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Intact shallow and mesophotic assemblages of large carnivorous reef fishes underscore the importance of large and remote protected areas in the Coral Triangle

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Abstract

1. Overfishing remains a threat to coral reef fishes worldwide, with large carnivores often disproportionately vulnerable. Marine protected areas (MPAs) can restore fish populations and biodiversity, but their effect has been understudied in mesophotic coral ecosystems (MCEs), particularly in the Coral Triangle.
2. Videos were analysed from baited remote underwater video systems deployed in 2016 to investigate the assemblage structure of large carnivorous fishes at shallow (4–12 m) and mesophotic (45–96 m) depths in two of the largest and most isolated MPAs in the Philippines: an uninhabited, fully no-take MPA enacted in 1988 (Tubbataha Reefs Natural Park) and an archipelagic municipality surrounded by an extensive but not fully no-take MPA declared in 2016 (Cagayancillo). Taxa focused on were groupers (Serranidae), snappers (Lutjanidae), emperors (Lethrinidae), jacks (Carangidae) and the endangered *Cheilinus undulatus* (Labridae).
3. Mean abundance and species richness were not greater in TRNP than in Cagayancillo regardless of depth despite long-term protection in the former. Limited impacts of fishing in Cagayancillo may explain this result. Differentiation of fish assemblages was evident between TRNP and Cagayancillo but more obvious between depths at each location, probably due more to habitat than MPA effects. In Cagayancillo, overall carnivorous reef fish, grouper and jack mean abundance were 2, 2 and 10 times higher, respectively, at mesophotic depths, suggesting that MCEs can serve as deep refugia from fishing.
4. These findings of differentiation between depths and higher abundance of certain taxa in mesophotic depths emphasize that MCEs are distinct from shallow reefs, serve as important habitat for species susceptible to overfishing and, thus, must be explicitly included in the design of MPAs. This study also highlights the value of maintaining strict protection of MPAs like TRNP for the Coral Triangle and an opportunity to safeguard intact fish assemblages in Cagayancillo by expanding its no-take zones.

KEYWORDS

baited camera, deep reefs, partially protected MPAs, Philippines, predatory fish, video analysis

1 | INTRODUCTION

Across the world, coral reefs and the ecosystem services they provide have declined substantially due to climate change and human activities that cause pollution, reef habitat destruction, and overfishing (Eddy et al., 2021). Marine protected areas (MPAs) are an important tool for the conservation of coral reefs and other marine ecosystems. In the Coral Triangle, the world's center of marine biodiversity, MPAs are regarded as one of the most feasible and effective approaches to secure and manage reef ecosystem services (White et al., 2014). If implemented successfully, not only do MPAs protect marine ecosystems from ecological degradation caused by human activities, but they also help to maintain ecosystem structure, function and connectivity, and preserve endangered species and overall biodiversity (Laffoley et al., 2019). MPAs are more likely to become effective if they are completely no-take, well-enforced, implemented over the long-term (>10 years), large (>100 km²), isolated from direct disturbance by humans, demographically linked with other MPAs and encompass a wide depth range (Edgar et al., 2014; Goetze et al., 2021).

The Philippines harbours the most threatened coral reefs in the Coral Triangle (Burke et al., 2012). The overall health of Philippine reefs has suffered over many decades due to poor land use practices, overfishing, destructive fishing and climate change (Burke et al., 2012; Licuanan et al., 2019). Unabated fishing pressure has already caused large declines in fish biomass and catch, which will likely further result in localized species loss, especially species that are more vulnerable to fishing (Lavides et al., 2016; Nañola et al., 2011). MPAs have become a widely accepted approach to conserve marine biodiversity and manage fisheries on coral reefs in the Philippines (Weeks et al., 2010). More than 1,800 MPAs have been enacted locally and nationally across the country in the hope of reversing these declines and protecting marine resources from further extraction and other destructive activities (Cabral et al., 2014). However, these are mostly small (<1 km²) coastal MPAs. The very limited cumulative protection Philippine MPAs provide relative to the vast coral reef area of the country can be mostly accounted for by just a few very large (>100 km²) MPAs that protect remote reefs (Weeks et al., 2010).

Coral reef fish species in higher trophic levels, specifically large carnivores, may be in greater need of MPA protection than other reef fishes (Eddy et al., 2021; MacNeil et al., 2015). Due to their larger body size, slower growth rates, later maturity, predatory nature and being highly preferred targets of fisheries, large carnivorous species such as ray-finned bony fishes (class Actinopteri) in the families Serranidae (groupers), Lutjanidae (snappers), Lethrinidae (emperors) and Carangidae (jacks) are more sensitive to overfishing (Abesamis et al., 2014). Large carnivorous reef fish species are also some of the slowest to recover in MPAs (MacNeil et al., 2015). Another large

carnivorous reef fish not included in the aforementioned taxa and that is sensitive to overfishing is the critically endangered, largest wrasse species *Cheilinus undulatus* (class Actinopteri, family Labridae) (IUCN, 2022). Compared to the other large carnivorous reef fish taxa, few studies have investigated the response of *C. undulatus* to MPA protection.

Although *C. undulatus* and fishes within the families Serranidae, Lutjanidae, Lethrinidae and Carangidae are more sensitive to overfishing and may be slower to recover in the absence of fishing, the effect of MPAs on the abundance of these large carnivores has been relatively understudied in deeper reef habitats. Mesophotic coral ecosystems (MCEs) are extensions of shallow coral reefs between depths of 30 and 150 m characterized by the presence of light-dependent corals and other associated taxa (Hinderstein et al., 2010). Mesophotic coral ecosystems are ecologically differentiated from shallow reefs in regard to the relative abundance of corals, macroalgae, sponges and unconsolidated substrata which has been shown to influence the structure of reef fish assemblages due to variations in benthic habitat and food availability from shallow to mesophotic depths (Rocha et al., 2018). Efforts to study MCEs have increased rapidly in the past decade due in part to the hypothesis that they can serve as 'deep refugia' for reef organisms from natural and man-made disturbances, but this remains open to debate (Laverick et al., 2018; Rocha et al., 2018). Higher abundance or species richness of fishery-targeted species at mesophotic depths may be considered as evidence for MCEs functioning as deep refugia from intense fishing on shallow reefs (Lindfield et al., 2016). However, the ecology of MCEs in the Philippines and other countries of the Coral Triangle remains poorly understood, including differences in human impacts between shallow and deep reefs and the effects of MPAs on many fishery-targeted species that use deeper reefs (Andradi-Brown et al., 2021). Furthermore, there has been little emphasis on protecting MCEs in this region (Weeks et al., 2010; White et al., 2014).

One of the primary reasons MCEs remain understudied is that deeper reefs are more difficult to sample than shallow reefs using diver-based methodologies (Loya et al., 2016; Rocha et al., 2018). Baited remote underwater video (BRUV) systems are a feasible means to extend ecological surveys to deeper reefs and have been proven useful in elucidating the effects of MPAs on shallow and mesophotic fish assemblages (Asher et al., 2017; Goetze et al., 2021). A BRUV system consists of bait and at least one video camera deployed on the seafloor, where the bait attracts mostly carnivorous fish to come into the field of view (Cappo et al., 2006). BRUV systems allow sampling to neither be restricted by diver safety limitations nor by behavioral changes in fishes caused by diver presence. Single-camera BRUVs can estimate fish diversity and abundance, while stereo-BRUVs can estimate fish body size and biomass, in addition to diversity and abundance (Cappo et al., 2006; Langlois et al., 2020).

This study compares the large carnivorous reef fish assemblages at two MPAs with different levels and durations of protection at shallow and mesophotic reefs: an uninhabited, fully no-take MPA enacted in 1988 [Tubbataha Reefs Natural Park (TRNP)] and an inhabited archipelagic municipality surrounded by an extensive but not fully no-take MPA declared in 2016 (Cagayancillo). Three hypotheses were tested: (1) Mean fish abundance and species richness per BRUV deployment station will be greater in TRNP than in Cagayancillo, regardless of depth; (2) fish assemblage structure will be distinct between the two locations and between depths (shallow vs. mesophotic) within the locations; and (3) mean fish abundance and species richness will still be relatively high at mesophotic depths in Cagayancillo despite decades of fishing by its residents, which may indicate MCEs serving as deep refugia from fishing.

2 | METHODS

2.1 | Study locations

Tubbataha Reefs Natural Park is a well-managed, no-take MPA, World Heritage Site, and world-renowned dive tourism destination located in the central Sulu Sea, approximately 150 km southeast of Puerto Princesa, the capital of the Palawan province (Figure 1). It was first declared as an MPA by the Philippine government in 1988 (Presidential Proclamation No. 306) because of reports of overfishing

and destructive fishing using cyanide and explosives. However, enforcement of the no-take policy did not gain traction until the middle to late 1990s (Dygico et al., 2006). The no-take core zone encompasses 970.3 km², which includes two atolls with lagoons (North Atoll and South Atoll, about 6 km apart), the submerged Jessie Beazley Reef (protected in 2006), their MCEs and surrounding deeper waters (Figure 1a,b). A wide buffer zone further protects the no-take zone from anthropogenic threats. TRNP holds extensive marine biodiversity with over 360 species of corals and 600 species of fishes (Dygico et al., 2013). It is uninhabited except for a small contingent of park rangers stationed at the southern part of the North Atoll. Regular seaborne patrols and radar surveillance are conducted by the park rangers to reduce the threat of poaching.

Cagayancillo is an archipelagic municipality of Palawan located approximately 270 km east of Puerto Princesa and 100 km northeast of TRNP (Figure 1a,b). It is composed of the main atoll of Cagayancillo, which has a lagoon surrounded by small islands, and other small islands approximately 20–60 km west and southwest of this atoll. Its population has remained relatively low in the past two decades, ranging from about 6,300 to 7,100 people (Dygico et al., 2016). Fisheries, seaweed farming and land-based farming are the primary livelihoods in the municipality. Fluctuations in seaweed farming due to external market demand are a major driver of the local population size and economy. Fishing on reefs in Cagayancillo is exclusive to residents (about 2000 fishers). Hook-and-line, nets and spearguns are the most common fishing gear. The main targets are high-value reef species

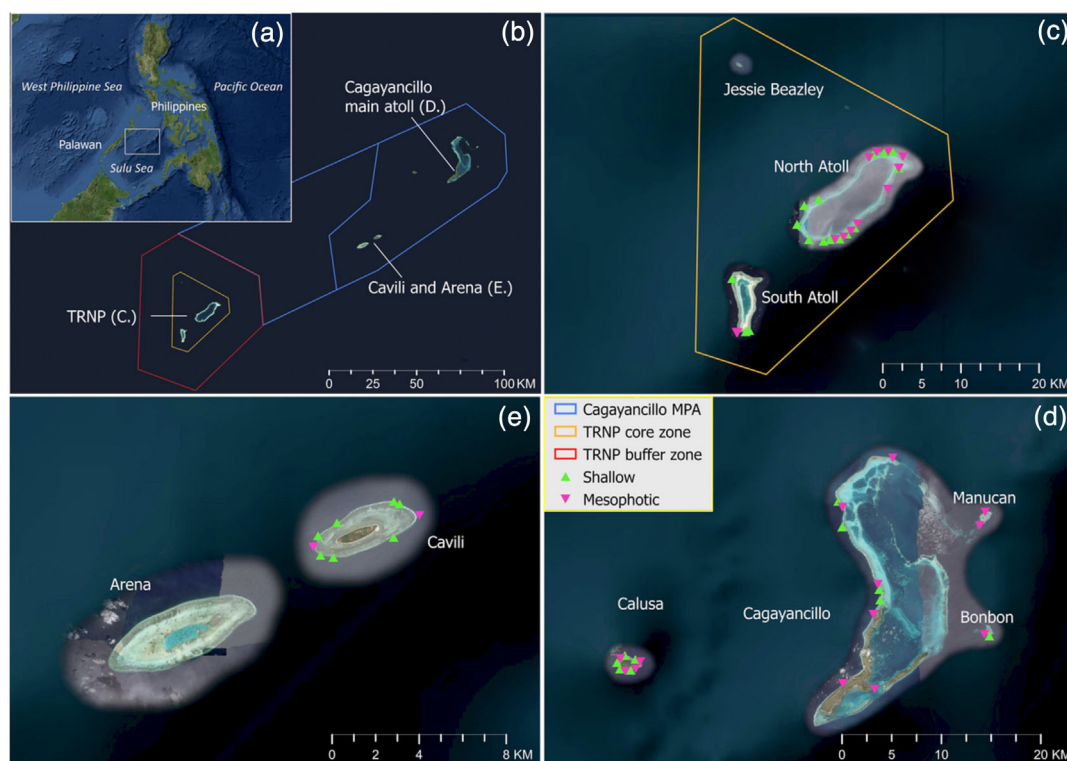


FIGURE 1 Map of the study region (a) and the two study locations (b): Tubbataha Reefs Natural Park (c), an old (created in 1988) fully no-take MPA, and Cagayancillo (d, e), a new (created in 2016) MPA that is not fully no-take. MPA boundaries and BRUV deployment stations are also shown. Map sources: Esri, Maxar, Earthstar Geographics and DeLorme.

including groupers (primarily for the live fish trade), snappers and jacks, as well as non-carnivorous fish (surgeonfishes and parrotfishes). Cagayancillo has eight small MPAs that were established by local communities at different times between 2000 and 2009, with a collective no-take area of approximately 4.5 km² that protects mostly shallow coral reefs. In September 2016, these MPAs became part of a much larger multi-use MPA that extends to deeper waters beyond the municipal boundaries, making Cagayancillo the largest managed marine area in the Philippines with a size of 10,133.4 km². However, unlike TRNP, the larger Cagayancillo MPA system allows regulated, non-destructive small-scale and commercial fishing outside of the small no-take zones. Interview surveys suggest that long before the establishment of the multi-use MPA, fishery resources in Cagayancillo had declined due to unsustainable fishing practices, including the use of cyanide for the live fish trade, explosives and the targeting of sharks (Dygico et al., 2016; Subade & Subade, 2006).

2.2 | Baited remote underwater video (BRUV)

Each BRUV unit consists of a single high-definition video camera (GoPro Hero 4) contained in a custom-made underwater housing rated to a maximum depth of 100 m (Supplementary Figure 1). Each camera was set to 1080p and 60 fps, mounted facing forward on a horizontal metal base bar, and protected by a metal frame. A rope with surface marker buoys was attached to the metal frame for BRUV deployment and retrieval. A bait container was suspended in front of the camera using a 1.2 m PVC pipe.

The BRUVs were deployed during the day (0700–1600) in TRNP and Cagayancillo in April and June 2016. Different habitats were haphazardly sampled, including lagoons, seagrass beds, reef slopes and mid-water at depths ranging from <10 to 100 m. Deployments on the seafloor between 15 to 60 m deep were usually avoided because of difficulties in setting BRUVs on steep reef slopes (Murray et al., 2019). For this study, 33 and 32 BRUV deployment stations on reef slopes in TRNP and Cagayancillo, respectively, were selected ($n = 65$ videos), which represented two depth categories at each location: shallow (4–12 m) and mesophotic (45–96 m) (Supplementary Table 1). The sample sizes were limited by the number of successful reef slope deployments per depth category at each location. Deployment stations were selected haphazardly without watching the videos prior to analysis. Selected BRUV samples were only replaced when the deployment was unsuccessful (e.g., camera was facing up). Furthermore, if there were two consecutive deployments within the same depth category that were too close to one another (<0.5 km), one was chosen. The subsample of 33 BRUV deployment stations in TRNP represented 94% of reef slope samples in this location distributed amongst the North and South Atolls (Figure 1c). The subsample of 32 BRUV deployment stations in Cagayancillo only represented 36% of the reef slope samples in this location. In selecting deployments from Cagayancillo, those that were chosen sampled reef slopes around the main atoll of Cagayancillo, two islands to the east (Bonbon and Manucan) and two islands (Calusa and Cawili)

in the westernmost and southernmost parts of the municipality, while keeping the total number of stations similar to TRNP (Figure 1d,e). While the surveys in Cagayancillo were conducted a few months before the extensive multi-use MPA was legally established, five of the selected deployments (<2% of the 32 stations) were situated within small, community-managed no-take MPAs that were 7–12 years old at the time of survey. These were in Calusa Island MPA ($n = 1$ shallow), Nusa MPA ($n = 1$ shallow, 2 mesophotic) and Bonbon Island MPA ($n = 1$ shallow).

The BRUV deployments in TRNP and Cagayancillo were originally designed to only examine the diversity and abundance of sharks (Murray et al., 2019), which were excluded in the present study. Sharks are generalist carnivores that may be attracted to many kinds of bait, but sardines (*Sardinella sp.*) or similar oily fish species may be the ideal bait to attract various carnivorous fishes in BRUV studies (Cappo et al., 2006; Wraith et al., 2013). However, due to difficulties of acquiring fresh sardines in the remote study locations, different species of fish were used as bait depending on their availability. In TRNP, sardines, barracuda (*Sphyrna barracuda*) and frigate tuna (*Auxis thazard*) were used while bluefin trevally (*Caranx melampygus*), black jack (*Caranx lugubris*) and skipjack tuna (*Katsuwonus pelamis*) were used at Cagayancillo. Approximately 500 g bait was used for each BRUV deployment.

2.3 | Video analysis

All 65 videos were analysed using the software EventMeasure (SeaGIS, 2022) to estimate fish abundance and species richness from the videos recorded at each BRUV deployment station. All visible individuals of large carnivorous reef fish species were identified and counted from the families Serranidae, Lutjanidae, Lethrinidae and Carangidae as well as the endangered species *C. undulatus*. Large carnivorous fishes were defined as species that are known to consume fish or macroinvertebrates (Froese & Pauly, 2022), estimated to reach a maximum total length of >30 cm (Allen et al., 2003), and are highly likely to be targeted or caught incidentally by commercial or subsistence fisheries in Palawan (Gonzales, 2013). The relative abundance of a species in a BRUV deployment station was given by MaxN, defined as the maximum number of individuals per species observed at any time in the video (Cappo et al., 2006). To avoid sampling fishes that were outside the immediate vicinity of the deployment station, each video was only analysed 10 min after the BRUV settled onto the seabed, and for 30 min thereafter. These ‘settling’ and viewing times were arbitrarily decided but likely included most species and individuals of large carnivorous fishes within the immediate vicinity of each deployment station (Birt et al., 2021).

2.4 | Data analysis

Tidyverse and ggplot packages from R were used to process and visualize the abundance and species richness data (Wickham, 2016;

Wickham et al., 2019). In analysing abundance, all recorded individuals were included, even those that were not identified to the species level ($n = 25$). Abundance per station was expressed in terms of overall (all large carnivorous fish species) and separately for Serranidae, Lutjanidae, Lethrinidae, Carangidae and *C. undulatus*. Overall abundance was calculated as the sum of all MaxN values per station. Abundances of Serranidae, Lutjanidae, Lethrinidae and Carangidae were calculated by summing the MaxN values of species that belong to each of these taxonomic groups per station. Abundance of *C. undulatus* was simply given by the MaxN of this species per station.

The individuals that could not be identified at the species level were removed in the analyses of species richness and fish assemblage structure. The non-parametric Chao1 estimator within the vegan package in R was used to model the overall species richness of all the analysed large carnivorous fishes per station (Chao et al., 2009; Oksanen et al., 2022). However, when examining the Chao1 estimator per each taxon (Serranidae, Lutjanidae, Lethrinidae and Carangidae), there was not enough data to apply the Chao1 estimator. Therefore, to analyse species richness per taxa, the raw number of species observations (observed species richness) was used.

The mixed command in the afex package in R was used to test the effects of study location and depth category on mean abundance and species richness per BRUV deployment (Singmann et al., 2016). The following statistical formula was applied: $y \sim \text{depth_category} * \text{study_location} + (1|\text{study_location}:\text{bait_type})$. Bait type was used as a random blocking factor nested within the study location because no bait types were shared between the two locations. Estimated marginal means and confidence intervals were obtained using the emmeans package (Lenth, 2022). The command `emmeans::contrast` was used to test for differences across treatment combinations (shallow*TRNP, mesophotic*TRNP, shallow*Cagayancillo, and mesophotic*Cagayancillo), and the false discovery rate was controlled at 0.05. The `multcomp::cld` command (Hothorn et al., 2012) was used to label and separate significantly different treatment combinations from the estimated marginal means. Estimated marginal means for abundance were modelled using the Poisson distribution. For overall species richness (Chao1 estimates) and species observations per taxonomic group, the gamma and Poisson distributions were used, respectively. Assuming Poisson and gamma distributions for overall abundance and species richness, respectively, a generalized linear model was also applied to separately test the effect of bait type on overall abundance and species richness. Since the same bait types were not used in TRNP and Cagayancillo, the effect of bait type was analysed separately at both study locations. The following formula was used: sum_max_n (abundance) or s_chao1 (species richness) $\sim \text{depth_category} * \text{bait_type}$. The effect of frigate tuna and sardines as bait was tested relative to barracuda in TRNP, and the effect of bluefin trevally and skipjack tuna was tested relative to black jack in Cagayancillo.

To further evaluate species richness and assess how well the BRUV deployments sampled species richness, sample size-based rarefaction and extrapolation curves were generated using the iNEXT

package in R, where diversity estimates are calculated using Hill numbers with respect to sample size (Chao et al., 2014; Hsieh et al., 2016). Separate rarefaction and extrapolation curves for overall species richness were created using pooled data from all stations and data from stations within each treatment combination (shallow*TRNP, mesophotic*TRNP, shallow*Cagayancillo and mesophotic*Cagayancillo). Rarefaction and extrapolation curves were also generated for the taxonomic groups Serranidae, Lutjanidae, Lethrinidae and Carangidae using pooled data from all stations. All pooled abundance data from the stations was transformed into incidence data. Incidence data was then input into iNEXT to derive estimates of species richness ($q = 0$). Extrapolation models were applied to examine species richness beyond the number of BRUVs that were deployed and to identify the asymptote across treatment combinations and taxonomic groups.

Similarities in fish assemblage structure among stations were quantified by generating a Bray–Curtis dissimilarity matrix from data on abundance (raw MaxN) per species. A non-metric multidimensional scaling (nMDS) plot was generated from this matrix using the `metaMDS` command in the vegan package to visualize patterns of similarity (Oksanen et al., 2022). Distance-based Redundancy Analysis (dbRDA) was performed with `vegan::dbRDA` to visualize the same data as used to generate the nMDS plot, constraining variance to the location and depth factors, as well as their interaction. Confidence ellipses (95%) were plotted to highlight treatment groupings. One outlier (a station in Cagayancillo) was removed from the nMDS and dbRDA plots to better discern patterns of similarity amongst the remaining stations. Using `vegan::adonis2`, two separate two-way PERMANOVAs were used to test differences in fish assemblages. The first tested the effects of depth category and study locations. The second tested the effects of depth category and bait type because bait type was not consistent across study locations and depths. Pairwise post-hoc tests were conducted using `pairwiseAdonis::pairwise.adonis` (Martinez Arbizu, 2020) while accounting for false discovery rate (Benjamini & Hochberg, 1995). Similarity percentage (SIMPER) analysis (command `vegan::simper` in the vegan package) was used to identify species that were influential in distinguishing fish assemblages (i.e., accounted for 75% of the total dissimilarity) between shallow and mesophotic depths within TRNP and Cagayancillo (Oksanen et al., 2022). Multilevel pattern analysis (`multipatt` in the `indicspecies` package in R) was used to identify indicator species associated with each of the station groups defined by the four treatment groupings (shallow-TRNP, mesophotic-TRNP, shallow-Cagayancillo and mesophotic-Cagayancillo) or combinations of these groups (De Cáceres & Legendre, 2009). Species were identified based on an indicator value index (IndVal), which is the product of two quantities: A (a measure of specificity)—the mean abundance of a species in a group, or combinations of groups, compared to all other groups; B (a measure of fidelity)—the relative frequency of occurrence of a species in the stations within a group or combinations of groups (Dufrêne & Legendre, 1997).

All R scripts for data manipulation and visualization are published and available on GitHub (Salvador & Bird, 2022).

3 | RESULTS

3.1 | Species composition

All large carnivorous reef fishes observed in the videos were successfully identified to the genus level and 93% to the species level due to good water clarity and natural lighting at all BRUV deployment stations, even at mesophotic depths. A total of 55 species ($n = 739$ total individuals) were recorded (Supplementary Table 2). These do not include 25 individuals in seven genera from the families Serranidae, Lethrinidae and Carangidae that could not be identified to the species level with high confidence due to the individuals swimming too far away from the camera (Supplementary Table 3). Most of the recorded species were generalist carnivores (prey on fish and invertebrates) (75%), whereas others specialized on fish (18%) or invertebrates (7%). Most recorded species were from Serranidae (33%), followed by Carangidae (25%). Species from the Lethrinidae and Lutjanidae comprised 22% and 18% of the total recorded species, respectively, and *C. undulatus* comprised 2%. The majority of the recorded species occurred in both TRNP and Cagayancillo (58%) and both shallow and mesophotic depths (56%). Relatively few species were recorded exclusively in TRNP (18%), Cagayancillo (24%), shallow depths (20%) or mesophotic depths (24%). Aside from *C. undulatus*, two species in the Serranidae are listed by the IUCN as threatened by extinction (IUCN, 2022). One was recorded in TRNP only (*Plectropomus areolatus*—vulnerable) and the other in both locations (*Epinephelus fuscoguttatus*—vulnerable).

3.2 | Abundance

Between the old, fully no-take, and uninhabited MPA (TRNP) and new, partially no-take and inhabited MPA (Cagayancillo), no significant individual effect of location on the estimated marginal means of overall abundance was detected ($p = 0.363$; Table 1). Overall abundances at shallow and mesophotic depths in TRNP were similar to each other and to shallow depths in Cagayancillo (Figure 2a; Supplementary Table 4). There was an individual effect of depth category and a significant interaction of location and depth category ($p = <0.001$; Table 1), which is consistent with mesophotic depths in

Cagayancillo having significantly higher overall abundance (Figure 2a; Supplementary Table 5). Mean abundance in Cagayancillo was approximately 2 times higher in mesophotic depths than in shallow depths (Figure 2a). However, bait type effects were present. In TRNP, there was a significant interaction between frigate tuna used as bait and the depth category shallow reef on overall abundance ($p = 0.006$; Supplementary Table 5). In Cagayancillo, there was a significant effect of the use of bluefin trevally ($p < 0.001$; Supplementary Table 5) as bait and a significant interaction of shallow reefs and bluefin trevally as bait on overall abundance ($p = 0.004$; Supplementary Table 5).

The estimated marginal means of abundance varied depending on the taxonomic grouping, with no consistent effects of depth category, location or their interaction (Figure 2; Supplementary Table 4). The Serranidae and Carangidae were significantly more abundant at mesophotic than shallow depths in Cagayancillo, having 2 to 10 times higher mean abundance at mesophotic depths, respectively ($p_{\text{Serranidae}} = 0.004$; $p_{\text{Carangidae}} = 0.030$, Supplementary Table 4; Figure 2b,e). Cagayancillo had 2 times higher mean overall abundance and 10 times higher mean abundance of Carangidae at mesophotic depths, likely due to large schools of *Caranx sexfasciatus*. Lutjanidae were significantly more abundant in shallow depths in Cagayancillo than in mesophotic depths ($p = 0.005$; Supplementary Table 4; Figure 2c). There was no significant difference in the abundance of the Lethrinidae between depth categories or study locations (Supplementary Table 4; Figure 2d). A total of 22 individuals of *C. undulatus* were recorded in TRNP and Cagayancillo, but their abundance did not differ significantly between the locations (Figure 2f; Supplementary Table 4). *C. undulatus* was significantly more abundant at shallow than mesophotic depths at TRNP ($p = 0.018$; Supplementary Table 4; Figure 2f).

3.3 | Species richness

Similar to overall abundance, there was no individual effect of location ($p = 0.104$) or depth category ($p = 0.163$) on the estimated marginal means of Chao1 overall species richness (Figure 3a), nor was there a significant effect of the interaction of depth category and location ($p = 0.814$). There was also no significant individual effect of bait type on overall species richness in either TRNP or Cagayancillo

TABLE 1 Summary of p values in testing the effect of depth category, study location and their interaction, on large carnivorous reef fish abundance.

Grouping	Effect of depth category	Effect of location	Effect of interaction between location and depth category
Overall	0.003	0.363	<0.001
Serranidae	0.002	0.389	0.147
Lutjanidae	<0.001	0.330	0.049
Lethrinidae	0.311	0.543	0.306
Carangidae	<0.001	0.697	<0.001
<i>Cheilinus undulatus</i>	0.016	0.704	0.191

Note: Significant results are highlighted in bold.

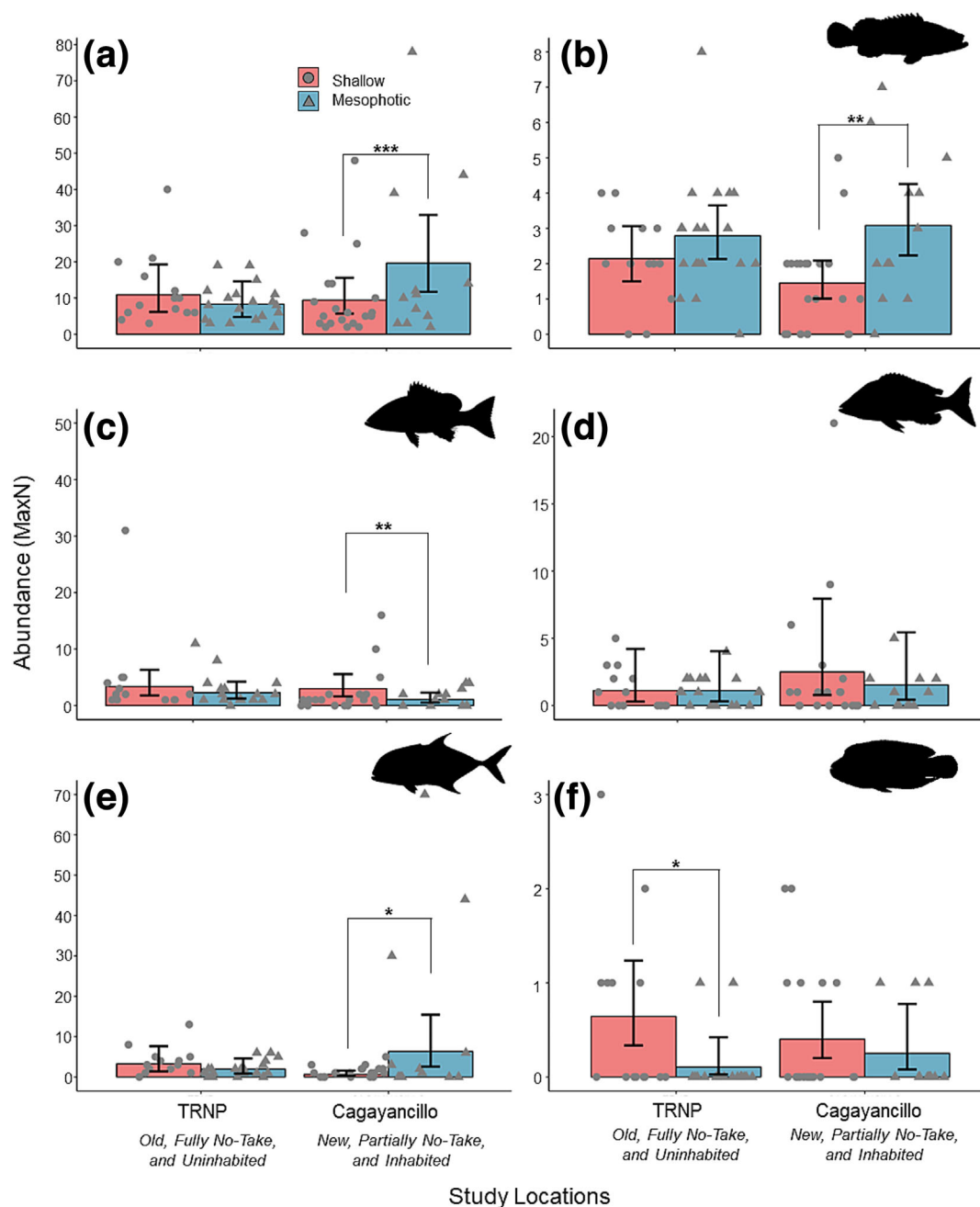


FIGURE 2 Bar plots of the estimated marginal means from a general linear model ($y \sim \text{depth category} * \text{study locations}$) of the overall abundance (Poisson distribution) and the abundance of different large carnivorous reef fish taxa (Poisson distribution) per BRUV station at two depth categories in the two study locations. (a) Overall abundance, (b) Serranidae, (c) Lutjanidae, (d) Lethrinidae, (e) Carangidae and (f) *Cheilinus undulatus*. Error bars represent 95% CI. Data points represent raw MaxN values per station and are allowed to jitter. Note different scales on y-axes. Asterisks indicate statistically significant difference: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Refer to Supplementary Figure 2 for histograms of abundance.

(Supplementary Table 7). In examining the treatment combinations, no significant differences in the estimated marginal means of Chao1 overall species richness were detected between shallow and mesophotic depths in TRNP ($p = 0.316$) and Cagayancillo ($p = 0.335$; Supplementary Table 6; Figure 3a).

No significant differences in the estimated marginal means of observed species richness were detected in the Serranidae, Lutjanidae and Lethrinidae across treatment combinations (Supplementary

Table 6; Figure 3b-d). However, the species richness of Carangidae at shallow depths was higher in TRNP than in Cagayancillo ($p = 0.033$, Supplementary Table 6; Figure 3e).

The rarefaction and extrapolation curves generated by iNEXT indicated that a total sample size of 65 BRUV deployment stations recorded almost all species of Lethrinidae and Carangidae in the two MPAs (Figure 4d,e). In contrast, this sampling effort was probably not adequate for the Serranidae, Lutjanidae and the large carnivorous fish

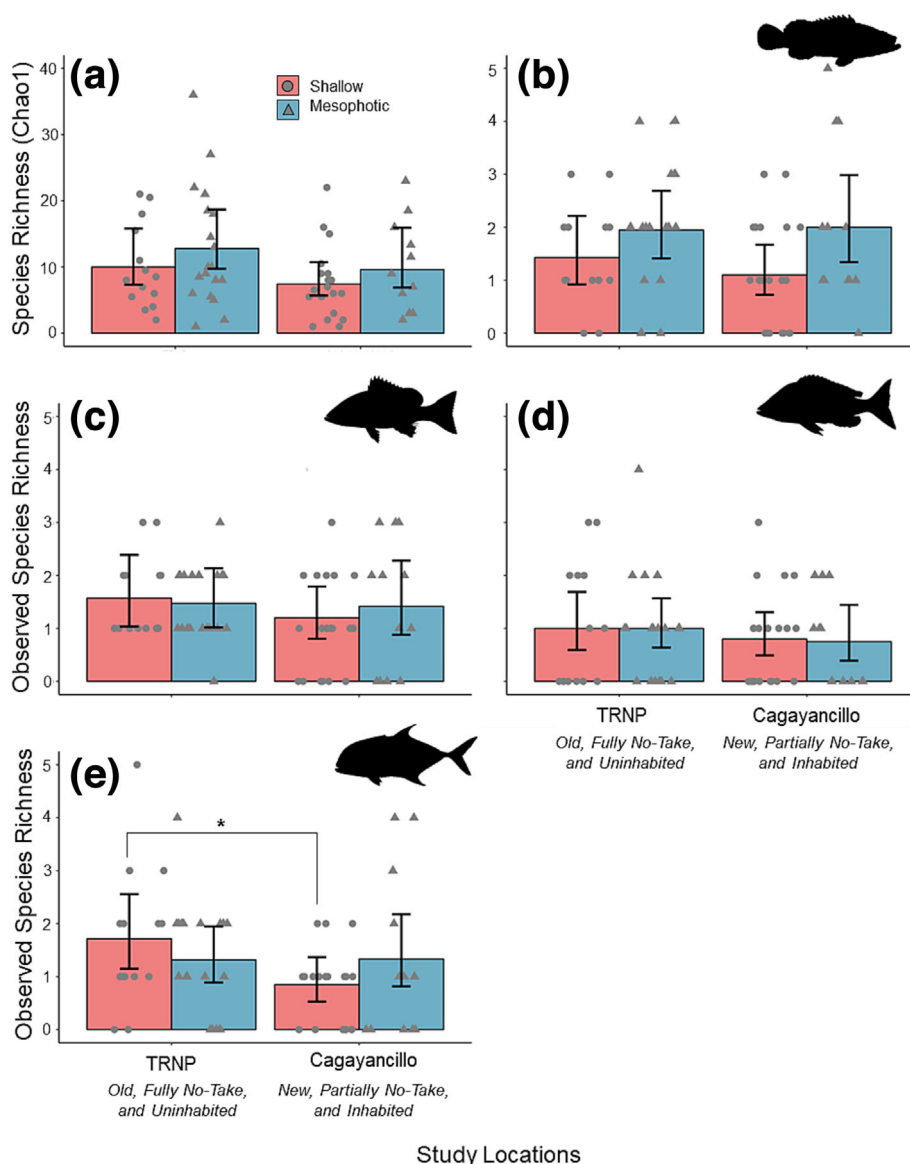


FIGURE 3 Bar plots of the estimated marginal means from a general linear model ($y \sim \text{depth category} * \text{study locations}$) of overall species richness (gamma distribution) and the observed species richness (Poisson distribution) of different large carnivorous reef fish taxa per BRUV station at two depth categories in the two study locations. (a) Overall species richness (Chao 1), (b) Serranidae, (c) Lutjanidae, (d) Lethrinidae and (e) Carangidae. Chao1 estimator was used to calculate overall species richness (Chao et al., 2009). For the four taxonomic groupings, raw number of species observations were used as species richness instead of the Chao1 estimator. Error bars represent 95% CI. Data points represent raw values of observed species richness and are allowed to jitter. Note different scales on the y-axis for overall species richness. Asterisks indicate statistically significant difference: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Refer to Supplementary Figure 3 for histograms of species richness.

assemblage as a whole (Figure 4a-c). Similarly, sampling effort was also probably insufficient to represent entire species assemblages in each of the four treatment combinations (depth category*study location) (Figure 5a-d). However, for the same sampling effort, species richness in TRNP was expected to be lower at shallow depths compared to mesophotic depths (Figure 5a,b) while in Cagayancillo, species richness was expected to be similar between shallow and mesophotic depths (Figure 5c,d), although there were very wide confidence regions for these curves. This contrasted with the results in the actual data, where overall species richness was similar across shallow and mesophotic depths in both TRNP and Cagayancillo (Supplementary Table 6; Figure 3).

3.4 | Assemblage structure

The nMDS plot revealed some differentiation in the fish assemblages between the two locations, where stations in TRNP were clustered

more tightly than those observed in Cagayancillo (Figure 6a). Within each location, the shallow assemblages were more distinctly separated from mesophotic assemblages along axis 1 of the nMDS. The 95% confidence ellipses indicated that differentiation among locations and depths was not clear cut. Ordination performed with dbRDA (Figure 6b) demonstrated a clear separation of location and depth treatments, with 13.8% of variance constrained by these factors. Location and depth accounted for 47.1% and 34.0% of constrained variance, and their interaction accounted for 18.9%. The results of the dbRDA ordination are consistent with the PERMANOVA analysis, which indicated that the effects of depth category, location and the interaction of these two factors on assemblage structure were significant (Table 2). The significant interaction indicated that the effect of depth category was not consistent between the two locations. Post-hoc pairwise comparisons indicate that each combination of depth category and study location was significantly differentiated ($p < 0.0039$). The PERMANOVA also suggested that the individual effect of bait type was significant on

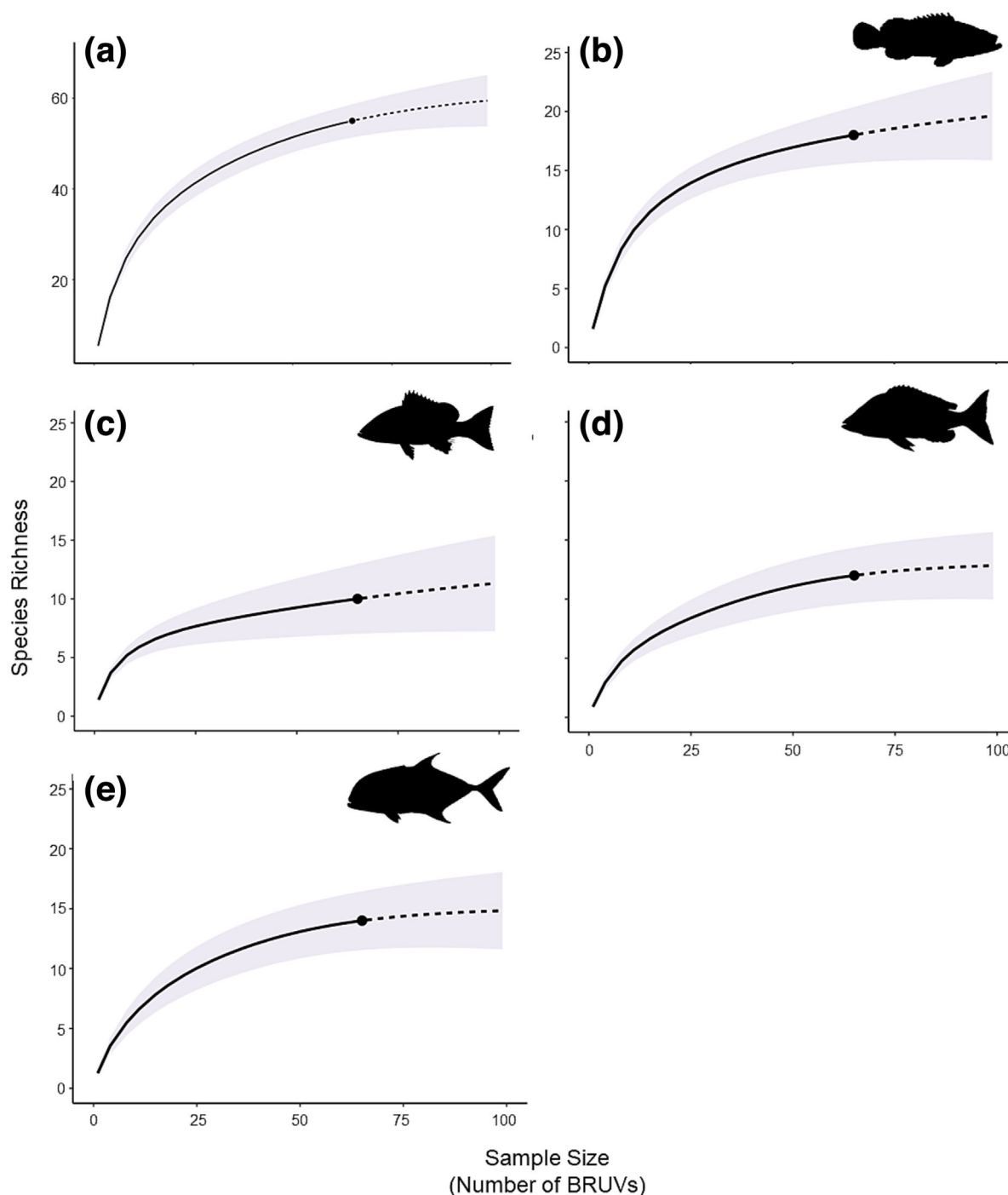


FIGURE 4 Species richness rarefaction and extrapolation curves generated by iNEXT based on the incidence of large carnivorous reef fishes, split by the groupings analysed ($n = 5$) and overall species richness. (a) Overall species richness, (b) Serranidae, (c) Lutjanidae, (d) Lethrinidae and (e) Carangidae. The solid line represents the rarefaction curve, the middle point represents the observed species richness at the sample size, and the dotted line represents the extrapolation curve. The fill represents the 95% confidence interval. Note different scales on the y-axis for overall species richness.

assemblage structure ($p < 0.001$; Table 2), but post-hoc pairwise comparisons indicated that only certain bait types were significantly different between depth categories (Supplementary Table 8).

A pool of 31 species was identified by SIMPER to be most influential in differentiating the fish assemblages, accounting for 75%

of the total dissimilarity between depth categories at each location (Table 3). Limiting the influential species to only those that were statistically significant, six species were identified for each of the two locations (TRNP—*C. melampygus*, *Lutjanus rivulatus*, *Aetholoperca rogaa*, *C. undulatus*, *Cephalopholis argus* and *Monotaxis grandoculis*;

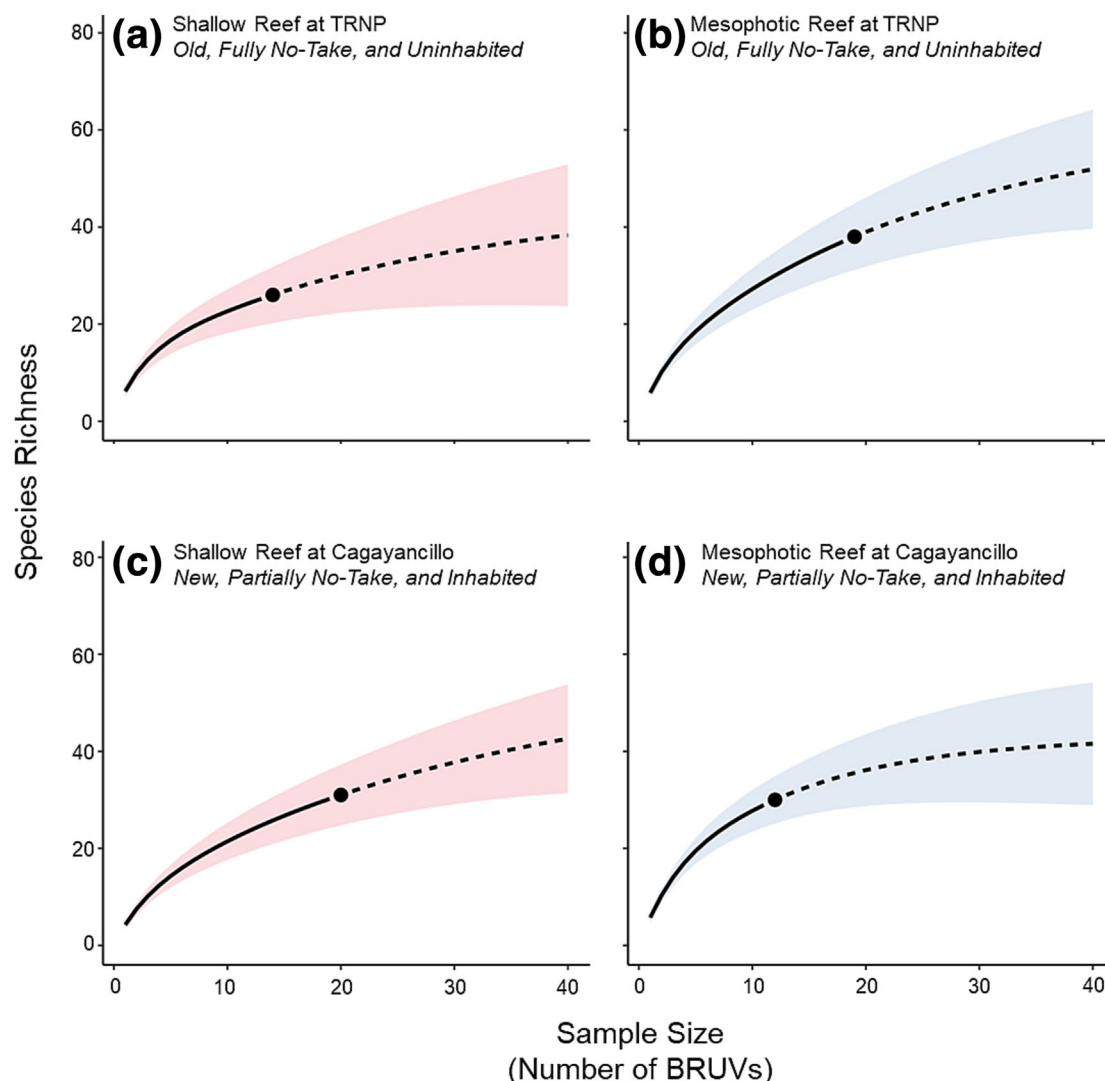


FIGURE 5 Species richness rarefaction and extrapolation curves generated by iNEXT based on the incidence of large carnivorous reef fishes, split by the study locations (TRNP and Cagayancillo) and two depth categories (shallow vs. mesophotic). (a) Shallow reef at TRNP, (b) mesophotic reef at TRNP, (c) shallow reef at Cagayancillo and (d) mesophotic reef at Cagayancillo. The solid line represents the rarefaction curve, the middle point represents the observed species richness at the sample size, and the dotted line represents the extrapolation curve. The fill represents the 95% confidence interval.

Cagayancillo—*C. sexfasciatus*, *Gracila albomarginata*, *Carangoides oblongus*, *Cephalopholis polleni*, *Aprion virescens* and *Plectropomus leopardus*). The six species in TRNP were all more abundant at shallow depths while the six species in Cagayancillo were all more abundant at mesophotic depths (Table 3).

Multilevel pattern analysis identified 14 species (IndVal ranging from 0.405 to 0.748) that were significantly associated with a particular station group or combinations of these groups (Table 4). Indicator species were identified for shallow-TRNP (*Aethaloperca rogaa*), mesophotic-TRNP (*Epinephelus maculatus*), shallow-Cagayancillo (*Lutjanus decussatus*) and mesophotic-Cagayancillo (*G. albomarginata*, *C. sexfasciatus*, *Gymnocranius griseus* and *Elagatis bipinnulata*) (Table 4). Several species were also identified to be associated with TRNP (*Lethrinus olivaceus* and *Lethrinus erythracanthus*), as well as shallow depths (*C. argus*) and mesophotic depths (*Variola louti*, *C. polleni* and

C. oblongus) regardless of location (Table 4). One species (*Lutjanus bohar*) was identified to be significantly associated with all station groups combined except for shallow-Cagayancillo (Table 4).

4 | DISCUSSION

This study investigated how assemblages of large carnivorous fishes would differ according to quality and duration of protection from fishing, and between shallow reefs and MCEs, in two of the most extensive and inaccessible MPAs in the Philippines. The first hypothesis that mean abundance and species richness would be greater in the shallow reefs and MCEs of TRNP (because it is an old, uninhabited and fully no-take MPA) was not supported by the results. The second hypothesis—differentiation of fish assemblage structure

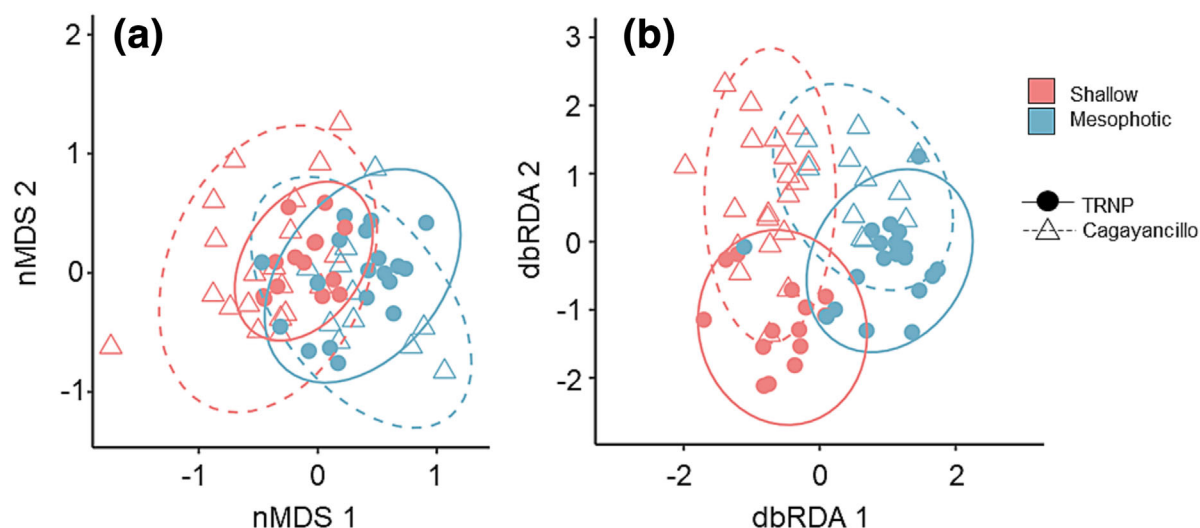


FIGURE 6 Two-dimensional (a) nMDS ($p = 0.012$; stress = 0.15) and (b) dbRDA plots of fish assemblage similarity (Bray–Curtis) among BRUV stations at different depths (colour) and study locations (point shape, line type). The ellipses represent 95% confidence intervals. One outlier (a mesophotic Cagayancillo station) was removed from the plot for clarity because it had a very high positive value along the first axis.

TABLE 2 Results of PERMANOVA testing the effects of depth category, study location, bait type and the interaction of these factors, on large carnivorous reef fish assemblage structure.

Factor	df	Sum of squares	R^2	F	Pr (>F)
Effect of depth category and study location					
Depth Category	1.00	1.61	0.064	4.56	<0.001
Location	1.00	1.19	0.048	3.38	<0.001
Depth Category * Location	1.00	0.684	0.027	1.94	<0.01
Residual	61.0	21.50	0.861		
Effect of depth category and bait type					
Depth Category	1.00	1.54	0.062	4.65	<0.001
Bait Type	6.00	4.31	0.172	2.17	<0.001
Depth Category * Bait Type	4.00	1.59	0.063	1.20	0.107
Residual	53.0	17.6	0.702		

Note: Significant results are highlighted in bold.

between TRNP and Cagayancillo—was supported, but this was more evident between shallow and mesophotic depths within the locations. There was some support for the third hypothesis that MCEs can serve as deep refugia from fishing in Cagayancillo, where the MPA is new, inhabited and only partially no-take. This was shown through the mean abundance of the overall fish assemblage and the mean abundance of two families (groupers and jacks) that were found to be greater at mesophotic depths. These results point to the importance of strictly enforcing large and remote no-take MPAs like TRNP, potentially expanding no-take zones in Cagayancillo to protect intact assemblages and explicitly including MCEs in the planning and design of future MPAs.

The lack of consistently higher mean abundance and species richness in TRNP was unexpected. However, this result seems unlikely to be indicative of ineffective enforcement of the no-take policy in this old, uninhabited MPA, considering previous studies and observations. Annual diver-based surveys from 1996 to 2011 documented a steady recovery in the biomass of fishery-targeted

species and stable coral cover in TRNP despite incidents of poaching by local and foreign fishers within this period (Dygico et al., 2013). Recovery likely occurred because the effects of poaching were minimal relative to the size of the MPA. Diver-based surveys conducted between 2006 and 2009 also showed that TRNP had the highest total reef fish biomass documented in the Philippines (Muallil et al., 2019). Furthermore, diver-based and BRUV surveys in 2015–2016 recorded densities of threatened shark species (*Carcharhinus amblyrhynchos* and *Triaenodon obesus*) at shallow and mesophotic depths that were among the highest in the world (Murray et al., 2019). With regard to *C. undulatus*, diver-based surveys on shallow reefs in 2017 showed that TRNP had the highest density of this species in the Philippines (Nañola et al., 2021), which is consistent with the present study showing high abundance of *C. undulatus* at shallow depths in TRNP. Rare natural behavior of *C. undulatus* hunting together with emperors and jacks as a group, which may be indicative of near-pristine conditions, was also documented in TRNP in 2016 (Sorgon & Abesamis, 2023). This body of evidence strongly suggests

TABLE 3 Results of SIMPER, showing the most influential species that accounted for 75% of the total dissimilarity in the fish assemblage between depth categories (shallow vs. mesophotic) within TRNP and Cagayancillo.

Location/species	Average dissimilarity	Standard deviation	Ratio	Average abundance at shallow depths	Average abundance at mesophotic depths	Cumulative %	p
TRNP							
<i>Caranx melampygus</i>	0.112	0.098	1.142	2.429	0.737	0.134	0.003
<i>Aethaloperca rogaa</i>	0.065	0.076	0.847	1.000	0.000	0.211	0.001
<i>Lutjanus rivulatus</i>	0.062	0.170	0.362	2.500	0.053	0.285	0.033
<i>Lutjanus bohar</i>	0.056	0.050	1.135	1.214	0.790	0.352	0.196
<i>Aphareus furca</i>	0.044	0.069	0.639	0.286	0.842	0.405	0.963
<i>Epinephelus maculatus</i>	0.038	0.064	0.602	0.000	0.790	0.451	0.918
<i>Cheilinus undulatus</i>	0.033	0.051	0.658	0.643	0.105	0.491	0.017
<i>Variola louti</i>	0.032	0.047	0.685	0.000	0.526	0.529	0.582
<i>Carangoides plagiotaenia</i>	0.031	0.048	0.644	0.500	0.158	0.566	0.102
<i>Lethrinus erythracanthus</i>	0.030	0.041	0.735	0.357	0.421	0.602	0.985
<i>Lethrinus olivaceus</i>	0.027	0.036	0.759	0.357	0.421	0.635	0.979
<i>Cephalopholisargus</i>	0.027	0.055	0.492	0.357	0.053	0.667	0.022
<i>Carangoides oblongus</i>	0.022	0.037	0.602	0.071	0.368	0.694	0.945
<i>Aprion virescens</i>	0.021	0.047	0.448	0.143	0.263	0.719	0.871
<i>Monotaxis grandoculis</i>	0.020	0.033	0.611	0.357	0.053	0.743	0.015
Cagayancillo							
<i>Caranx sexfasciatus</i>	0.132	0.252	0.524	0.000	7.583	0.142	0.039
<i>Caranx melampygus</i>	0.070	0.090	0.775	0.850	1.167	0.216	0.870
<i>Monotaxis heterodon</i>	0.067	0.135	0.496	1.550	0.333	0.288	0.959
<i>Lutjanus gibbus</i>	0.051	0.143	0.356	2.000	0.000	0.343	0.971
<i>Cephalopholis argus</i>	0.050	0.077	0.647	0.750	0.083	0.396	0.798
<i>Gracila albomarginata</i>	0.040	0.051	0.788	0.200	0.833	0.439	0.027
<i>Carangoides oblongus</i>	0.037	0.112	0.333	0.000	0.833	0.479	0.030
<i>Elagatis bipinnulata</i>	0.037	0.104	0.357	0.050	2.750	0.519	0.196
<i>Lutjanus bohar</i>	0.037	0.057	0.643	0.400	0.500	0.558	0.873
<i>Cephalopholispolleni</i>	0.035	0.051	0.700	0.000	0.500	0.596	0.002
<i>Cheilinus undulatus</i>	0.029	0.054	0.543	0.400	0.250	0.628	0.874
<i>Lutjanus decussatus</i>	0.026	0.042	0.615	0.500	0.167	0.656	0.927
<i>Aprion virescens</i>	0.022	0.049	0.445	0.000	0.250	0.679	0.006
<i>Plectropomus leopardus</i>	0.022	0.056	0.393	0.000	0.250	0.703	0.022
<i>Aphareus furca</i>	0.022	0.037	0.592	0.200	0.333	0.726	0.852
<i>Lethrinus semicinctus</i>	0.020	0.071	0.284	0.000	0.333	0.747	0.070

Note: Also shown are estimates of average abundance (MaxN) of each species per depth category. Significant results are highlighted in bold.

that the no-take protection of TRNP has been quite successful, allowing fishes, including those that are highly sensitive to overfishing, to recover for at least two decades. These surveys in TRNP also suggest that the abundance, and perhaps species richness, of large carnivorous reef fish at shallow and mesophotic depths in TRNP in 2016 that were reported here were much higher than in other Philippine regions and may have been approaching peak levels.

Compared to TRNP, Cagayancillo is not fully no-take, is inhabited by thousands of people, and was declared as an MPA only a few

months before sampling for this study was conducted. Ecological and socio-economic factors operating in Cagayancillo may largely explain the lack of strong differences in fish abundance and species richness compared to TRNP and indicate that fishing in the municipality has had a limited impact on local populations of large carnivorous reef fishes. Cagayancillo has a very small human population relative to its extensive reefs (a few tens of people per km² reef) both by Philippine and global standards (Newton et al., 2007). It is also relatively close to TRNP and may be benefiting from the success of this adjacent no-

TABLE 4 Indicator species identified by multilevel pattern analysis.

Indicator species	S-T	M-T	S-C	M-C	A	B	IndVal	<i>p</i>
Associated with one group								
<i>Aethaloperca rogae</i>	1				0.870	0.643	0.748	0.001
<i>Epinephelus maculatus</i>		2			0.826	0.421	0.590	0.002
<i>Lutjanus decussatus</i>			3		0.695	0.350	0.493	0.025
<i>Gracila albomarginata</i>				4	0.660	0.500	0.574	0.009
<i>Caranx sexfasciatus</i>				4	0.991	0.250	0.498	0.010
<i>Gymnocranius griseus</i>				4	1.000	0.167	0.408	0.026
<i>Elagatis bipinnulata</i>				4	0.982	0.167	0.405	0.028
Associated with two groups								
<i>Lethrinus olivaceus</i>	5	5			0.903	0.364	0.573	0.007
<i>Lethrinus erythracanthus</i>	5	5			0.854	0.303	0.509	0.042
<i>Cephalopholis argus</i>	6		6		0.891	0.412	0.606	0.004
<i>Variola louti</i>		7		7	0.933	0.323	0.549	0.007
<i>Cephalopholis polleni</i>		7		7	1.000	0.290	0.539	0.008
<i>Carangoides oblongus</i>		7		7	0.944	0.290	0.523	0.018
Associated with three groups								
<i>Lutjanus bohar</i>	8	8		8	0.862	0.600	0.719	0.041

Note: Station groups are shallow-TRNP (S-T), mesophotic-TRNP (M-T), shallow-Cagayancillo (S-C) and mesophotic-Cagayancillo (M-C). Station groups or combinations of station groups for which indicator species were identified are labelled from 1 to 8. A (specificity) and B (fidelity) are the components of the indicator value index. IndVal is the square root of the indicator value index. Significant results are highlighted in bold.

take MPA through reef fish recruitment subsidies via long-range larval connectivity (Williamson et al., 2016). Moreover, the municipal government had implemented conservation measures as evidenced by the enactment of small no-take MPAs and the large multi-use MPA. These conditions would confer greater resilience to the impacts of fishing. Moreover, reef fisheries in Cagayancillo are quite isolated from external market pressures due to their distance from major cities (Dygico et al., 2016). Such isolation has been demonstrated to have a direct relationship with reef fish biomass and presence of large carnivorous reef fish (Andradi-Brown et al., 2021; Cinner et al., 2018). Lastly, fishing intensity on reefs in Cagayancillo had decreased significantly several years prior to 2016. This was caused by a municipal ban on live fish trade operations in 2014 due to concerns about cyanide fishing. By 2015, most fishers shifted to seaweed farming while fishing was done primarily for subsistence (Dygico et al., 2016). The combination of low fishing pressure, inaccessibility and probable larval connectivity with an adjacent MPA may have stabilized the large carnivorous reef fish populations in Cagayancillo at levels comparable with TRNP.

The lack of differences in abundance and species richness between TRNP and Cagayancillo seems consistent with the notion that either partially protected MPAs or well-managed fisheries can provide benefits similar to fully no-take MPAs. Some have argued that implementing more conventional fishing regulations, such as seasonal fishery closures, may be as effective as no-take MPAs (Hilborn, 2018). However, many other studies examining fish assemblages between no-take MPAs and partially protected areas have shown otherwise;

no-take MPAs have often conferred greater benefits to fish assemblages in terms of higher densities and biomass of marine organisms (Hall et al., 2023). Nonetheless, it is important to acknowledge the caveats of comparing two MPAs with different levels of protection. Due to the lack of appropriate controls (i.e., reef areas similar to TRNP or Cagayancillo), it is difficult to know if a difference in fish abundance or species richness was due to MPA protection rather than other confounding factors such as habitat differences between the two locations. Also, the different taxonomic groups of fishes may have different responses to full versus partial protection based on their life history and behavioral traits (Gilman et al., 2019).

Several lines of evidence, including PERMANOVA, SIMPER, and multilevel pattern analysis indicate differentiation of assemblages of large carnivorous fishes between TRNP and Cagayancillo and between shallow and mesophotic depths at each location. The PERMANOVA indicated significant effects of location, depth category and their interaction, which were consistent with the patterns shown by the nMDS, and more clearly, the dbRDA. The different sets of species identified by SIMPER in each location accounted for a large proportion of the assemblage dissimilarity between shallow and mesophotic depths. Potential indicator species were not only identified for shallow reefs and MCEs at each location but also for TRNP regardless of depth and for shallow reefs and MCEs regardless of location. However, MPA protection was probably not the main influencing factor behind the observed structuring of fish assemblages given the lack of strong differences in mean abundance and species

richness between the locations. It seems more likely that habitat variation at different scales between locations, and between shallow coral reefs and MCEs, had a stronger influence.

An effect of larger-scale habitat differences between locations is suggested by the ordination analyses, which showed that stations in TRNP are more similar to each other compared to stations in Cagayancillo, regardless of depth category (Figure 6a). One possible driver of this pattern is differences in gross reef geomorphology between locations, particularly the presence of or proximity to a lagoon (Figure 1). The stations in TRNP were distributed around two neighboring atolls that have lagoons. In contrast, most stations in Cagayancillo (about 70%) were far from, or had no direct access to, the lagoon in its main atoll (note that Arena, a small atoll with a lagoon was not successfully sampled; Figure 1e). Lagoons have been implicated in shaping the fish assemblages of isolated coral reef systems due to their importance as wave-sheltered recruitment or nursery habitats for many reef fish species (Bennett et al., 2018). A well-documented case is that of Christmas Island in the eastern Indian Ocean, which does not have a lagoon. Certain large carnivorous reef fishes that use lagoons as juveniles, such as *C. undulatus*, and some species of groupers, emperors and sharks, were found to be much fewer there compared to atolls with lagoons in the same region (Bennett et al., 2018). In certain cases, this geomorphological effect may be a more influential driver of fish assemblage structure than fishing pressure or local habitat conditions such as coral cover (Bennett et al., 2018).

Habitat variables that operate at more local scales may also play a significant role in differentiating the reef fish assemblages between the locations, and between shallow coral reefs and MCEs, as demonstrated by previous studies (Abesamis et al., 2020; Quimpo et al., 2019). These habitat variables include relative cover of biotic (hard corals, soft corals, sponges and algal assemblages) and abiotic substrata (rock, rubble and sand) and structural complexity (Kahng et al., 2019), which are indicative of the availability of shelter or food for fish. Characterizing habitat at each BRUV station was beyond the scope of the present study, so the extent to which local habitat conditions influenced the observed assemblage patterns remains unknown. Previous studies, however, indicate that the effects of local habitat conditions on the assemblage structure of large carnivorous reef fishes (i.e., generalist carnivores and piscivores) are weaker compared to other trophic groups (Abesamis et al., 2020; Asher et al., 2017). A likely reason for this is the tendency of large carnivorous reef fishes to be less site-attached, utilizing a wider range of habitat types and depths in search of prey (Green et al., 2015). This notion is consistent with the higher proportion of species shared between TRNP and Cagayancillo and between shallow and mesophotic depths, as opposed to the proportion of species exclusive to one location or depth category (Supplementary Table 2).

The present study detected higher mean abundance of the overall fish assemblage, groupers (Serranidae) and jacks (Carangidae) at mesophotic depths compared to shallow depths in Cagayancillo. These results were interpreted as indicative of MCEs serving as deep refugia from fishing because similar patterns were not detected in any

taxa in TRNP which is fully closed to fishing. However, some caution is warranted because potential differences in habitat quality between shallow reefs and MCEs cannot be ruled out. Furthermore, there is no available data to suggest that fishing pressure on large carnivorous reef fishes in Cagayancillo is greater on shallow reefs than on MCEs. The few studies that provide compelling evidence for MCEs providing refuge from fishing usually implicate depth-limited fishing methods, specifically spearfishing (Goetze et al., 2011; Lindfield et al., 2016). In Cagayancillo, spearfishing is just one of several techniques that are employed by fishers and the use of hook-and-line, which can access mesophotic depths, appears to be common. In other regions of the Coral Triangle where hook-and-line is prevalent, evidence for MCEs providing refuge from fishing is lacking (Abesamis et al., 2020; Andradi-Brown et al., 2021). Further studies focused on the deep refugia from fishing hypothesis that account for potential habitat effects, local fishing patterns and fisheries catch are required to verify the findings of the present study.

Another main limitation in this study is the lack of bait type of consistency between each BRUV deployment and both study locations. The use of bait in BRUV deployments is necessary to differentiate reef fish assemblages across habitats because bait increases the number of individuals and species sampled at each deployment compared to unbaited deployments (Harvey et al., 2007). When sampling abundance and species richness, consistent bait type in BRUV deployments is critical, as different bait types have been shown to impact the diversity of carnivorous fishes they attract (Wraith et al., 2013). Sardines and other oily fishes are the ideal bait for BRUVs (Cappo et al., 2006). Bait type consistency was not considered in the initial design of the BRUV deployments, as the deployments were initially meant to only examine shark abundance in TRNP (Murray et al., 2019), and sharks are considered as generalist carnivores. Additionally, logistical difficulties in sourcing or maintaining fresh or frozen sardines in the remote study locations constrained the ability to standardize bait type. Some effects of bait type on overall abundance were identified, in that there was a significant positive interaction between frigate tuna and shallow reef sites at TRNP, but there was no significant effect of the individual bait type. At Cagayancillo, there was evidence for lower overall abundance when bluefin trevally was used as bait, and this effect was variable between depths. No such evidence for bait type effects on species richness was detected. Lastly, the PERMANOVA indicated that bait type did have a significant effect on the overall assemblage structure across the two study locations. Future studies that attempt to use BRUVs to characterize reef fish assemblages should standardize bait type across all deployments to avoid significant effects of bait type on abundance, species richness and assemblage structure.

There are other limitations to the findings of this study and interpretations apart from the lack of habitat, fisheries, time series data and inconsistent bait type. First, the study employed single-camera BRUVs and therefore could not provide estimates of fish biomass, which is a better indicator of the effects of MPAs or fishing because it incorporates fish body size and, to some extent, age (i.e., bigger fish of the same species would be older). Follow-up

studies should measure fish biomass using stereo-BRUVs (Langlois et al., 2020). Second, the sample size may not have been adequate to capture the entire large carnivorous reef fish assemblage and specifically estimate relative species richness for the different taxonomic groups, except for the Lethrinidae and Carangidae. Inadequate sampling may be due to the BRUV deployments being originally designed to target sharks rather than the more diverse assemblages of large carnivorous reef fishes in TRNP and Cagayancillo. Furthermore, results showing no effect of study location or the interaction of depth category on study location may just be attributed to the relatively small sampling size and limited statistical power. Greater sampling effort would thus be advantageous. The rarefaction and extrapolation curves suggest that a desirable sample size would be about double that of the present study (Figures 4 and 5), or approximately 25–40 BRUV deployments depending on depth category and location. Future BRUV-based studies that include reef regions outside of TRNP and Cagayancillo that are open to fishing will likely require greater sample sizes, as the occurrences of large carnivorous reef fishes would be lower due to high fishing mortality.

Marine protected areas are considered indispensable in preserving biodiversity and restoring fisheries throughout the Coral Triangle (White et al., 2014). However, there is less appreciation for the importance of protecting MCEs within MPAs in this region due to the lack of ecological studies that extend beyond shallow reefs (Andradi-Brown et al., 2021). Aside from being one of the first to provide baseline data for the newly protected Cagayancillo MPA, this study is one of the few in the Coral Triangle to investigate MPA effects at mesophotic depths, which was made possible by BRUVs. It is also one of the few that focused on assemblages of large carnivorous reef fish species outside of sharks, which contributes to raising awareness about remote reefs in the region where these species remain relatively abundant. This study showed that there is a distinction between shallow and mesophotic communities, which emphasizes the need to conserve MCEs in addition to shallow reefs. Conservation of MCEs can be achieved by explicitly including deeper ecosystems in the planning and design of individual MPAs or MPA networks and not just focusing on the more familiar shallow ecosystems. Furthermore, this study underscores the importance of upholding the strict protection of old, large and fully no-take MPAs such as TRNP and points towards an opportunity to safeguard a rich assemblage of higher trophic level fishes in Cagayancillo, which can be realized by increasing its no-take zones. Large and remote MPAs in the Coral Triangle that include MCEs such as TRNP and Cagayancillo are crucial to maintaining marine biodiversity and must be protected permanently.

AUTHOR CONTRIBUTIONS

Mikaela L. Salvador, David T. Gauthier, Christopher E. Bird and Rene A. Abesamis conceived the study. Ryan Murray, Segundo F. Conales and Kymry Delijero conducted field data collection. Mikaela L. Salvador, Jean Asuncion T. Utzurum, David T. Gauthier, Christopher E. Bird and Rene A. Abesamis carried out video and data

analysis. Mikaela L. Salvador and Rene A. Abesamis drafted the manuscript. All authors contributed to improving the manuscript and approved it for submission.

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CONFLICT OF INTEREST STATEMENT

The authors declare that there is no conflict of interest.

DATA AVAILABILITY STATEMENT

All data and data analyses are available at <https://github.com/Ph-IRES/salvador>.

ETHICS AND PERMIT STATEMENT

This project was completed with approval from the Tubbataha Management Office and the local government of Cagayancillo. All work strictly adhered to the guidelines of the Tubbataha Reefs Natural Park (TRNP) Act of 2009. Large Marine Vertebrates Research Institute (LAMAVE) received prior consent from the Protected Area Management Board (PAMB) of the TRNP.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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