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

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2 **systems**

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7 Running title: Pelagic species composition and functional traits
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29 **Abstract**

30 The link between biodiversity and ecosystem functioning has been the topic of

31 considerable research, but it remains unclear how biodiversity decline is compromising

32 ecosystem functionality, particularly in the pelagic realm. Here, we explore how pelagic fish

33 species diversity relates to functional diversity by sampling two locations, which, on the

34 basis of biogeography, environmental conditions, and human pressures, were expected to

35 host pronounced differences in species composition and abundances, and therefore

36 functionality. Strings of five drifting mid-water Baited Remote Underwater Video Systems

37 were used to survey pelagic vertebrate diversity and abundance in two isolated oceanic

38 island systems, the Malpelo Fauna and Flora Sanctuary – a large, 25-year-old marine

39 protected area – and an unprotected area in Cape Verde. Functional diversity, which offers

40 insight into a community's resilience against disturbance, was analysed using six key

41 functional traits of marine fishes. Abundance was recorded as Max$N$, the maximum

42 number of individuals of a given species in a single frame during the 2-hour deployment

43 time. Cape Verde showed high overall abundance (Total Max$N$ 873) and low biomass (3,559

44 kg), with a predominance of smaller fishes. Malpelo showed high biomass (7,839 kg) but

45 lower abundance (Total Max$N$ 465), with a predominance of large species. Species and

46 functional diversity were marginally different between locations. Multivariate analysis of

47 species relative abundances showed significant divergence between locations, although

48 community functional traits overlapped strongly, suggesting that both communities share

49 a similar structure and vulnerability. The existence of a common functional 'backbone' in

50 diverging species communities across the oceans, under different productivity regimes,

51 and under different protection levels, suggests that although pelagic communities may

52 differ considerably in terms of species composition, this does not translate into a differing

53 functional structure and resilience potential. Whether this vulnerability is a common

54 feature of pelagic communities and how this contrasts with benthic systems warrants

55 further research.

56

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58 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

88 vulnerable, due in part because of limited pelagic sampling methodologies (Letessier et al.
89 2017).

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

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

102

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

113 Malpelo is a remote oceanic island located in the Tropical Eastern Pacific, approximately
114 500 km west of Buenaventura, Colombia. The interaction of multiple seasonal currents
115 results in distinct cold and warm water seasons at Malpelo (Bessudo et al. 2011). The survey
116 at Malpelo was conducted between 18 and 28 March 2018, 8:00 AM to 5:00 PM local time,

117 during the cold season, which occurs between January and April and is characterized by a

118 shallow thermocline – around 15 m depth – decreased visibility due to high primary

119 production caused by upwelling, and an average sea surface temperature of about 25° C

120 (Soler et al. 2013). An area of 8,575 km² surrounding Malpelo is designated as the Malpelo

121 Flora and Fauna Sanctuary, a marine protected area (MPA) since 1995 (UNESCO 2019).

122 Though it is a no-take MPA, some illegal, unreported, and unregulated (IUU) fishing activity

123 is believed to occur (Bessudo et al. 2011).

124 The Republic of Cape Verde is an archipelago nation located around 600 km west of

125 Senegal, with a population of approximately 550,000 (United Nations 2019). It falls within

126 the Tropical Eastern Atlantic biogeographic region and is subject to the seasonal influences

127 of both the Canary Current and the North Equatorial Countercurrent (Wirtz et al. 2008).

128 The survey in Cape Verde took place from 27 September to 1 October 2017, 9:00 AM to

129 4:30 PM local time, in the warmer months, during which average sea-surface temperature

130 is around 27°C (Stobberup et al. 2004). Domestic artisanal and commercial fishing occur

131 throughout the area, including vessels flagged from the European Union and China (Medina

132 et al. 2015). Substantial IUU fishing also contributes to overall fisheries landings (Medina

133 et al. 2015). Pelagic target species include tuna, billfish and mackerel scad, with sharks as

134 important bycatch (Santos et al. 2013).

135 *Sampling protocol*

136 The pelagic community in each location was assessed using drifting mid-water BRUVS

137 (Bouchet & Meeuwig 2015). Each rig consisted of a metal frame with two GoPro cameras

138 in underwater housings mounted on a bar perpendicular to an arm supporting a bait

139 canister filled with 1 kg of crushed fish (tuna and mackerel). The two cameras were

140 intended to be used for stereo measurements, but could not be calibrated in the field, so

141 only footage from the right-hand camera of each rig was used for analysis. The rigs were

142 suspended from buoys at a depth of 10 m (Bouchet & Meeuwig 2015). BRUVS rigs were

143 deployed in groups of five – hereafter referred to as "strings" – with each rig connected to

144 the next one by a 200 m line. This distance was a trade-off between field practicalities and

145 maximising the distance between rigs (Bouchet et al. 2018). The strings were allowed to

146 drift for approximately two hours, an effective duration for mid-water BRUVS (Bouchet et
147 al. 2018).

148 *Data analyses*

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

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

175   Each species was functionally described using a set of 6 complementary traits describing

176   their key ecological features (Mouillot et al. 2014, Villéger et al. 2017). The traits were size,

177   mobility, period of activity, schooling, position in water column, and diet (Table S2). Values

178   for the adult stage of each species were gathered from FishBase and other literature

179   (Supplementary material). A multidimensional functional space was calculated following

180   the methods of Maire et al. (2015). First, a dissimilarity matrix quantifying the functional

181   distance between species was computed using Gower's distance, which is able to

182   accommodate categorical traits. A Principal Coordinates Analysis (PCoA) was performed

183   with this matrix, and the mean squared deviation (mSD) was used to select the best quality

184   functional space. The mSD quantifies the "mean squared deviation between the initial

185   functional distance and the scaled distance in the functional space" and – when using

186   Gower's distance – ranges from 0 to 1, the closest value to zero indicating the most robust

187   functional space (Maire et al. 2015). The four-dimensional space – or the space using the

188   first four axes of the PCoa – was the highest quality space with an mSD of 0.0026 (Fig. S1).

189   Three complementary functional diversity indices were calculated using species position in

190   the multidimensional space: functional richness (FRic), functional evenness (FEve), and

191   functional divergence (FDiv) (Villéger et al. 2008). These metrics are favoured for functional

192   diversity analysis because they can work with multiple traits. FRic measures how much

193   functional space is filled by a species community and accounts only for species position in

194   the multidimensional range. FEVe and FDiv account for species abundance and measure

195   regularity and variance within the occupied space, respectively (Villéger et al. 2008). To

196   further explore functional overlap between communities, functional beta-diversity and its

197   percentage due to species turnover were computed using Jaccard's dissimilarity index

198   (Villéger et al. 2013). All analyses were performed in R statistical software (R Core Team

199   2018), including the *mFD* package for computation of functional space and functional

200   diversity indices (https://cmlmagneville.github.io/mFD/).

201

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

263 unique resilient traits associated with either positive or negative ecosystem outcomes
264 (Cinner et al. 2016).

265 Our survey included different biogeographical provinces and covers contrasting ends of
266 environmental and human pressure gradients, although -due to time constraints, is limited
267 to a snap-shot view of the species diversity and abundance. Nevertheless our results
268 presents preliminary evidence that pelagic ecosystems may share a common 'backbone' of
269 functional traits related to mobility and predatory diet. Such a backbone of 21 common
270 traits has already been documented to exist within global reef ecosystems (McLean et al.
271 2021). Since ecological disturbance is likely to affect species with identical functional traits
272 in similar ways (Mouillot et al. 2013), low trait diversity within pelagic ecosystems may
273 make the pelagic faunas particularly vulnerable to disturbance. A lack of fish length stereo-
274 measurements means our biomass estimates must be interpreted with caution. We
275 propose that further study specifically aims to determine whether this is a consistent
276 feature of the pelagic realm, and the degree to which it may affect the resilience of mid-
277 water communities.

297   All code is referenced in the text
298
299   Author's contribution
300   MS conceived and conducted the analysis, and as part of her MSc thesis. TBL supervised
301   and managed the study, and co-wrote the first draft together with MS. TBL and JB
302   coordinated the BRUVS deployment, with assistance from RH, LP, CP, AP, and VM. DM and
303   SV advised on the functional analysis. DM is the PI of the Monaco Exploration 'Megafauna'
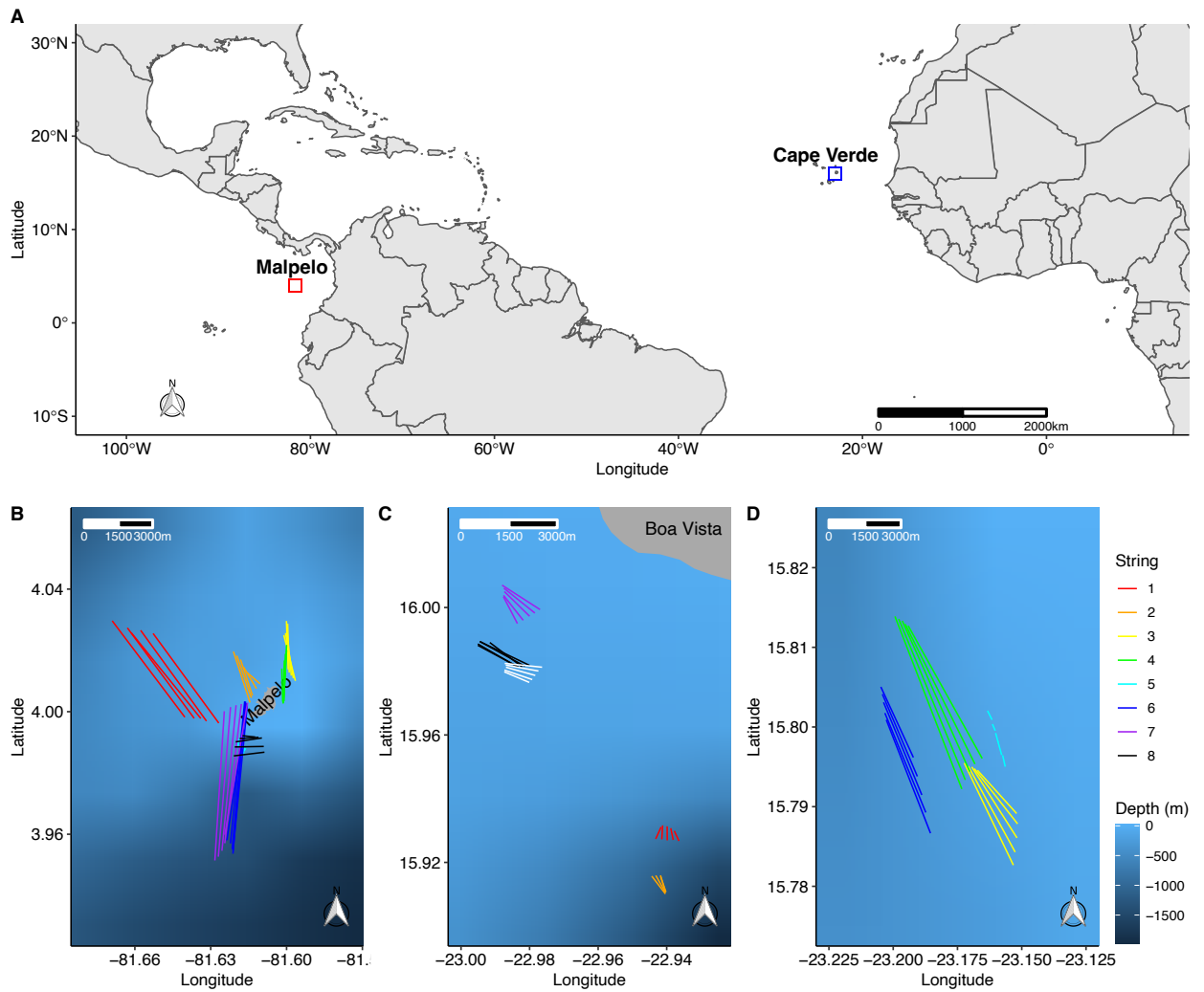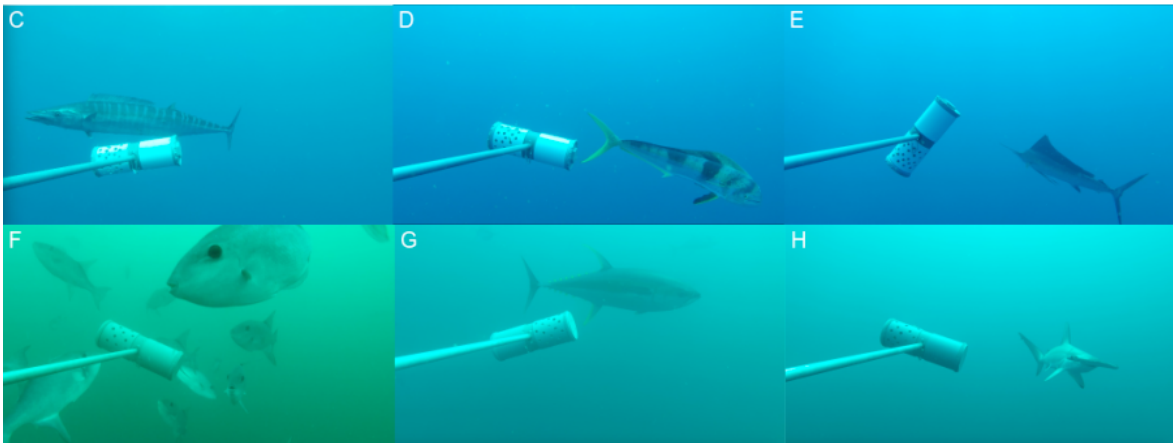304   team. All authors helped revise the manuscript.
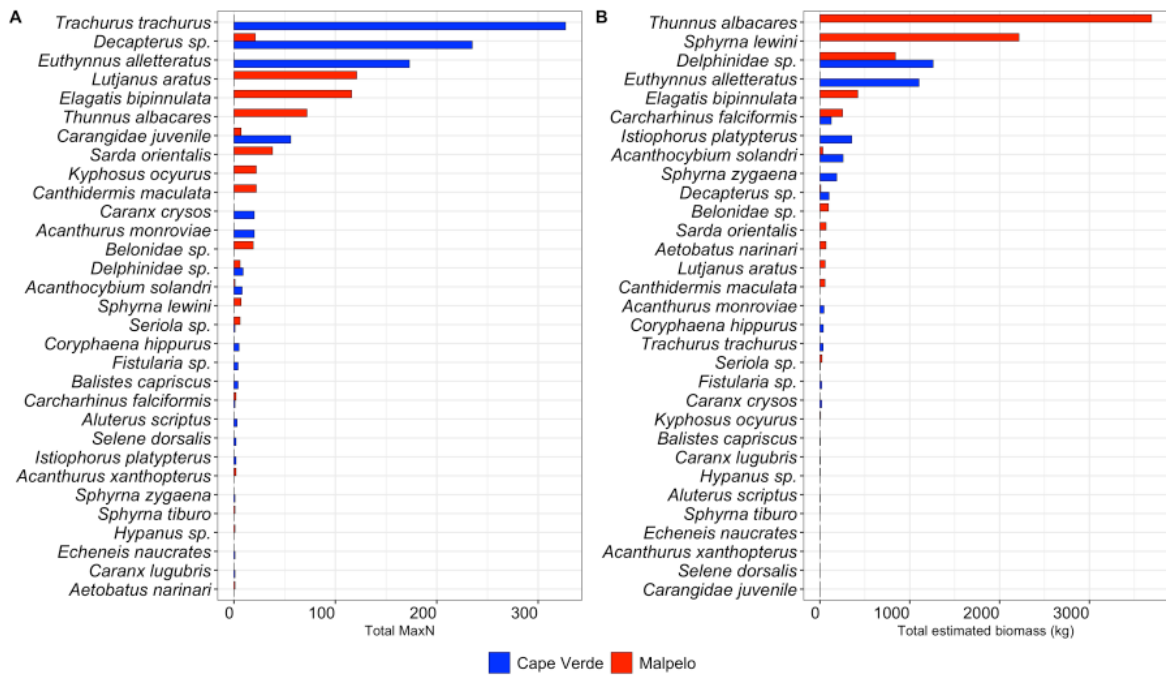305
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308
309 **Figures**

310

311 **Fig. 1** Sampling locations and deployment sites. Sampling locations (A) and BRUVS
312 deployment sites in Malpelo (B) and Cape Verde (C, D). Line segments indicate BRUVS
313 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.
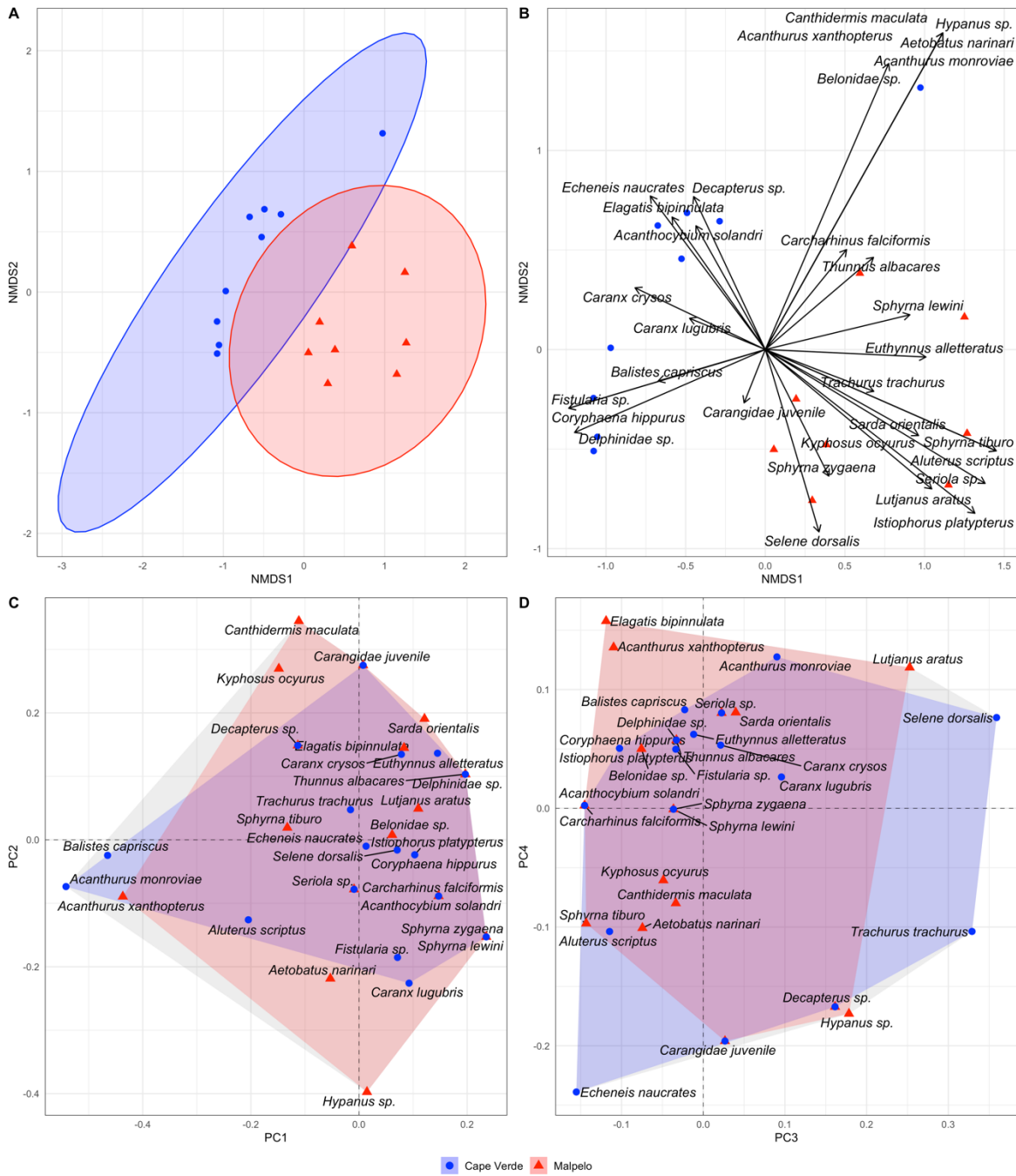
Fig. 3 Species community differences and functional similarity in Malpelo and Cape Verde. Two-dimensional NMDS ordination plot with 95% confidence level ellipses based on ANOSIM results from samples (BRUVS strings) from Cape Verde and Malpelo (A). NMDS plot of samples with vectors showing species correlation (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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