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Madeline Steinberg, Jean-Baptiste Juhel, Virginie Marques, Clara Péron, Régis Hocdé, et al.. Similar trait structure and vulnerability in pelagic fish faunas on two remote island systems. Marine Biology, 2022, 169 (1), 10.1007/s00227-021-03998-6 . hal-03566643

HAL Id: hal-03566643

https://hal.umontpellier.fr/hal-03566643v1

Submitted on 6 Oct 2022

Similar trait structure and vulnerability in pelagic fish faunas on two remote island systems

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Running title: Pelagic species composition and functional traits

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Abstract

The link between biodiversity and ecosystem functioning has been the topic of considerable research, but it remains unclear how biodiversity decline is compromising ecosystem functionality, particularly in the pelagic realm. Here, we explore how pelagic fish species diversity relates to functional diversity by sampling two locations, which, on the basis of biogeography, environmental conditions, and human pressures, were expected to host pronounced differences in species composition and abundances, and therefore functionality. Strings of five drifting mid-water Baited Remote Underwater Video Systems were used to survey pelagic vertebrate diversity and abundance in two isolated oceanic island systems, the Malpelo Fauna and Flora Sanctuary – a large, 25-year-old marine protected area – and an unprotected area in Cape Verde. Functional diversity, which offers insight into a community's resilience against disturbance, was analysed using six key functional traits of marine fishes. Abundance was recorded as Max*N*, the maximum number of individuals of a given species in a single frame during the 2-hour deployment time. Cape Verde showed high overall abundance (Total Max*N* 873) and low biomass (3,559 kg), with a predominance of smaller fishes. Malpelo showed high biomass (7,839 kg) but lower abundance (Total Max*N* 465), with a predominance of large species. Species and functional diversity were marginally different between locations. Multivariate analysis of species relative abundances showed significant divergence between locations, although community functional traits overlapped strongly, suggesting that both communities share a similar structure and vulnerability. The existence of a common functional 'backbone' in diverging species communities across the oceans, under different productivity regimes, and under different protection levels, suggests that although pelagic communities may differ considerably in terms of species composition, this does not translate into a differing functional structure and resilience potential. Whether this vulnerability is a common feature of pelagic communities and how this contrasts with benthic systems warrants further research.

Key words: Biodiversity, Functional diversity, Pelagic fish, Islands, Mid-water BRUV

Introduction

The pelagic realm is the world's largest habitat, covering 71% of Earth's surface (1368.10^6 km^2), and providing millions of tons of fish biomass annually (Chassot et al. 2010). Pelagic systems have a massive influence on global nutrient cycling, food production, and climate change, each of which may be influenced by the abundance and composition of pelagic communities (Duffy & Stachowicz 2006, Sala et al. 2021). Yet, the vast pelagic area with dynamic environmental conditions (Breitburg et al. 2018)) and heterogeneous distribution of animals (Denderen et al. 2018) make it difficult to monitor and understand pelagic faunas (Briscoe et al. 2016), challenging the design of marine protected areas (Sala et al. 2021) and the appropriate management of fisheries (Pons et al. 2018).

Pelagic ecosystems hold unique characteristics compared to the benthos, with likely implication for vulnerability and resilience. While pelagic diversity is considered relatively low compared with that of demersal fish communities (Tittensor et al. 2010), pelagic communities may show high local diversity, as a function of biogeography, bathymetry, and productivity (Bouchet et al. 2020). Oceanic islands, banks, and seamounts are notable hotspots of species richness (Letessier et al. 2019), which predictably aggregate fish biomass, including mobile predators, by acting as navigation points and reliable feeding grounds (Hosegood et al. 2019). Because prey density in the open ocean is generally low, predators need to forage over a wide range to fulfil their energetic requirements, leading to resource translocation from other habitats and promoting food web connectivity (Heupel et al. 2014).

Ecosystem functioning and resilience are increasingly assessed using trait-based analyses (McLean et al. 2019), an approach that determines which functional roles are being filled and by which species (Mouillot et al. 2013). At the community level, functional traits explain differences of vulnerability between species: for example, predators and large individuals may be preferentially targeted by fishing (Mbaru et al. 2020). In the face of increasing fisheries pressure and environmental change, a trait-based approach may capture novel aspects of pelagic community vulnerability missed by classic community-based analyses. However, it remains unclear to which degree different pelagic systems are similarly vulnerable, due in part because of limited pelagic sampling methodologies (Letessier et al. 2017).

Here, we use mid-water Baited Remote Underwater Video Systems (BRUVS, Bouchet & Meeuwig 2015) to assess how pelagic fish communities differ taxonomically and functionally. Our study took place in Malpelo Island and in Cape Verde, two remote tropical island systems located in different biogeographical provinces (Kulbicki et al. 2013), which are exposed to contrasting levels of both environmental conditions and human pressures. We hypothesise that species community differences in taxonomy and relative abundance at each location may lead to trait dissimilarity, with implication for resilience and vulnerability.

Our objectives were to 1) describe and contrast species communities on each island using mid-water BRUVS and multivariate analyses, and 2) assess the extent to which any species dissimilarity translates into functional dissimilarity, using multivariate trait-based analyses, and then (3) make general inference concerning pelagic vulnerability.

Materials and Methods

Study locations

Our study aimed to target features such as islands and seamounts known to provide key habitat for top predators and migratory species. In Malpelo Island, BRUVS were deployment at four sites around the island, located within 3°57’5.184” to 4°1’46.704” N, and 81°40’8.256” to 81°35’47.4” W, with seabed depths ranging from 25 m to 1500 m (Fig. 1). In Cape Verde, BRUVS deployments focusing on the areas southwest of the island of Boa Vista, and on the João Valente Bank seamount between 15°47’40.452” to 16°0’25.2” N, and 23°12’17.316” to 22°56’11.148” W, with seabed depths ranging from 25 to 500 m (Fig. 1).

Malpelo is a remote oceanic island located in the Tropical Eastern Pacific, approximately 500 km west of Buenaventura, Colombia. The interaction of multiple seasonal currents results in distinct cold and warm water seasons at Malpelo (Bessudo et al. 2011). The survey at Malpelo was conducted between 18 and 28 March 2018, 8:00 AM to 5:00 PM local time, during the cold season, which occurs between January and April and is characterized by a shallow thermocline – around 15 m depth – decreased visibility due to high primary production caused by upwelling, and an average sea surface temperature of about 25° C (Soler et al. 2013). An area of 8,575 km² surrounding Malpelo is designated as the Malpelo Flora and Fauna Sanctuary, a marine protected area (MPA) since 1995 (UNESCO 2019). Though it is a no-take MPA, some illegal, unreported, and unregulated (IUU) fishing activity is believed to occur (Bessudo et al. 2011).

The Republic of Cape Verde is an archipelago nation located around 600 km west of Senegal, with a population of approximately 550,000 (United Nations 2019). It falls within the Tropical Eastern Atlantic biogeographic region and is subject to the seasonal influences of both the Canary Current and the North Equatorial Countercurrent (Wirtz et al. 2008). The survey in Cape Verde took place from 27 September to 1 October 2017, 9:00 AM to 4:30 PM local time, in the warmer months, during which average sea-surface temperature is around 27°C (Stobberup et al. 2004). Domestic artisanal and commercial fishing occur throughout the area, including vessels flagged from the European Union and China (Medina et al. 2015). Substantial IUU fishing also contributes to overall fisheries landings (Medina et al. 2015). Pelagic target species include tuna, billfish and mackerel scad, with sharks as important bycatch (Santos et al. 2013).

Sampling protocol

The pelagic community in each location was assessed using drifting mid-water BRUVS (Bouchet & Meeuwig 2015). Each rig consisted of a metal frame with two GoPro cameras in underwater housings mounted on a bar perpendicular to an arm supporting a bait canister filled with 1 kg of crushed fish (tuna and mackerel). The two cameras were intended to be used for stereo measurements, but could not be calibrated in the field, so only footage from the right-hand camera of each rig was used for analysis. The rigs were suspended from buoys at a depth of 10 m (Bouchet & Meeuwig 2015). BRUVS rigs were deployed in groups of five – hereafter referred to as “strings” – with each rig connected to the next one by a 200 m line. This distance was a trade-off between field practicalities and maximising the distance between rigs (Bouchet et al. 2018). The strings were allowed to drift for approximately two hours, an effective duration for mid-water BRUVS (Bouchet et al. 2018).

Data analyses

The BRUVS footage was analysed using the video analysis software VidSync (Neuswanger et al. 2016). Analysis began when the camera settled underwater and ended when the duration of the recording reached two hours. Species were identified to the lowest possible taxonomic level using information and photographs available from reference books and FishBase (Froese & Pauly 2019, Humann & DeLoach 2004, Humann & DeLoach 2014). Where species-level identifications could not be made, genus or family names were used. For each species, we recorded Max*N*, the maximum number of individuals present in a single frame, thereby preventing double-counting (Priede et al. 1994). Due to the proximity between each rig, abundance for each species was reported at the level of the string, using the maximum Max*N* value across each rig (Bouchet et al. 2018). We opted for this approach as 200 m separation between rigs is probably not sufficient to guarantee independence, certainly not for large sharks, which can cover more than this distance during the 2-hour soak time. In the absence of stereo measurements, the biomass of each species was computed using common lengths and Bayesian length-weight coefficients available from FishBase and scaled by abundance (Table S1). These biomass estimates are speculative since they are based on calculations from FishBase rather than true measurements. The conclusions on biomass patterns from this study are therefore rough estimates. Future studies should include stereo measurements to more accurately assess patterns in fish biomass.

Total abundance and biomass by deployment or site were analysed using PERMANOVA. Biomass was reported by species, but was not analysed further. The differences between species communities at each site were tested with an analysis of similarities (ANOSIM) on Bray-Curtis dissimilarity between all pairs of communities. A similarity percentage (SIMPER) analysis using Bray-Curtis dissimilarity and 1,000 permutations were used to compare species groups by site. Species community abundance were illustrated using non-metric multidimensional scaling (NMDS).

Each species was functionally described using a set of 6 complementary traits describing their key ecological features (Mouillot et al. 2014, Villéger et al. 2017). The traits were size, mobility, period of activity, schooling, position in water column, and diet (Table S2). Values for the adult stage of each species were gathered from FishBase and other literature (Supplementary material). A multidimensional functional space was calculated following the methods of Maire et al. (2015). First, a dissimilarity matrix quantifying the functional distance between species was computed using Gower's distance, which is able to accommodate categorical traits. A Principal Coordinates Analysis (PCoA) was performed with this matrix, and the mean squared deviation (mSD) was used to select the best quality functional space. The mSD quantifies the "mean squared deviation between the initial functional distance and the scaled distance in the functional space" and – when using Gower's distance – ranges from 0 to 1, the closest value to zero indicating the most robust functional space (Maire et al. 2015). The four-dimensional space – or the space using the first four axes of the PCoa – was the highest quality space with an mSD of 0.0026 (Fig. S1).

Three complementary functional diversity indices were calculated using species position in the multidimensional space: functional richness (FRic), functional evenness (FEve), and functional divergence (FDiv) (Villéger et al. 2008). These metrics are favoured for functional diversity analysis because they can work with multiple traits. FRic measures how much functional space is filled by a species community and accounts only for species position in the multidimensional range. FEVe and FDiv account for species abundance and measure regularity and variance within the occupied space, respectively (Villéger et al. 2008). To further explore functional overlap between communities, functional beta-diversity and its percentage due to species turnover were computed using Jaccard's dissimilarity index (Villéger et al. 2013). All analyses were performed in R statistical software (R Core Team 2018), including the *mFD* package for computation of functional space and functional diversity indices (https://cmlmagneville.github.io/mFD/).

Results and discussion

Eight strings, a total of 40 individual rigs (80 video hours in total), were deployed in Malpelo and nine strings, a total of 44 individual rigs as one string had only 4 rigs (88 video hours in total), were deployed in Cape Verde. In line with expectations, we observed distinct species compositions between locations. BRUVS observations yielded 29 fish species, one juvenile group (Carangidae) and one mammal (family Delphinidae), with 18 species present in Malpelo and 19 species present in Cape Verde (Fig. 2A). Species ubiquitous to both sites were wahoo (*Acanthocybium solandri*), silky shark (*Carcharhinus falciformis*), mackerel scad (*Decapterus* sp.), amberjack (*Seriola* sp), and juveniles of family Carangidae. Strings recorded on average fewer species in Cape Verde (5.22 ± 2.11 SD per string) than in Malpelo (6.25 ± 2.19 SD), albeit not significantly (PERMANOVA $F_{1,15}$ = 0.3011, p-value = 0.773). Abundance was higher in Cape Verde (873 individuals total, mean 97 ± 128.9 SD per string), than in Malpelo (465 individuals total, mean 58.1 ± 59.9 SD per string), whereas biomass in Malpelo (7,838 kg total, mean 979.8 ± 506.3 SD per string) far exceeded the biomass observed in Cape Verde (3,558 kg total, mean 395.44 ± 563.1 SD per string, Fig. 2B). An ANOSIM test revealed significantly dissimilar clusters between locations (R = 0.5, p = 0.001, Fig. 3A and B). Fifteen species were responsible for 95% of the dissimilarity between sites (Table S3, SIMPER). Mackerel scad (*Decapterus* sp.), rainbow runner (*Elagatis bipinnulata*), yellowfin tuna (*Thunnus albacares*), and little tunny (*Euthynnus alletteratus*) cumulatively contributed 55% of the difference in abundance between Cape Verde and Malpelo, while rainbow runner, yellowfin tuna, scalloped hammerhead (*Sphyrna lewini*), and cornetfish (*Fistularia* sp.) contributed significantly to (p < 0.05).

In contrast with expectations, communities from the two locations filled the same amount of the functional space (functional richness Malpelo: 0.542, Cape Verde: 0.452), and species abundance were similarly distributed in the filled space (functional divergence: Malpelo: 0.833, Cape Verde 0.913) in both locations. While the volume of the overall space occupied by each location was relatively high, the majority of the species were densely distributed in one area of the space, displaying low functional evenness (0.425 for Cape Verde, and 0.346 for Malpelo). The first two dimensions showed most species clustered on the right-hand side (Fig. 3C), defined by mobility, whereas the outliers on the left side of the space had a more restricted range (Fig. S2A). Highly mobile species, clustered into two groups, one characterised by purely pelagic species of very small, and medium size, and with a planktivorous or omnivorous diet and one by large or very large, benthopelagic species living solitary or in small groups, and with either a piscivorous or invertivorous diet. The third and fourth dimensions of the functional space showed some of the same stratification observed on the first two dimensions. However, the species which diverged from the main group were planktivores and invertivores which fed on mobile prey (Fig. 3D), with loose grouping according to different daily activity patterns (Fig. S2B).

Functional divergence and functional evenness are indices of the variance and regularity of species' distribution within the functional space, respectively, weighted by abundance (Villéger et al. 2008). A highly divergent and minimally even community is one in which some functional roles are much better represented and insured than others, which leaves points of exposure to disturbance, particularly when – as was the case here - dominant and common species are sensitive (McLean et al. 2019). The most dominant species overall across either location, the Atlantic horse mackerel (*Trachurus trachurus*) is listed as Vulnerable (Smith-Vaniz et al. 2015). The most abundant by weight, yellowfin tuna (*Thunnus albacares*), was at the time of sampling listed as Near Threatened, although has since been listed as Least Concern (Collette et al. 2021). Furthermore, ecologically important top predators like the silky shark and scalloped hammerhead that were ubiquitous in both locations are listed as Vulnerable (Rigby et al. 2017) and Critically Endangered (Rigby et al. 2019), respectively.

Overall functional beta-diversity between the locations was 0.6, to which species turnover contributed 90.3%. The remaining proportion arose from distinct trait combinations, often between confamilials like the triggerfishes (mobile in Malpelo, and reef-associated in Cape Verde), surgeonfishes (large in Malpelo and small in Cape Verde) and jacks (large and piscivorous in Malpelo, and medium and invertivore in Cape Verde). Fishing remains the primary threat to pelagic elasmobranchs and teleosts (Pacoureau et al. 2021). Although the bulk of the functional space was similar between locations, the presence of such unique trait combinations suggests that some nuanced differences in sensitivity may still render certain locations more or less resilient (Villéger et al. 2013). Future research should aim to identify pelagic systems which overperform compared to expectations, in order to identify unique resilient traits associated with either positive or negative ecosystem outcomes (Cinner et al. 2016).

Our survey included different biogeographical provinces and covers contrasting ends of environmental and human pressure gradients, although -due to time constraints, is limited to a snap-shot view of the species diversity and abundance. Nevertheless our results presents preliminary evidence that pelagic ecosystems may share a common 'backbone' of functional traits related to mobility and predatory diet. Such a backbone of 21 common traits has already been documented to exist within global reef ecosystems (McLean et al. 2021). Since ecological disturbance is likely to affect species with identical functional traits in similar ways (Mouillot et al. 2013), low trait diversity within pelagic ecosystems may make the pelagic faunas particularly vulnerable to disturbance. A lack of fish length stereo-measurements means our biomass estimates must be interpreted with caution. We propose that further study specifically aims to determine whether this is a consistent feature of the pelagic realm, and the degree to which it may affect the resilience of mid-water communities.

Acknowledgements

We thank Monaco Explorations for supporting the fieldwork and The Bertarelli Foundation for TBL's time and salary in the field. We are grateful to the Master and Crew of the RV Yersin for supporting sampling activities. We thank Dr. Christophe Eizaguirre for his support as a teacher and adviser to MS.

Declarations

Fundings

Field activities were funded by Monaco Explorations. The Bertarelli Foundation funded TBL's salary

Conflict of interest

We declare no conflict of interest

Ethics approval

As none of the authors are resident in Cape Verde, research there was conducted under authorization No. 08/GP-CA.AMP/2017.

Data/Code availability

All code is referenced in the text

Author's contribution

MS conceived and conducted the analysis, and as part of her MSc thesis. TBL supervised and managed the study, and co-wrote the first draft together with MS. TBL and JB coordinated the BRUVS deployment, with assistance from RH, LP, CP, AP, and VM. DM and SV advised on the functional analysis. DM is the PI of the Monaco Exploration 'Megafauna' team. All authors helped revise the manuscript.

Figures

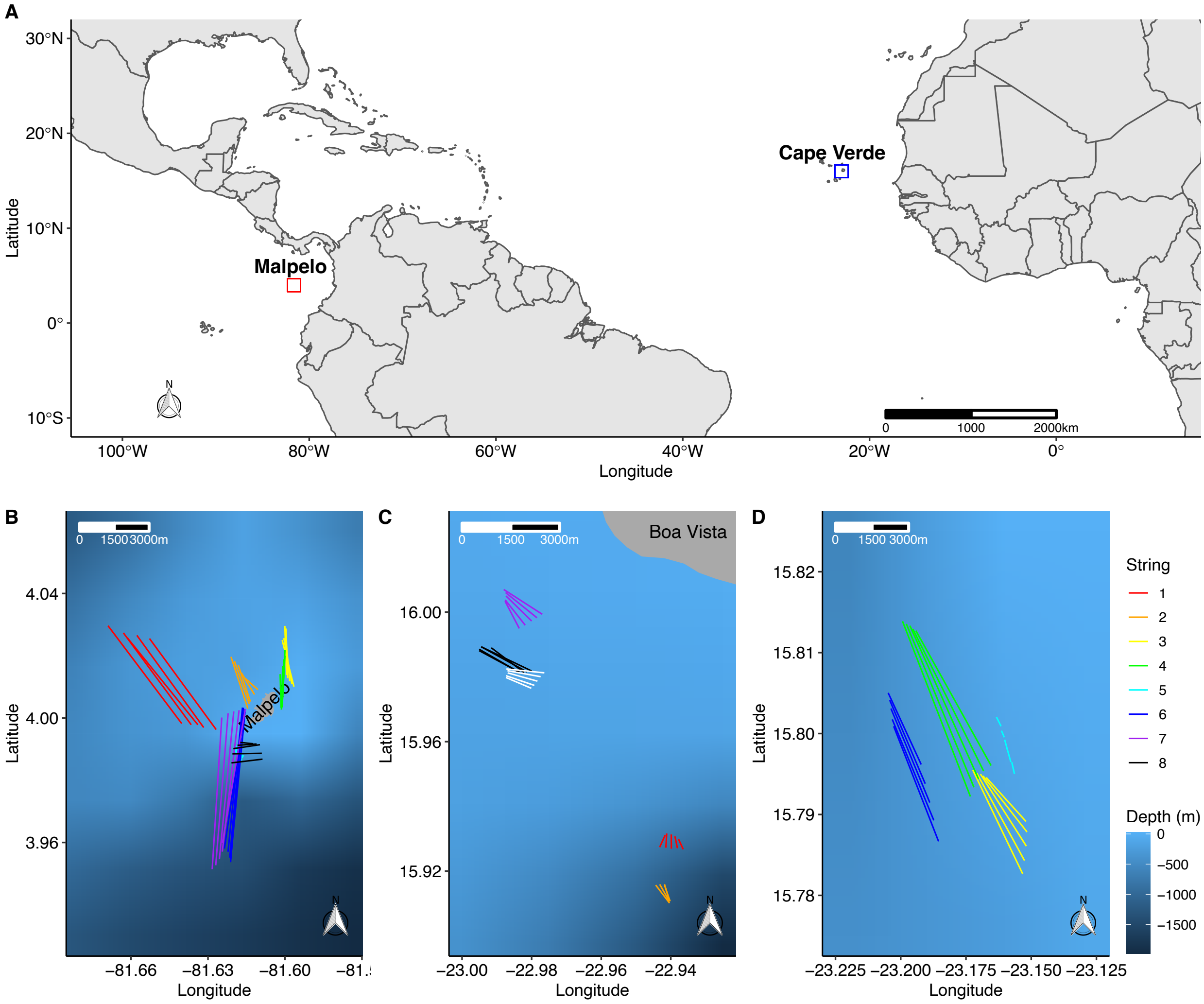

Fig. 1 Sampling locations and deployment sites. Sampling locations (A) and BRUVS deployment sites in Malpelo (B) and Cape Verde (C, D). Line segments indicate BRUVS trajectories and are color-coded by string, with each line representing an individual rig.

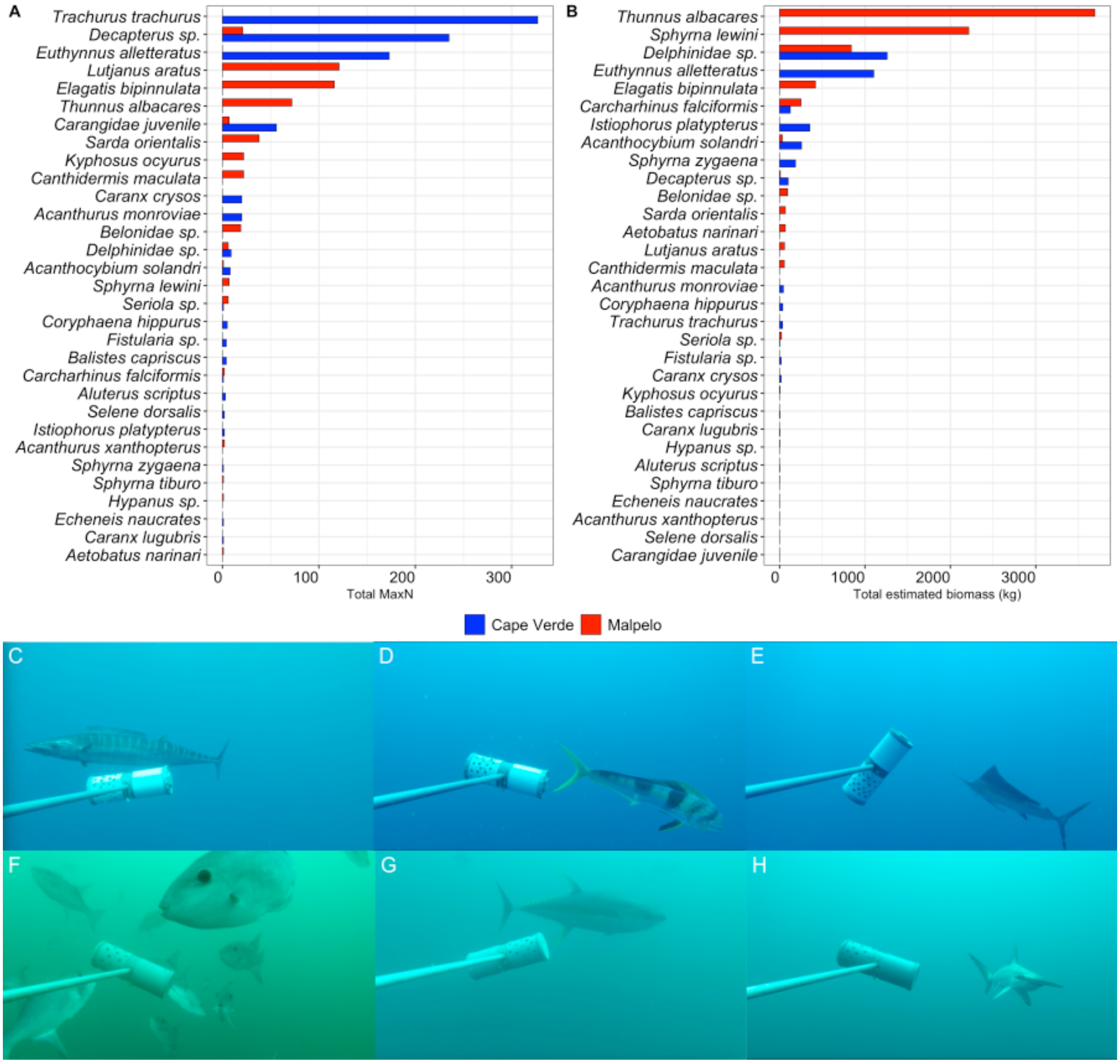

Fig. 2 Fish community composition in Malpelo and Cape Verde. Ranked abundance (A) and biomass (B) of species recorded in either location, and examples of species observed using BRUVS. Stills (C) through (E) are from Cape Verde: (C) *Acanthocybium solandri* – Wahoo; (D) *Coryphaena hippurus* – Common dolphinfish; (E) *Istiophorus platypterus* – Indo-Pacific sailfish [This identification reflects the increasingly common belief that there is only one pantropic species of sailfish (e.g Collette et al. 2011), rather than *I. albicans* in the Atlantic and *I. platypterus* in the Indo-Pacific]. Stills (F) through (H) are from Malpelo: (F) *Canthidermis maculata* – Rough triggerfish; (G) *Thunnus albacares* – Yellowfin tuna; (H) *Sphyrna lewini* – Scalloped hammerhead.

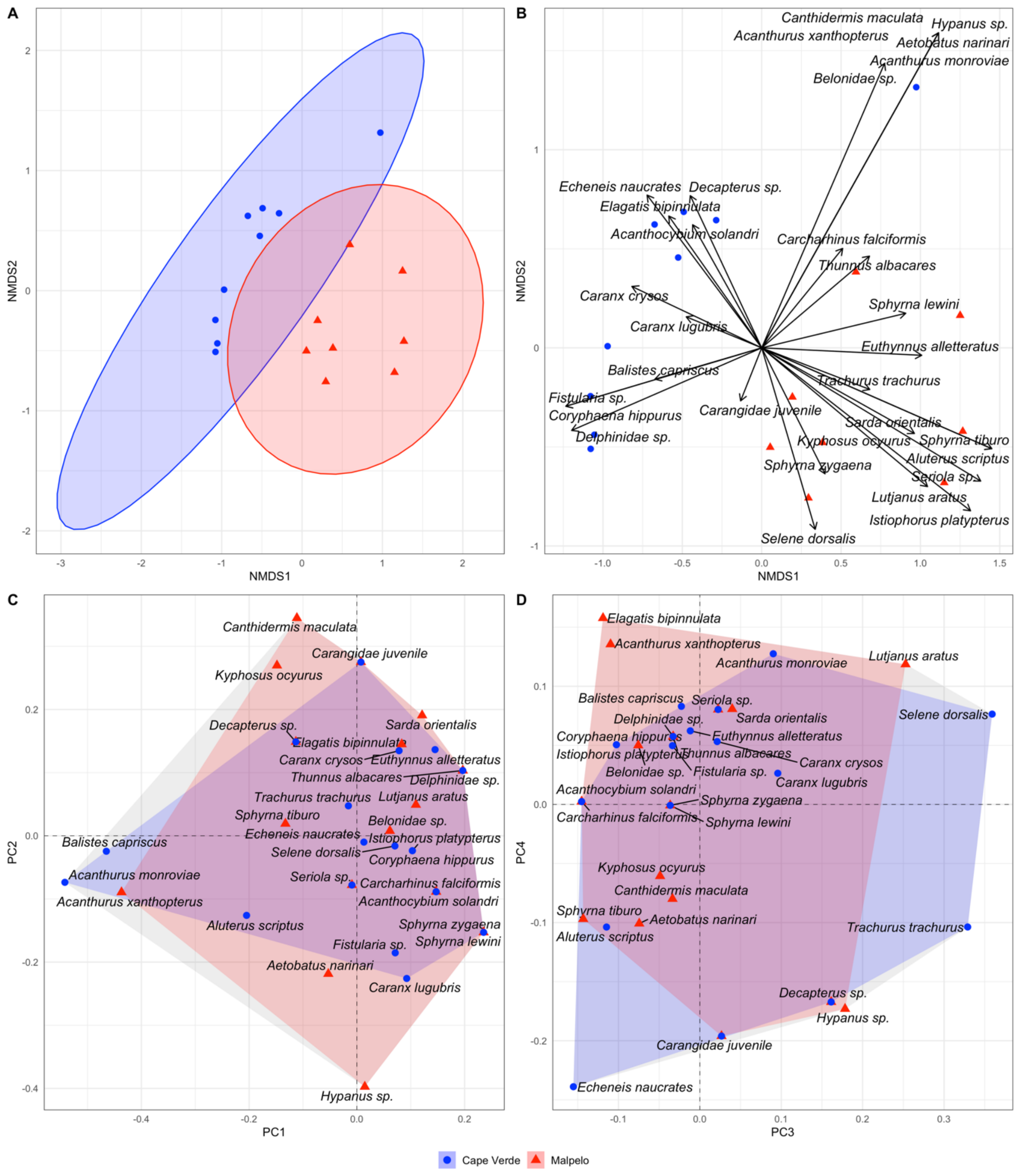

Fig. 3 Species community differences and functional similarity in Malpelo and Cape Verde. Two-dimensional NMDS ordination plot with 95% confidence level ellipses based on ANOSIM results from samples (BRUVS strings) from Cape Verde and Malpelo (A). NMDS plot of samples with vectors showing species correlation (B). Distribution of species in the first and second (C) and third and fourth (D) dimensions of the functional space. Grey hull indicates overall volume of the functional space on the two axes shown. Red (Malpelo) and blue (Cape Verde) hulls contain positions of all species found at each site.

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