent to category la (Strict Nature Reserve) from the IUCN (Dudley et al., 2013). Two Take Zones, areas where fishing is unrestricted, were selected as comparison for evaluation, chosen for having similar bottom depth ranges, similar hydrodynamic exposure, and proximity to the NTZs: Mar Virado Island (MV) and Ponta do Espia (PE) (Fig. 1). The habitats at the four sites were physically similar: semi-protected areas consisting of turf-covered rocks and occasional boulders, with the presence of some palythoa coverage, colonies of Mussismilia hispida, and the occurrence of sea


Figure 1. Study area and the sample locations. The triangles denote NTZ sampling sites: Anchieta Island (red) and Palmas Island (yellow). The circles denote samples in Take Zones: Mar Virado Island (blue) and Ponta do Espia (green). The dashed lines surrounding the islands indicate the No-take Zones; the dashed line around Palmas Island is protected as part of Tupinambás Ecological Station; the dashed line delineates the Portaria SUDEPE 56 protection zone surrounding Anchieta Island State Park.
urchins, such as Echinometra lucunter observed at some sampling points. Each site was sampled six times, using randomly selected sampling locations during daylight hours. One sample was lost at PI, resulting in a total of 23 collection points among all sites (details in Table SM 1).

## Sampling method

The samples were collected using two Baited Remote Underwater Video (BRUV) structures deployed almost simultaneously at nearby locations in randomly assigned pairs. Each BRUV was baited with approximately 400 g of Sardinella brasiliensis (whole) inside a mesh plastic bag (3 cm mesh). The bait was fixed 1.5 meters away from the camera (GoPro Hero 3) on a polyvinyl chloride (PVC) pipe, 2.5 cm in diameter. The BRUV structure was a trapezoid made of steel rebar, 0.8 cm diameter, with a square base and attached ballast for added stability. The GoPro was installed inside the pyramid, 0.5 m from the base, at the same height as the PVC bait pole, showing a wide angle, horizontal field of view, with the bottom visible. The BRUV structure was easily placed on and removed from the sea floor using a rope tied to a buoy, lowered from a small boat.

At each sample location, the BRUV structure was placed six times, sampling 70 minutes of
video. The first 10 minutes of each video were discarded to avoid interference from equipment placement and boat noise, resulting in one hour of useful video per sample. As a sample at PI was lost, a total of 23 hours of video from the 23 samples was analyzed.

The samples were collected over five consecutive days in March of 2016, aiming to be as close to synoptic as possible. Samples were collected between 8:30 AM and 6:00 PM, with all days having similar light conditions. The four to six sites sampled per day were randomly distributed among the zones to prevent habitat sampling bias. Any simultaneously collected samples were separated by at least 100 m to avoid bias of the same individuals visiting both BRUVs.

The intent of the video samples was to record fish from rocky reef environments. For this, BRUVs were installed either directly in the rocky environment or in the adjacent sandy area surrounding the reef edge, in both cases < 5 m from the other environment type to ensure sample similarity. BRUVs were placed at depths ranging from five to twelve meters in areas protected from waves. Secchi depth measurements were collected from each site before sampling to assess visibility conditions.

## Video analysis

With the help of identification keys (Luiz Jr. et al., 2008; Humann and DeLoach, 2014), a single annotator conducted all the video analysis to maintain consistency in the accuracy of fish identification and counting. Species identification, used for assessments such as richness, included all fish within the camera field of view, rather than only those attracted to the bait. Abundance was estimated by counting the maximum number of individuals from the same species that appeared simultaneously in one frame (Nmax) of video, then using the largest Nmax recorded for each species once the whole video was analyzed; this avoided counting the same individual more than once (Unsworth et al., 2014). All individuals were identified to the lowest possible taxonomic level. The trophic categories were defined as carnivore, roving herbivore, territorial herbivore, mobileinvertebrate feeder, sessile-invertebrate feeder, piscivore, planktivore, and omnivore (Floeter et al., 2007; Luiz Jr. et al., 2008; IUCN, 2021; Froese and Pauly, 2021).

## Statistical analysis

To assess the effectiveness of short period BRUV deployments in distinguishing fish communities between Take Zones and NTZs, the four sites were analyzed nested within each protection status [PE/MV(Take Zones); Al/ PI(NTZ)].

Ecological descriptors such as abundance ( n ), species richness ( S ), Shannon's diversity index ( $H^{\prime}$ ), and Pielou's evenness ( $J^{\prime}$ ) were calculated and tested for differences among sites and between protection statuses using a 2-way nested ANOVA. These variables have been log-transformed (log $x+1$ ) to meet normality and homoscedasticity assumptions. Differences between pairs were tested with a post-hoc HSD-Student's test.

Differences between fish community composition between zone protection statuses ( $Z$ ) and sites ( Si ) were tested using a 2-way nested permutational multivariate analysis of variance (PERMANOVA) using Bray-Curtis dissimilarity measure. Due to low possible permutations for achieving suitable $p$-values, these probabilities were adjusted using the Monte Carlo approach.

Similarity percentage analysis (SIMPER) was used to evaluate species contribution to the community similarity within each site and to identify the species that contributed the most to differences between sites and protection status types. A non-metric multidimensional scaling (nMDS) plot was used to represent the similarities among samples, comparing sites and protection status. Species abundance was square-root transformed to weigh down the influence of the most abundant species in the multivariate analyses. Multivariate community analyses were performed using Primer 6 + Permanova software (Clarke et al., 2014), and parametric tests were run on JMP®, Version 9. SAS Institute Inc., Cary, NC, 1989-2019.

The efficiency o $f t$ his "snapshot" B RUV assessment method and the adequacy of the sample size in sampling the fish community within each protection status were tested with rarefaction curves using the S(est) estimate (formerly Mao Tau), pooling the data into Take or No-take groups and using the "randomize samples with substitution" option in EstimateS 9.1.0 (Colwell, 2013) along with $95 \%$ confidence intervals. This allowed determination of the expected number of new species with further BRUV sampling for both the Take and No-take zones. For curves that approach the asymptote, sample diversity is approaching true diversity (Lande et al., 2000), with the understanding that the Sobs method provides a very conservative estimate. Higher curves indicate higher diversity, with curve intersection indicating the sample with lower richness has higher diversity (Lande et al., 2000). Curves with $95 \%$ confidence intervals that do not overlap indicate significant differences at a level of $5 \%$ among the expected diversities (Chao and Jost, 2012).

To evaluate whether the 60 -minute BRUV duration was sufficient, $r$ esults $f$ rom a nother BRUV study at the MV and PI sites were compared (Rolim et al., 2019). That study used stereo-BRUV with a longer sampling duration, 90 minutes, and twice as many deployments, with some sampling periods fortuitously overlapping in time between studies. The sampling effort of each study was compared, as were rarefaction curves, to assess
whether increasing the recommended deployment time would result in any appreciable benefit.

The effectiveness of using only short period BRUV as a low-cost alternative to comprehensive long-term survey methods was evaluated in the waters surrounding AI. A long-term survey that included the use of diving, snorkeling, BRUV, scientific fishing, and bottom trawling from ships was presumed to have generated a comprehensive list of all species present, that could then be compared to results from our shortterm BRUV. Using surveys spanning >20 years, the species recorded by the comprehensive survey were measured by multiple research teams that spent 142 hours on snorkeling and diving, with additional hours spent on trawling and other non-diver survey methods, including their BRUV implementation (Souza et al., 2018). The list of species detected was compared to those recorded by this rapid-implementation, low manpower BRUV survey results with six hours of tape collected at Al. To normalize data from these different sources, survey effort was assessed using the hours of BRUV tape in this study in comparison to the diving hours reported in the comprehensive study, disregarding the further unknown number of hours spent trawling or for BRUV recordings.

Species from both studies were indexed both by average adult body size for the species and dominant feeding preferences to look for biases in the BRUV implementation versus the comprehensive study. Because size cannot be determined from single-camera BRUV or for data collected in the other study being compared, the size for each species was classified according to the average adult size from reference publications (Froese and Pauly, 2021). This generalization was made for comparison to the long-term study at the same site, noting that body sizes were also not available for that comparison study. While this does not account for the natural variation in body size among a single species, the average body size should be the same for any species when comparing to the Al site as a whole.

In terms of financial costs, initially creating a BRUV structure was $\sim \$ 20$ for the structure itself, a negligible cost for bait, and would be $\sim \$ 96-580$ for a Go Pro camera, depending on the model selected.

Use in the field for this study required five days of boat rental and operation by a single snorkeler. In comparison, a basic underwater survey would require daily SCUBA gear rental for two divers ( $\sim 40$ per day per person, plus added costs for the additional tanks or fills if available) and 7-8 days of boat rental to cover the same sites. In LMIC regions, there is also the logistical complication of low availability of this type of equipment near some of the potential sites requiring monitoring, thus arranging gear rentals and sufficient tanks cannot always be achieved with less than a few days' notice.

## RESULTS

## Evaluation of Take and No-take Zones

During the 23 successful BRUV deployments, 737 individuals were recorded, comprising 51 fish species. The highest numbers of species were recorded at the two NTZ sites: 34 at AI and 27 at PI (Fig. 2, Table SM 2). Among the tTake zZone sites, nineteen species were recorded at MV and seven along the mainland site Ponta do Espia (PE) (Fig. 2).

NTZs were significantly richer in species (S) and abundance ( n ), and more diverse ( $\mathrm{H}^{\prime}$ ) when compared to take areas (Fig. 3; Table 1). PE had the lowest species richness, diversity, and abundance among all sites. MV was midway between PE and the two NTZs for these parameters. Of the NTZs, Al had higher richness and diversity but lower abundance than Pl (Fig. 2).

Communities from sites classified as NTZs differed from Take Zones (PERMANOVA Pseudo-F $=3.4144, \mathrm{df}=3, \mathrm{p}(\mathrm{MC})=0.031$ ) (Supplement 1). Fish assemblages at sites with the same protection status did not differ (PERMANOVA Pseudo-F = $1.2014, \mathrm{df}=998, \mathrm{p}(\mathrm{MC})=0.286)$.

Communities under different protection status differed in at least $70 \%$ of their species composition (Fig. 4). Communities at MV were more heterogeneous, with more diverse samples (MV1, MV2, and MV4) resembling those from protected areas, while low diversity samples harbored two species (MV3 and MV5) or one individual from one species (MV6 - Balistes capriscus). The samples Al1 and Pl1 (56\%


Figure 2. Bubble plot showing both abundance (n) and Shannon diversity ( $\mathrm{H}^{\prime}$ ) by site, with increasing bubble size indicating increasing abundance and the transition from green to red indicating increasing Shannon diversity. Anchieta Island (AI) and Palmas Island (PI) are No-take Zones; Mar Virado (MV) and Ponta do Espia (PE) are Take Zones. The samples from PI6 and PE6 had no data.


Figure 3. Average species richness (S; A), abundance (n; B), Shannon's diversity index (H'; C) and Pielou's evenness (J'; D) for the No-take Zones Anchieta Island (AI) and Palmas Island (PI) and the fished Take Zones Mar Virado (MV) and Ponta do Espia (PE). Different letters above each column indicate significant differences in the post-hoc HSD-Student's $t$ -

Table 1. Results of the 2-way nested ANOVA for ecological indexes ( S - species richness, n - abundance, $\mathrm{H}^{\prime}$ Shannon diversity index, and J'- Pielou's evenness) among sites and protection statuses (Take and No-take). Asterisks indicate p-values < $5 \%$ probability. $Z$ indicates the zone's protection status and Si indicates sites nested within each protection status.

| Ecological index | Source | df | Mean Square | F | p |
| :---: | :---: | :---: | :---: | :---: | :---: |
| S | Z | 1 | 7.10 | 19.92 | $<0.01^{*}$ |
|  | $\mathrm{Si}[\mathrm{Z}]$ | 2 | 0.39 | 1.12 | 0.34 |
| n | Z | 1 | 17.14 | 20.45 | $<0.01^{*}$ |
|  | $\mathrm{Si}[\mathrm{Z}]$ | 2 | 1.42 | 1.69 | 0.21 |
| $\mathrm{H}^{\prime}$ | Z | 1 | 1.24 | 8.56 | $<0.01^{*}$ |
|  | $\mathrm{Si}[\mathrm{Z}]$ | 2 | 0.08 | 0.59 | 0.55 |
| $\mathrm{~J}^{\prime}$ | Z | 1 | 0.01 | 0.52 | 0.48 |
|  | Si [Z] | 2 | 0.02 | 1.27 | 0.30 |



Figure 4. Non-metric multidimensional scaling (nMDS) plot showing the differences in the species composition of the fish assemblages among samples. Circles represent Bray-Curtis similarities over $20 \%$ (solid line) and $30 \%$ (dashed line) among samples. Take Zones (green and blue symbols) and Notake Zones (yellow and red symbols) are mostly dissimilar from each other at the $20 \%$ level. $\mathrm{Pl}=\mathrm{Palmas}$ Island, $\mathrm{Al}=$ Anchieta Island, MV= Mar Virado Island and PE= Ponta do Espia.
similarity) were grouped due to low richness (six and five species, respectively) and the presence of large Caranx latus schools in these samples, 70 individuals in Al1 and 77 individuals in PI1, decreasing the community evenness ( $\mathrm{J}=0.29$ and $J=0.25$, respectively). PE5 is an outlier relative to all samples as only two individuals from different species (Mugil curema and Diplodus argenteus) were registered for this sample. Sample Al3 recorded the presence of an individual from the territorial sandy bottom grey triggerfish Balistes capriscus and a single individual Caranx latus.

The NTZs contained $82.35 \%$ ( $n=42$ ) of the total species observed, with higher average species richness, abundance, and diversity than Take Zones, in which $45.09 \%$ ( $n=23$ ) of the total species were observed (Fig. 5, Table SM 3). Besides being richer and more diverse, NTZs were also more consistent in species occurrence among samples (SIMPER average NTZ similarity $=34.56 \%$ ) than those samples from Take Zones (SIMPER average Take similarity = 22.71\%) (Fig. 5). Dissimilarities in species composition between samples from these areas were $82.48 \%$ (SIMPER dissimilarity). The


Figure 5. Total number of individuals ( $n$ ) per fish species in the four sites (No-take: AI and PI; Take: MV and PE). The order of the 20 fish species in the horizontal axis is given by the percentage of contribution of each species to the dissimilarity between Take and No-take Zones. Species ( $n=31$ ) that contributed less than $80 \%$ of the dissimilarity between these areas were pooled as "Other species".
presence of the species Caranx latus contributed most to dissimilarities between Take and No-take Zones ( $13.41 \%$ ) as well as to similarities among sites within the Take Zone, $88.39 \%$, and among NTZs, $22.96 \%$. C. latus accounted for $94 \%$ of the abundance observed from the Carangidae family, present in $89 \%$ of the video samples. Abundance in those records varied from one to a school of 77 individuals (at PI), with the other largest schools distributed among the other test sites: 71 (AI), 22 (MV), and 11 (PE) individuals.

In general, the top contributors to species composition differences between Take Zones and NTZs were Caranx latus, Haemulon aurolineatum, Abudefduf saxatilis, Epinephelus marginatus, Mugil curema, Kyphosus sp., Holocentrus adscensionis, Pomacanthus paru, Chaetodon striatus, Diplodus argenteus, and Acanthurus bahianus, accounting for $64.57 \%$ dissimilarity ( $80.26 \%$ unweighted), all more abundant in the NTZs (Fig. 5, Table SM 3). Among these species, only two of the 81 sergeant major, Abudefduf saxatilis, a mobile Pomacentridae species with
high abundance more typically associated with areas with human visitation (Ilarri et al., 2008; Feitosa et al., 2012; Albuquerque et al., 2014) individuals were found in Take Zones. For the fished dusky grouper Epinephelus marginatus, a Serranidae, only one individual was recorded in a Take Zone (MV1), versus 25 in NTZs. This fish appeared in $81 \%$ of the NTZ samples in abundances of 1-4 individuals. The squirrelfish Holocentrus adscensionis (a target of smallscale fisheries), sea chub Kyphosus sp., and angelfish Pomacanthus paru were found only in the NTZs. The white mullet Mugil curema had similar average abundance in both areas, 1.18 individuals for Take Zones and 1.91 individuals for NTZs. Analysis by site, however, revealed that individuals of this species were observed in only two samples in Take Zones (12 at MV4 and 1 at PE5), but distributed more evenly between four samples at NTZ sites. Among less common species, such as Chloroscombrus chrysurus, and Stegastes variabilis, some were found only in Take Zones. These contributed $1.3 \%$ (one individual in
two Take Zone samples) and 1.07\% (a school of eleven individuals in one Take Zone sample) to the Take Zone and NTZ dissimilarity, respectively.

## Effectiveness of Short Period BRUV as an NTZ Assessment Technique

After establishing that the takeTake Zone and no take zones NTZs were distinguishable statistically, the short-period BRUV method was examined in more detail. Using datamining of results from previously published studies at some of the same sites, we assessed (1) the sufficiency of the recording time and number of samples, and (2) the percentage of species potentially present that were being detected without the supplemental use of longer-term collection methods such as UVC.

Comparing this study with a BRUV study (Rolim et al., 2019) conducted for a longer period at two of the four study sites (MV and PA ), our rapid-implementation study recorded $44.3 \%$ of total species using $28 \%$ of the survey effort. Examining the rarefaction curves to look at species by sample using the Mao Tau estimator revealed that this study is expected to detect $\sim 6$ species fewer per sample using 60 minutes versus 90 minutes. When rarefaction is reexamined using species over time instead of per sample, the curves overlap (Fig. 6).

The effectiveness of short period BRUV as a low-cost alternative to a comprehensive longterm survey was evaluated at AI, comparing the compiled species detection list (Souza et al., 2018) to the six hours of BRUV recordings collected at the same AI site. A total of 112 fish species were recorded between these two studies at AI. For the purposes of this comparison, the assumption will be made from this point on that this species total represents $100 \%$ of the fish that can be found at this site, understanding that this may be an underestimate due to undetected rare fish (Colwell et al., 2012). Of these 113, the comprehensive long-term survey observed 103 species (91.1\% of those present), while BRUV deployments in this study recorded 34 species ( $30 \%$ of species present). To normalize, survey effort for BRUV was $4.2 \%$ of the hours used in the comprehensive assessment.

For fish in the two size classes larger than $15 \mathrm{~cm}, \sim 36 \%$ of species in each class were observed by BRUV. For fish less than 15 cm , only $\sim 13 \%$ of the species were observed (Fig. 7a). Because not all fish will be attracted to the bait or presence of a structure, detection rate differences were examined according to feeding strategy. For AI, BRUV did not capture the presence of planktivorous or territorial herbivorous fish (Fig. $7 b)$. In contrast, BRUV captured $58 \%$ of the roving herbivores, $43 \%$ of the sessile invertebrate feeders, $33 \%$ of the omnivores, $39 \%$ of mobile invertebrate feeders, and $12 \%$ of piscivores.

Despite the extent of the comprehensive survey, nine species were observed via BRUV that were not recorded in the long-term diverbased survey (Table 2). The majority were larger fish (>30 cm).

## DISCUSSION

## Evaluation of Take and No-take Zones

In the studied area, human actions appear to be downsizing and homogenizing the fish assemblage (Araújo et al., 2016). Fish assemblages in NTZs were richer and harbor more individuals compared to Take Zones, as found in other studies (Worm et al., 2006; Lester et al., 2009). The NTZs accounted for $84.6 \%$ of total species abundance. BRUV identified sixteen species that appeared exclusively inside the boundaries of a protected area and seven exclusively outside. Although the species richness and abundance in Take Zones were lower, differences in diversity (Shannon) and evenness (Pielou's) between Take and NTZs were less evident or non-existent, respectively. This result indicates, besides lowering species richness, that a species turnover from commercial fishes (Silvano and Begossi, 2012) towards unfished species may be ensuing in Take Zones. Greater abundance of fisheries target species in NTZs was found in the region of the study area by Rolim et al. (2019), but differences in the abundance of non-target species in NTZs versus Take zones were not observed.

The lowest species richness and abundance were found at PE. Greater species richness and abundance for one of the study's Take Zones over


Figure 6. Rarefaction curves (showing site PI here for illustration) for species detected by BRUV, illustrating the species observed S(est) / Mao Tau, using sample substitution with $95 \%$ confidence intervals. The species observed in each sample for the present study and that of Rolim et al., (2019) are compared using the number of BRUV samples and then plotted again using minutes of sampling time with the same data.to assess if the sample size of BRUV showed substantial improvement with a 90 minute vs. 60 minute duration.
the other may be partially due to a site effect. While effort was made to conduct sampling in NTZs and Take Zones with high similarity between habitats while randomly choosing areas at the interface of soft and hard substrates, the MV Take Zone is on
an island as are the NTZs, while the PE Take Zone is attached to the mainland, thus located closer to urban developed areas with greater anthropogenic pressures. PE may receive more fishing effort than MV ; the latter is only accessible by vessel and is


Figure 7. Species Observed at the Anchieta Island site, grouped by Size Class (a) and by Feeding Preference (b), showing this rapid BRUV implementation compared to available data from a long-term multi-method long term diving and trawling survey at the No-take Anchieta Island site (Souza et al., 2018). Total column height indicates the cumulative number of species observed in both studies, with the lower dark section indicating the number recorded by BRUV. Feeding preferences listed are CAR = Carnivores, MIF = Mobile invertebrate feeders, OMN = Omnivores, PIS = Piscivores, PLK = Planktivores, ROVH = Roving herbivores, SIF = Sessile invertebrate feeders, and TERH = Territorial herbivores.
more distant from human occupation, so access to these fishing grounds is more difficult (Floeter et al., 2006). Greater fishing effort is related to decreased fish abundance and richness of target species. Furthermore, the fish assemblages respond to a variety of other direct and indirect factors from human population density and proximity, such as tourism and harbor activities, sedimentation, habitat degradation, and sewage
(Richards et al., 2012). The species richness of target and non-target species and the abundance of non-target species increase with distance from the São Paulo coast, coinciding with the distance from human occupation (Rolim et al., 2019).

The abundance and richness of fishes at MV was midway between the other Take Zone, PE, and the two NTZs. The lower diversity at PE does not appear to be an artifact of sampling;

Table 2. List of species recorded by BRUV that were not detected in the long-term multi-method diving and trawling survey at the Anchieta Island site (Souza et al., 2018), indicating feeding strategy and the average adult size class for those species.

| Species unique to BRUV | Feeding Strategy | Size Class cm |
| :---: | :---: | :---: |
| Pomacentridae (fam.) | Roving herbivore | $<15$ |
| Caranx hippos | Carnivore | $>30$ |
| Selene vomer | Carnivore | $>30$ |
| Lagocephalus laevigatus | Carnivore | $>30$ |
| Balistes capriscus | Mobile invertebrate feeder | $>30$ |
| Halichoeres radiatus | Mobile invertebrate feeder | $>30$ |
| Sphyraena guachancho | Piscivore | $>30$ |
| Sparisoma amplum | Roving herbivore | $>30$ |
| Sparisoma axillare | Roving herbivore | $>30$ |

while turbidity does reduce the observed area and lower the ability to observe fish in the background that did not directly access the bait, Secchi depth measurements indicate very similar visibility between MV and PE sites. But it is important to consider the lack of physical and biological variables that could influence the composition of the fish assemblages of each site, including the NTZs sites, like exposure to waves, currents, topographic complexity, recruitment from planktonic larvae, interactions among the species, and the history of disturbance - e.g. physical, biotic, and even fishing (Ferreira et al., 2001; Floeter et al., 2006; Pinheiro et al., 2010; TeixeiraNeves et al., 2015).

Between the NTZ sites, Pl is the most restrictive towards human access (only permitted for scientific purposes), while tourism is permitted at Al. The effect of anthropogenic impact differences between these areas was not clearly identified using this rapid BRUV assessment technique. The species richness, diversity, and evenness at Al is larger, with higher variation between samples for richness and diversity. Meanwhile, the abundance of fish is higher at PI (Fig. 7), again with higher variation between samples at AI. In this case, while the averages for diversity, richness, and abundance are similar, tourism impacts could be partly responsible for the higher variability between samples at AI. These differences might also be due to the heterogeneity in habitat complexity between BRUV sampling locations at AI, which had a larger overall protection area, an
effect that could be tested in the future with more BRUV samples at each site (Rolim et al., 2019) or by collecting more physical and biological data from the environment.

## Effectiveness of Short Period BRUV as an NTZ Assessment Technique

The efficac yof alow-cost, low-manpower sampling method was demonstrated for monitoring the effectiveness of protected areas in LMIC regions with limited resource availability, allowing a more even geographic distribution of such surveys along the entire coastline in these regions than currently exists. Regions with sites that have rapid variations in turbidity and visibility could also benefit from BRUV surveys, as the method can attract the fishes to the field view and be rapidly implemented on favorable days. The potential for rapid variations in visibility conditions found in the study region can potentially hamper effective visual identification, so techniques that can attract the fishes to the field view and be rapidly implemented on favorable days, such as BRUV, have an advantage.This study used BRUV operated by only two boat-based researchers to survey the sites of interest quasi-synoptically, rather than a resource-intensive Underwater Visual Census. While BRUV is known to detect fewer species than UVC (Francour et al., 1999; Stobart et al., 2007; Lowry et al., 2011; Langlois et al., 2020), it has been demonstrated to effectively assess the presence of reef-associated species (Lowry
et al., 2011). Regardless of method, marine reserve studies may underestimate species richness due to the typically small sampling area (Lester et al., 2009). To account for the inherent species undersampling using BRUV, NTZ effectiveness was successfully measured by comparing the species to those found in nearby Take Zones, finding a $29.4 \%$ increase in richness for protected over unprotected areas. On a global scale, richness was $21 \%$ higher inside NTZs (Lester et al., 2009), suggesting that this rapid BRUV method was successful in capturing a reasonable subset of the species present, sufficient for NTZ success evaluation.

BRUV can record species from multiple trophic categories, from roving and territorial herbivores to omnivores and piscivore fishes (Cappo et al., 2007; Andrade-Brown et al., 2016). While carnivore species would be recorded due to attraction to the bait plume, other trophic category species are recorded because of attraction to the BRUV structure, to the activity of other fishes feeding and aggregating around the BRUV, occupation of the territory within the field of view of the camera, and species that are indifferent to the BRUV, but present in, or passing through, the field of view during the deployment. Herbivorous species tend to be visible 4-7 m beyond the bait basket grazing or swimming by (Harvey et al., 2007). The absence of planktivorous or territorial herbivorous in our data could be because the low visibility makes it difficult to identify individuals that are far away, thus reducing the sampling distance beyond the bait. Fish smaller than 15 cm also have their identification impaired by visibility. This may account for differences in detection rate among feeding strategy categories found by our rapid BRUV implementation. Increasing the sampling time in future implementations would increase the likelihood that these individuals would eventually pass close enough to the camera to be identified.

BRUV captured the presence of species below and above 15 cm with different levels of success, $13 \%$ and $>36 \%$ respectively, when looking at the AI dataset. When examining a set of globally distributed NTZs for richness, comparing
individuals $>25 \mathrm{~cm},<25 \mathrm{~cm}$, and both sets of individuals jointly, species richness increased only for individuals $>25 \mathrm{~cm}$ (Edgar et al., 2014). This indicates a food chain effect: increases in biomass and richness for these larger fish coincide with decreases in richness and biomass of smaller individuals, top-down control (Roberts and Polunin, 1991). The bias towards detection of fish larger than 15 cm therefore is not likely to affect evaluation of NTZ success. BRUV also exhibited a bias against certain feeding behaviors, as it did not detect any of the planktivores or territorial herbivores noted in the comprehensive multimethod survey at AI. A previous study comparing BRUV and UVC noted a bias against detection of cryptic species, as they live within the reef structure itself (Lowry et al., 2011).

Future diver-based surveys, such as an Underwater Visual Census, should consider using BRUV as an additional tool. The nine species recorded by BRUV in the present study but not by the more extensive underwater survey compiled from multiple survey types for Al could be explained by a variety of reasons, some inherent to differences between the two methods (Lowry et al., 2011), such as avoidance of divers and snorkelers or differences in attraction to bait. The low detection rate of the overall number of species present in the area ( 24 of 113) is partially due to the rapid nature of this implementation of BRUV, conducted during a single week to be nearly synoptic, as well as sampling biases of the BRUV method previously noted by others (Francour et al., 1999; Stobart et al., 2007; Langlois et al., 2020). The underwater survey used 142 hours of diving whereas the present study used only 6 hours of video at the same site, meaning that with $4.2 \%$ of the survey effort, the BRUV method detected $21.2 \%$ of the species at the site.

For future implementations, 90-minute deployments are recommended to detect a greater number of species in general. This stems from a comparison between this study and that of Rolim et al. (2019) conducted at the MV and PI sites. Examining the rarefaction curves using species observed vs. samples, the Mao Tau estimator indicates that the observations from this study fall below that of Rolim et al. (2019). When
the Rarefaction curve is examined using species observed vs. time, the curves overlap and follow the same path. This indicates that the low-cost BRUV sample technique used in this research has similar success to a high-cost stereo-BRUV structure when examined using the amount of time recorded. The increase in recording time would also increase the sampling effort where simultaneous replications are not ideal, in small sample areas. To adapt the low-cost technique to a 90-minute sample time, the bait housing should be modified to a container with increased difficulty for entry, such as a cage made of steel or hard plastic, to increase the bait duration.

## Using BRUV to evaluate NTZ EFFECTIVENESS FOR INDIVIDUAL SPECIES

In general, NTZ effects on a population are a complex relationship that varies by species, depending on species characteristics such as history of fishing pressure, trophic level, mobility in the environment and reproductive behavior (Jennings,2000;Claudetetal.,2008;Babcocketal., 2010). Effects also depend on NTZ characteristics such as size, period of implementation, habitats preserved, and their connectivity with other NTZs and with Take Zones (Edgar et al., 2014). This rapid BRUV implementation can be used by managers to quickly identify target species showing possible benefits from NTZs for further in-depth investigation, such as species with risk factors for future vulnerable or threatened status, such as endemism or targeting by ornamental fisheries (Bender et al., 2013) and long-term monitoring. If the goal, however, were to determine the specific effects of distinctions between the two NTZ sites rather than determine overall effectiveness, a comprehensive diving census or long-term, high sample number BRUV study would be required to examine these factors simultaneously (Mallet and Pelletier, 2014).

The distance for ensuring the independence of the replicate samples is a function of the mobility of the species, feeding activity, habitat, seabed currents, soak time, and plume dispersion of the bait (Cappo et al., 2001; Bond et al., 2018; Langlois et al., 2020). Cappo et al., (2004) formalized relations of these variables in one
equation, where the effective range of attraction is a function of soak time, fish velocity, and current velocity. Our sampling design used the minimum distance of 100 m between the replicates. It would be reasonable to use the calculated distance of 560 m for 70 minutes of soak time, $0.6 \mathrm{~ms}^{-1}$ of fish velocity, and $0.2 \mathrm{~ms}^{-1}$ of current velocity. Despite that, experiments using BRUV suggested that large schools of carangids could cover one kilometer of seabed in 90 minutes (Cappo et al., 2001). Our study registered large schools of this family, but was not recorded on both BRUVs that were implemented simultaneously. Therefore, there is no evidence that our samples replicates were not independent with a minimum of 100 m spacing, but in future BRUV studies it is still recommended to use greater distances (Langlois et al., 2020) as a precaution.

This rapid BRUV implementation proved adequate to distinguish clear differences between protected and fished areas, including elucidating interesting details regarding effects on particular species. Species of commercial interest, such as M. curema, C. latus and E. marginatus, showed greater abundances in NTZs.

SIMPER analysis in this study indicated that the presence of the Carangidae Caranx latus contributed most to the dissimilarity between NTZs and Take Zones. Carangids were shown to benefit from other NTZs in the region (Rolim et al., 2019). The size and connectivity of the NTZs can positively influence their biomass (Edgar et al., 2014). Their schooling behavior was observed at one sample in each study location, but with an abundance three times greater at the NTZ sites. This species is highly mobile (Chapman and Kramer, 2000), which could provide the benefit of biomass export beyond the boundaries of NTZs (Gell and Roberts, 2003). The benefit of an NTZ for a highly fished and mobile species occurs only while it is inside the protected area (Wetherbee et al., 2004; Kerwath et al., 2009; Pinheiro et al., 2010). The NTZ not only provides protection, particularly during the more vulnerable stages of life, but also increased feeding opportunities. C. latus, for instance, can feed by following other fish species, such as Bodianus rufus and Halichoeres poeyi, and preying upon the smaller fish startled
by their foraging activities (Silvano, 2001). NTZ effectiveness thus also depends on the health of populations of species that fulfil this function (Edgar et al., 2014). H. poeyi were spotted both in Take Zones (three in MV) and NTZs (two per area). B. rufus individuals were recorded only in NTZs (four in PI and two in AI), suggesting possible increased feeding opportunities in NTZs for C. latus over Take Zones. The white mullet Mugil curema is a highly sought species via small-scale net fisheries in Brazil (Mendonça and Bonfante, 2011; Pinto et al., 2015). Kyphosus sp. is another regularly fished species (Pinheiro et al., 2010) solely registered at NTZs that can take advantage of these protected areas to forage on algae undisturbed by fishing activities (Silvano and Güth, 2006). If NTZ effectiveness for $C$. latus were a specific goal, first using this rapid BRUV implementation would lead managers to target further investigations towards variations in school sizes and in populations of utilized forager species through increased sampling.

The high abundance of the mobile $A$. saxatilis almost exclusively in NTZ's in this study would also merit further investigation to explore both tourist visitation frequency in the NTZs and dominant surface cover variations between sites. A. saxatilis is found on reefs across Brazil (Molina et al., 2006; Araújo et al., 2020) but expected in greater abundance where areas have had recent or ongoing tourist visitation (llarri et al., 2008). Being found almost exclusively in the NTZs would thus prompt exploration of human visitation frequency in the NTZs. However, the presence of abundant $A$. saxatilis could also indicate a potential difference in reef cover composition between sites, being more commonly observed in reef areas with high proportions of the soft coral Palythoa caribaeorum rather than macroalgal cover in Brazil, for instance (Francini-Filho and Moura, 2010). This result would prompt exploration of differences in fish composition in relation to habitat surface cover, requiring more study sites in an expanded region if deemed of interest. The effectiveness of rapidimplementation BRUV at detecting differences between Take and No-take Zones in this study suggests that using this method at a larger number of sites in combination with photoquadrats or Diver

Operated stereo-Video (stereo-DOV) samples of bottom cover before deployment would be an effective yet low-cost method of assessing this phenomenon if deemed of interest.

For evaluation of target species with high fidelity to chosen areas, a rapid BRUV study including site comparison may be sufficient without further intensive investigations. The slow-moving dusky grouper Epinephelus marginatus, a Serranidae, is considered overexploited in Brazil, with prohibitions against fishing, transport, handling, storage, and marketing and globally categorized as vulnerable by the IUCN (Pollard et al., 2018). Typically hiding under rocks in a single area, E. marginatus benefits from NTZ protection from fishing in any case where that location is within NTZ limits (Harmelin and Harmelin, 1999; Chapman and Kramer, 2000; Hackradt et al., 2014). Here, only one of the 26 individuals recorded was found in a Take Zone (MV1). In NTZs, this species appeared in $81 \%$ of the samples in abundances of 1-4 individuals, averaging 2.27 among samples. The NTZ protection effect seen here has been previously observed in other regions for Epinephelus marginatus (Edgar et al., 2014; Hackradt et al., 2014; Malcolm et al., 2015; Anderson et al., 2019) and recently by a stereo-BRUV study that included the PI NTZ site (Rolim et al., 2019), finding larger individuals inside the NTZs. Body size differences are important observations for species management, as larger body sizes suggest higher fecundity in their population given their late maturation and slow growth rate (Jennings et al., 2001; Andrade et al., 2003; Fennessy, 2006). The low mobility of the species, coupled with extreme differences in abundance between NTZs and Take Zones recorded using this implementation of BRUV, suggests that these protected areas may be effective for assisting recovery of Epinephelus marginatus.

## CONCLUSION

BRUV can be used to assess NTZ effectiveness using a low number of samples by comparing them with similar habitats in nearby unprotected areas.

This may be of particular interest in LMIC regions where funding needed for more intensive or longterm studies is not easily available. Using six BRUV deployments per site revealed higher abundance, richness, and diversity in fish populations for the No-take Zones. Because this implementation requires only a simple easily-obtainable GoPro camera and a baited steel frame, it is well suited for use from small boats in areas with little to no support infrastructure. The BRUV frame is light and compact in this implementation, thus is also recommended for areas with rapidly changing visibility conditions; it can be deployed quickly when conditions are favorable, with successful species identification in visibility as low as 4 m Secchi depth. Bias inherent in the BRUV method indicated that it should be used only in conjunction with other complementary methods if the goal is to develop a comprehensive list of all species present. Similar to a previous finding that BRUV has a low detection rate for cryptic reef species and those hiding within the reef structure itself (Lowry et al., 2011), these results indicated a bias against detection of fish $<15 \mathrm{~cm}$ and against fish that will not be attracted to the bait due to feeding behavior, such as planktivores and territorial herbivores.

Our findings support recommending BRUV for widespread use as a low cost and rapid method for long-term monitoring of NTZs as an early signal or sentinel indicator (to be complemented when appropriate) for spatial and temporal changes in fish communities and assessing the overall status of MPAs in comparison to nearby unprotected sites.

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## AUTHOR CONTRIBUTIONS

M.F.T: Field work; Formal Analysis; Investigation; Writing - original draft; Writing - review \& editing;
L.G.W.: Supervision; Formal Analysis; Investigation; Writing - original draft; Writing review \& editing;
I.C.S.C.: Conceptualization; Supervision; Field work; Investigation; Writing - original draft; Writing - review \& editing;
A.Z.G.: Formal Analysis; Investigation; Writing review \& editing;
A.T.: Supervision; Resources; Funding Acquisition; Writing - review \& editing;

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Table SM 1. Results of the 2-way nested permutational multivariate analysis of variance (PERMANOVA) using Bray-Curtis distances testing for differences on the composition of fish assemblages between Protection Status Areas (Z) and among Sites within each Protection Status Areas (Si[Z]). P-values were adjusted using the Monte Carlo approach $[p(M C)]$. Asterisk indicates $<5 \%$ probability.

| Source | df | SS | MS | Pseudo-F | p (MC) |
| :---: | :---: | :---: | :---: | :---: | :---: |
| Z | 1 | 11188 | 11188 | 3.41 | $0.03^{*}$ |
| Si[Z] | 2 | 6553.3 | 3276.6 | 1.20 | 0.28 |
| Res | 18 | 49094 | 2727.4 |  |  |
| Total | 21 | 66164 |  |  |  |

Table SM 2. Protection status, geographic coordinates, depth (in meters), species richness (S), abundance ( n ), Pielou's evenness ( $\mathrm{J}^{\prime}$ ) and Shannon's diversity ( $\mathrm{H}^{\prime}$ ) of each site (AI = Anchieta Island; MV = Mar Virado Island; PE = Ponta do Espia; $\mathrm{PI}=$ Palmas Island). Secchi depth is listed as bottom depth at sites where visibility exceeded bottom depth. ${ }^{\dagger}$ indicates a sample that recorded no fish, likely due to nearby boat noise. $\ddagger$ indicates a lost sample.

| Protection status | Site | Sample | Latitude (S) | Longitude <br> (W) | Depth <br> (m) | Secchi <br> Depth <br> (m) | Species richness <br> (S) | n | Pielou's evenness <br> (J') | Shannon's diversity ( $\mathrm{H}^{\prime}$ ) |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Take | MV | 1 | 23³3'47.9" | $45^{\circ} 09{ }^{\prime} 8.8{ }^{\prime \prime}$ | 8.8 | 8.8 | 10 | 33 | 0.76 | 1.76 |
|  |  | 2 | $23^{\circ} 33^{\prime} 40$ " | $45^{\circ} 09{ }^{\prime} 16.4{ }^{\prime \prime}$ | 6.5 | 6.5 | 8 | 10 | 0.97 | 2.03 |
|  |  | 3 | $23^{\circ} 33^{\prime} 35{ }^{\prime \prime}$ | $45^{\circ} 09^{\prime 26.9 "}$ | 6.0 | 4.5 | 2 | 23 | 0.26 | 0.18 |
|  |  | 4 | 23³3'40" | $45^{\circ} 09^{\prime} 31{ }^{\prime \prime}$ | 5.0 | 4 | 6 | 19 | 0.69 | 1.23 |
|  |  | 5 | 23³3'47.1" | $45^{\circ} 09^{\prime} 35.9{ }^{\prime \prime}$ | 5.0 | 4 | 2 | 4 | 0.81 | 0.56 |
|  |  | 6 | 23³3'49.7" | $45^{\circ} 09^{\prime} 39.2^{\prime \prime}$ | 6.0 | 4 | 1 | 1 | - | - |
|  | PE | 1 | 23³1'02.7" | 45 ${ }^{\circ} 04^{\prime} 49.6 "$ | 7.0 | 5 | 1 | 4 | - | - |
|  |  | 2 | 23³1'14.1" | $45^{\circ} 04^{\prime} 53.5^{\prime \prime}$ | 6.7 | 4.5 | 2 | 2 | 1.00 | 0.69 |
|  |  | 3 | 23³0'29.2" | $45^{\circ} 04^{\prime} 40.5^{\prime \prime}$ | 5.5 | 4.5 | 1 | 10 | - | - |
|  |  | 4 | 23³0'25.9" | $45^{\circ} 04{ }^{\prime} 36.5^{\prime \prime}$ | 7.0 | 5 | 4 | 12 | 0.71 | 0.98 |
|  |  | 5 | 23³1'02.2" | $45^{\circ} 05^{\prime} 01.9^{\prime \prime}$ | 5.0 | 5 | 2 | 2 | 1.00 | 0.69 |
|  |  | $6{ }^{+}$ | $23^{\circ} 31^{\prime} 0.6{ }^{\prime \prime}$ | $45^{\circ} 05^{\prime} 06.4{ }^{\prime \prime}$ | 7 | 5 | - | 0 | - | - |
| No-take | AI | 1 | 23³1'38.2" | $45^{\circ} 03^{\prime} 34.9{ }^{\prime \prime}$ | 5.7 | 4 | 6 | 81 | 0.31 | 0.55 |
|  |  | 2 | 23³1'36.4" | $45^{\circ} 03^{\prime} 30{ }^{\prime \prime}$ | 6.7 | 6 | 18 | 44 | 0.89 | 2.58 |
|  |  | 3 | 23³1'41.4" | 45 $04^{\prime} 41.3^{\prime \prime}$ | 5.5 | 5.5 | 2 | 2 | 1.00 | 0.69 |
|  |  | 4 | 23 $31{ }^{\prime} 42.8{ }^{\prime \prime}$ | 4504'33.3" | 6.0 | 6 | 14 | 46 | 0.86 | 2.28 |
|  |  | 5 | 23³1'39.6" | 45º3'24.9" | 8.2 | 8 | 19 | 42 | 0.87 | 2.57 |
|  |  | 6 | 23³1'40.3" | $45^{\circ} 03^{\prime} 16.5^{\prime \prime}$ | 7.0 | 7 | 14 | 44 | 0.87 | 2.30 |
|  | PI | 1 | 23³2'39.7" | $45^{\circ} 01^{\prime} 38{ }^{\prime \prime}$ | 6.0 | 6.5 | 5 | 86 | 0.30 | 0.48 |
|  |  | 2 | 23³2'43.4" | 4501'41.2" | 6.4 | 6.4 | 11 | 47 | 0.55 | 1.31 |
|  |  | 3 | 23³2'45.7" | 45 ${ }^{\circ} 01^{\prime} 47.7^{\prime \prime}$ | 11.0 | 10 | 13 | 49 | 0.85 | 2.18 |
|  |  | 4 | $23^{\circ} 32^{\prime} 47{ }^{\prime \prime}$ | $45^{\circ} 01^{\prime} 52.6^{\prime \prime}$ | 8.0 | 8 | 15 | 87 | 0.68 | 1.84 |
|  |  | 5 | 23 ${ }^{\circ} 2^{\prime} 48.9{ }^{\prime \prime}$ | 4501'56.2" | 8.0 | 8 | 15 | 89 | 0.75 | 2.03 |
|  |  | $6^{\ddagger}$ | 23³2'50.6" | $45^{\circ} 01^{\prime} 58.2^{\prime \prime}$ | 10 | 10 | - | - | - | - |

Table SM 3. Dissimilarity between the composition of fish assemblages from Take and No-take Zones from Similarity Percentages (SIMPER) analysis. The average Bray-Curtis dissimilarity between Take and No-take Zones is 82.48 . Species are listed in decreasing order of percentage contribution to the dissimilarities between protection status areas.

| Species | Average abundance |  | Dissimilarity |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Take | No-take | Average | Diss/SD | Contribution |  |
|  |  |  |  |  | \% | $\begin{gathered} \text { Cumulative } \\ \% \end{gathered}$ |
| Caranx latus | 1.78 | 2.88 | 11.06 | 0.77 | 13.41 | 13.41 |
| Haemulon aurolineatum | 0.56 | 2.87 | 9.70 | 1.29 | 11.75 | 25.17 |
| Abudefduf saxatalis | 0.18 | 1.89 | 6.21 | 1.09 | 7.53 | 32.70 |
| Epinephelus marginatus | 0.09 | 1.32 | 4.50 | 1.80 | 5.46 | 38.16 |
| Mugil curema | 0.41 | 0.80 | 4.07 | 0.72 | 4.93 | 43.09 |
| Kyphosus spp. | 0 | 1.08 | 3.92 | 1.19 | 4.75 | 47.84 |
| Holocentrus adscensionis | 0 | 1.15 | 3.81 | 0.97 | 4.62 | 52.46 |
| Pomacanthus paru | 0 | 0.75 | 2.77 | 0.97 | 3.36 | 55.82 |
| Chaetodon striatus | 0.09 | 0.79 | 2.63 | 1.17 | 3.18 | 59.00 |
| Diplodus argenteus | 0.09 | 0.62 | 2.43 | 0.74 | 2.95 | 61.95 |
| Acanthurus bahianus | 0 | 0.69 | 2.16 | 0.67 | 2.62 | 64.57 |
| Balistes capriscus | 0.18 | 0.18 | 2.10 | 0.42 | 2.55 | 67.12 |
| Bodianus rufus | 0 | 0.55 | 1.85 | 1.04 | 2.25 | 69.37 |
| Anisotremus virginicus | 0.09 | 0.44 | 1.82 | 0.71 | 2.20 | 71.57 |
| Halichoeres poeyi | 0.22 | 0.31 | 1.54 | 0.68 | 1.87 | 73.43 |
| Chromis multilineata | 0.09 | 0.39 | 1.37 | 0.48 | 1.66 | 75.09 |
| Priacanthus arenatus | 0 | 0.40 | 1.22 | 0.56 | 1.48 | 76.57 |
| Chloroscombrus chrysurus | 0.18 | 0 | 1.07 | 0.33 | 1.30 | 77.87 |
| Lutjanus analis | 0 | 0.27 | 0.95 | 0.60 | 1.15 | 79.02 |
| Gymnothorax funebris | 0 | 0.27 | 0.92 | 0.60 | 1.11 | 80.13 |
| Stegastes variabilis | 0.30 | 0 | 0.88 | 0.30 | 1.07 | 81.20 |
| Chaetodipterus faber | 0 | 0.27 | 0.85 | 0.60 | 1.03 | 82.23 |
| Sparisoma axillare | 0 | 0.27 | 0.85 | 0.60 | 1.03 | 83.26 |
| Haelmulon plumierii | 0 | 0.26 | 0.83 | 0.47 | 1.01 | 84.27 |
| Caranx bartholomaei | 0 | 0.18 | 0.82 | 0.31 | 1.00 | 85.26 |
| Selene vomer | 0.09 | 0.09 | 0.78 | 0.40 | 0.95 | 86.21 |
| Pseudupeneus maculatus | 0 | 0.22 | 0.75 | 0.46 | 0.91 | 87.12 |
| Haemulon parra | 0.09 | 0.09 | 0.74 | 0.41 | 0.90 | 88.01 |
| Anisotremus surinamensis | 0 | 0.18 | 0.70 | 0.46 | 0.85 | 88.87 |
| Sparisoma amplum | 0 | 0.18 | 0.65 | 0.46 | 0.79 | 89.66 |
| Odontoscion dentex | 0.13 | 0.09 | 0.63 | 0.43 | 0.76 | 90.42 |
| Halichoeres radiatus | 0 | 0.18 | 0.62 | 0.46 | 0.76 | 91.18 |
| Diplodus holbrookii | 0.18 | 0 | 0.61 | 0.42 | 0.74 | 91.92 |
| Caranx crysos | 0.13 | 0 | 0.56 | 0.27 | 0.68 | 92.60 |
| Caranx hyppos | 0 | 0.16 | 0.51 | 0.31 | 0.62 | 93.22 |
| Sphyraena guachancho | 0 | 0.13 | 0.47 | 0.31 | 0.56 | 93.78 |

Continued. Table SM 3.

| Lagocephalus laevigatus | 0 | 0.09 | 0.46 | 0.31 | 0.56 | 94.34 |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
| Seriola dumerili | 0 | 0.09 | 0.41 | 0.31 | 0.50 | 94.84 |
| Lutjanus synagris | 0 | 0.09 | 0.41 | 0.31 | 0.50 | 95.34 |
| Ogcocephalus sp. | 0 | 0.09 | 0.41 | 0.31 | 0.50 | 95.84 |
| Gymnura micrura | 0.09 | 0 | 0.41 | 0.26 | 0.50 | 96.33 |
| Scomberomorus sp. | 0.09 | 0 | 0.40 | 0.27 | 0.48 | 96.81 |
| Haemulon album | 0.09 | 0 | 0.35 | 0.28 | 0.42 | 97.23 |
| Calamus penna | 0.09 | 0 | 0.34 | 0.28 | 0.41 | 97.64 |
| Haemulon carbonarium | 0 | 0.09 | 0.29 | 0.31 | 0.36 | 98.00 |
| Sparisoma sp. | 0 | 0.09 | 0.29 | 0.31 | 0.36 | 98.36 |
| Aluterus sp. | 0 | 0.09 | 0.29 | 0.31 | 0.36 | 98.71 |
| Halichoeres cyanocephalus | 0 | 0.09 | 0.27 | 0.31 | 0.33 | 99.04 |
| Stegastes fuscus | 0 | 0.09 | 0.27 | 0.31 | 0.33 | 99.37 |
| Sphoeroides spengleri | 0.09 | 0 | 0.27 | 0.30 | 0.32 | 99.69 |
| Scarus zelindae | 0 | 0.09 | 0.26 | 0.31 | 0.31 | 100 |


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