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## Comparison of mesozooplankton communities at three shallow seamounts in the South West Indian Ocean

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### Abstract :

Seamounts are recognised as hotspots of biodiversity, attracting large numbers of top predators, but the underlying mechanisms are still unclear. We studied mesozooplankton abundance and size distribution at three shallow seamounts (60m, 240m and 18m deep) in the South West Indian Ocean, along a latitudinal gradient (19°S, 27°S and 33°S). Samples were analysed using a ZooScan, allowing the use of a size-based approach. Differences were observed between seamount areas, but overall zooplankton communities did not seem to be affected by the changes in topography. Only in the lee of La Pérouse seamount was the zooplankton community slightly more concentrated than upstream, suggesting that zooplankton were flushed downstream of the seamount. The southernmost and shallowest seamount, Walters Shoal, had low abundance and its size spectrum differed greatly from the two other seamounts further north. These differences were attributed to seasonality and mesozooplankton population dynamics, whereas the other two seamounts exhibited a more “typical” oligotrophic pelagic ecosystem, at equilibrium and dominated by small organisms. At the time of sampling, the unnamed seamount south of Madagascar was influenced by a mesoscale dipole that impacted the zooplankton distribution, potentially masking any seamount effect. The normalised biomass spectrum approach contributed to a better understanding of the ecosystem dynamics (i.e. equilibrium vs. non-steady state) but revealed little variability within a stable oligotrophic environment.

**Keywords :** Normalised Biovolume Size Spectrum (NBSS), mesoscale eddies, topography, oligotrophic environment, pelagic ecology

## 38 1. Introduction

39 Seamounts have been identified as “hotspots” of biodiversity and productivity, inhabited by  
40 large fish aggregations (e.g. Genin, 2004; Morato et al., 2010a; Rogers, 2018, 1994). In  
41 recent years, they have been increasingly studied by oceanographers to understand their  
42 functioning, as well as by conservation entities attempting to preserve a pristine ecosystem  
43 and avoid overexploitation (e.g. Campos et al., 2019; Morato et al., 2010b; Warner, 2018).  
44 The underlying mechanisms that explain these aggregations of top predators are  
45 nonetheless far from being understood and many hypotheses have been put forward  
46 (Genin, 2004; Pitcher and Bulman, 2007). As described by Bakun (2006), three mechanisms  
47 must co-occur to allow an increase in biomass within a certain location: retention,  
48 enrichment, and concentration; and seamounts have the potential to satisfy all three  
49 criteria. Retention mechanisms that entrap a body of water on top of seamounts, such as  
50 Taylor columns, have been observed in very specific environments depending on currents,  
51 the size and the location of the seamount (Chapman and Haidvogel, 1992; White et al.,  
52 2007). Enrichment associated with seamounts has rarely been observed (reviewed by  
53 Rogers, 2018) but is often attributed to localised upwelling, induced by the topography and  
54 uplift of nutrients into the euphotic layer (Lemos et al., 2018; Mendonça et al., 2012).  
55 Advection, together with entrapment, will also result in increased production, and will be  
56 even more pronounced if the advected water mass is already enriched due the proximity of  
57 a continental shelf or another seamount.

58 *In situ* measurements have shown that zooplankton biomass is, in many cases, either not  
59 affected, or sometimes lower above the summit compared to the surrounding waters,  
60 especially over shallow seamounts that penetrate the euphotic zone (Carmo et al., 2013;  
61 Denda and Christiansen, 2014; Dower and Mackas, 1996; Genin et al., 1994; Haury et al.,

2000; Martin and Christiansen, 2009). The main reason put forward is the increase in predation pressure by benthic-pelagic or pelagic predators associated with seamounts (e.g. Frederick et al., 2018; Haury et al., 2000, 1995; Hosegood et al., 2019; Martin and Christiansen, 2009). Shallow topography (including continental shelves) concentrates zooplankton as the same number of organisms are contained within a shallower depth. Zooplankton that undergo diel vertical migration (DVM) can be trapped on the summit during their daily descent, known as topography blockage (Genin, 2004; Martin and Christiansen, 2009). This rise in zooplankton concentration, together with an intensifying flow on top of seamounts, increases prey encounter rates. Some pelagic predators would thus simply need to maintain their position above the seamount to benefit from an enhanced prey abundance passing through, therefore called the “feed rest” hypothesis (Genin, 2004). The impact of this predation can also be detected downstream of the seamount, with the formation of “gaps” in the zooplankton distribution (Dower and Mackas, 1996; Genin et al., 1994; Haury et al., 2000). Some authors have also suggested that zooplankton are ‘washed’ downstream of the seamount due to stronger currents above the seamount and are thus found in higher concentrations downstream compared to upstream of the seamount (Dower and Mackas, 1996; Genin, 2004). The last and more speculative hypothesis is related to the capacity of zooplankton, especially larger organisms, to horizontally avoid abrupt topography (Martin and Christiansen, 2009; Rogers, 1994). The mechanisms causing this behaviour are, however, not yet known.

Besides influencing zooplankton biomass, seamounts can also change the composition of the zooplankton community in their vicinity (Frederick et al., 2018; Martin and Christiansen, 2009). Inter- and intra-species interactions, as well as allochthonous growth, may alter the trophic structure of the advected zooplankton community. Amongst the approaches to investigate changes in zooplankton communities, size spectra have been widely used over the past two decades (reviewed by Sprules and Barth, 2015), partially related to the increase in technologies allowing semi-automated measurement and identification of plankton. Size structure is considered a useful metric for monitoring changes in plankton community structure and energy flux within a system (e. g. Basedow et al., 2010; Dai et al., 2016; García-Comas et al., 2014; Giering et al., 2018; Quinones et al., 2003; San Martín et al., 2006; Zhou et al., 2004). Size spectrum theory is based on predator-prey relationships and predicts a negative linear fit between biomass and size on a log-log scale (Platt and

94 Denman, 1977; Silvert and Platt, 1978). The most common metric used is the normalised  
95 biomass size spectrum. The parameters extracted from the normalised biomass size  
96 spectrum are inherent properties of the zooplankton community. One of these parameters,  
97 the slope, provides an index of the size distribution of the plankton and should be close to -1  
98 in a system that includes several trophic levels (Brown et al., 2004). A steeper slope  
99 indicates a higher proportion of small to large organisms, which could indicate an increase in  
100 reproduction and thus productivity (Zhou, 2006). The linear fit of the normalised biomass  
101 size spectrum is related to the stability of the ecosystem meaning that a deviation from  
102 linearity (i.e. low linear fit) can imply pulses of energy passing through the system and thus a  
103 non-steady state (e. g. Quinones et al., 2003; Rodriguez and Mullin, 1986).

104 It is generally assumed that season, the shape and depth of a seamount as well as the  
105 mesoscale current dynamics around it are important factors influencing the ecosystem  
106 associated with the seamount (Rogers, 2018, 1994). In this study, we selected three  
107 seamounts characterised by different topography and mesoscale conditions, and located  
108 along a latitudinal gradient in the South West Indian Ocean (SWIO). We used zooplankton  
109 abundance, biovolume and biovolume size spectrum parameters to investigate differences  
110 in the zooplankton communities at these three seamount ecosystems, and to explore  
111 whether topography had a discernible effect on zooplankton, stronger than the other  
112 drivers affecting the waters surrounding the seamounts.

113

## 114 **2. Methods**

### 115 *2.1. Study areas*

116 The three studied seamounts, La Pérouse, an unnamed seamount on the Madagascar Ridge  
117 - named MAD-Ridge hereafter, and Walters Shoals, are located along a latitudinal gradient  
118 in the SWIO at 19.43°S, 27.29°S and 33.12°S, respectively (Fig. 1). La Pérouse is 60m deep  
119 surrounded by depths of about 3000m, with a very uneven contour and steep slopes. It is in  
120 the path of the westward-flowing South Equatorial Current (SEC) and subject to limited  
121 mesoscale activity (Annasawmy et al., this issue). The two other seamounts are located on  
122 the Madagascar Ridge which has a bottom depth varying between approximately 1000 and  
123 2500m. MAD-Ridge is located about 225 km south of the southern tip of Madagascar with  
124 its summit at 240m depth. This seamount is influenced by the South-East Madagascar

125 Current (SEMC) and by strong mesoscale activity with many eddies formed all year round  
126 (de Ruijter et al., 2004a; Halo et al., 2014). Walters Shoal has a caldera-like shape with  
127 shallow circular walls, reaching ~ 18 m depth at its sides, with a deeper centre at about 50m.  
128 It is located near the Southern Indian Subtropical Gyre, and mesoscale turbulence in the  
129 vicinity is very low (Pollard and Read, 2017). All three seamounts have been identified as  
130 foraging areas for birds and other predators (Roberts et al., this issue).

131

## 132 2.2. Sampling

133 Mesozooplankton samples were collected at 46 stations during three cruises: La Pérouse  
134 (DOI: 10.17600/16004500) from 21-27 September 2016, MAD-Ridge (DOI:  
135 10.17600/16004800) from 14-22 November 2016, both on the *R/V Antea*, and Walters Shoal  
136 (DOI: 10.17600/17002700) from 30 April to 7 May 2017 on the *R/V Marion Dufresne* (Table  
137 1 sup. material). Ten stations were sampled at La Pérouse, 23 at MAD-Ridge and 13 at  
138 Walters Shoals. For La Pérouse and MAD-Ridge, stations were classified as either “on” or  
139 “off” the seamount based on the topography. The “on” stations were located above the  
140 summit and over the slopes of the seamount (6 at La Pérouse and 6 at MAD-Ridge) while  
141 the bottom depth of the “off” seamount stations was similar to the seafloor in the greater  
142 vicinity of the seamount ( $n = 4$  and 15 stations at La Pérouse and MAD-Ridge, respectively).  
143 The stations “off” the seamount were generally more than 15km away from the seamount,  
144 except for station 2 at La Pérouse which was only 7km away from the seamount. At MAD-  
145 Ridge, an extra 3 stations were sampled on the northern side of the south-north transect  
146 and which were classified as “shelf” stations being influenced by the Madagascan shelf  
147 productive waters (Fig. 2). These stations were sampled to have a zooplankton “shelf”  
148 signature to compare with the offshore stations as cross-shelf transport exists in this region  
149 and can influence zooplankton composition within eddies (Noyon et al, 2018). At Walters  
150 Shoal, due to the draught of the ship (~7m), no samples were taken on top of (or inside) the  
151 seamount, and due to ship time constraints, no “off” seamount stations were sampled. Only  
152 stations on the slopes were sampled, all around the seamount ( $n = 13$ ).

153 Zooplankton samples were collected using a Bongo net (0.28 m<sup>2</sup> mouth area) at La Pérouse  
154 and Walters Shoals, and using a Hydrobios Midi Multinet (0.25 m<sup>2</sup> mouth area) at MAD-  
155 Ridge, towed obliquely at about 1.5 to 2 knots, from 200m depth to the surface, or

156 shallower when the bottom depth was less than 200m (*i.e.* on the seamount). All the nets  
157 were fitted with 200  $\mu\text{m}$ -sized mesh and a flowmeter. Zooplankton samples were preserved  
158 in buffered formaldehyde (4% final concentration). Sampling was conducted during day time  
159 only. One zooplankton sample was collected at each station, and for MAD-Ridge the five  
160 nets of the Multinet were analysed individually.

161 At each station, a seabird 911+ CTD-F (conductivity, temperature, depth – fluorescence) was  
162 deployed to measure environmental parameters of the water column down to 1000 m  
163 depth, or to the bottom when shallower. The fluorescence sensors were calibrated using  
164 discrete *in situ* chlorophyll *a* (Chl *a*) concentrations, measured by High Performance Liquid  
165 Chromatography (HPLC) and collected at various depths on all three cruises. Integrated Chl  
166 *a* concentration ( $\text{mg m}^{-2}$ ) was calculated for the upper 200m of the water column or the  
167 whole water column when the bottom depth was shallower than 200m. The mixed layer  
168 depth (MLD) was determined as the depth at which the density increases by  $0.08 \text{ kg m}^{-3}$   
169 from a depth of 10m. The depth of the nutricline was defined as the depth where the  
170 concentrations of nitrate and nitrite reach  $1 \mu\text{g Kg}^{-1}$  (Dufois et al., 2014). As the nutrients  
171 were measured using discrete samples, the concentration between two depths was  
172 extrapolated using a linear regression.

173 Fortnightly averages and standard deviations of sea surface temperature (SST, in  $^{\circ}\text{C}$ ) and  
174 surface Chl *a* concentration ( $\text{mg m}^{-3}$ ) were calculated using MODIS-Aqua products from  
175 2003 to 2018 (for more details see Demarcq et al., this issue) over each seamount area (red  
176 boxes in Fig. 1).

### 177 2.3. Zooplankton sample analysis

178 The zooplankton samples were analysed using a Hydroptic ZooScan as described in Gorsky  
179 et al. (2010). Briefly, an aliquot of each sample of  $\sim 1000$  to 15000 particles was poured into  
180 the scanning tray. The raw images were processed and divided into thumbnails using  
181 ZooProcess and subsequently images containing more than one organism were separated  
182 digitally and reprocessed (Vandromme et al., 2012). All thumbnails were uploaded and  
183 classified on the Ecotaxa website (Picheral et al., 2017), using a pre-existing learning set and  
184 the random forest method. The pre-sorted thumbnails were then manually validated and  
185 moved into their correct category when prediction failed. The volume of each particle ( $\text{mm}^3$ )  
186 was calculated based on an ellipsoidal shape, using the major and minor axes. Particle size

187 was expressed as equivalent spherical diameter (ESD in mm). Each count and volume  
188 measured was then calculated for the whole sample and divided by the amount of seawater  
189 filtered by the net to provide abundance (ind m<sup>-3</sup>) and biovolume (mm m<sup>-3</sup>).

190 We grouped the taxa into 13 groups as shown in Tables 3 and 4. The category “gelatinous  
191 zooplankton” regroups all hydrozoa, siphonophora and thalicea. “Harosa” corresponds to  
192 the broad category of protists (e.g. radiolaria, phaeodaria, foraminifera, spumellaria). Parts  
193 of organisms, images of multiple organisms as well as unidentified organisms were removed  
194 from the counts presented here.

195 The size spectra were computed using 14 size bins of logarithmically increasing biovolume  
196 interval, from 0.18 mm ESD ~ 0.0031 mm<sup>3</sup> to 6.50 mm ESD ~ 144.31 mm<sup>3</sup>. The biovolume  
197 and Normalised Biovolume Size Spectra (NBSS) were computed by plotting the biovolume  
198 and the log<sub>10</sub> of normalised biovolume, respectively, on the Y-axis, against the log<sub>10</sub> of the  
199 volume of each size bin (Platt and Denman, 1977; Zhou and Huntley, 1997). The normalised  
200 biovolume (in m<sup>-3</sup>) was obtained by dividing the total biovolume in each size bin by the  
201 volume of that bin interval  $\Delta V$  (in mm<sup>3</sup>). A linear regression was fitted to the NBSS using the  
202 least squares method. To take into account the bias of not properly sampling the small  
203 organisms, which are not always retained by a 200  $\mu\text{m}$ -mesh nets, the smallest size bin used  
204 for the linear regression was the mode of the NBSS (García-Comas et al., 2014). In this case,  
205 the 4<sup>th</sup> size bin was used as the lowest limit of the linear fit (0.369 mm ESD ~ 0.0263 mm<sup>3</sup>).  
206 From this linear regression, the slope, the intercept and the linear fit ( $R^2$ ) are used in this  
207 study.

208 We also calculated a size diversity index ( $H'$ ), based on the Shannon diversity index and  
209 using a kernel distribution to estimate the frequency parameter  $p_i$  (Quintana et al., 2008):

$$H' = \sum_i^s p_i \log p_i$$

210 Because sometimes NBSS diverts from the theoretical linear model, this index takes into  
211 account irregularities in the size distribution, such as “domes” and “dips” that sometimes  
212 occur in NBSS. In theory, the flatter the slope is, the higher the size diversity index should  
213 be.

214

## 215 2.4. Data analysis

216 The zooplankton parameters that were tested throughout this study were total abundance  
217 and total biovolume, abundance and biovolume of specific taxa, slope, intercept and linear  
218 fit ( $r^2$ ) of the NBSS as well as the size diversity index ( $H'$ ). At MAD-Ridge, each net sample (5  
219 per station) were analysed individually with the ZooScan. To enable comparison between  
220 the 3 cruises, we combined the 5 nets at each station only in the calculation *a posteriori*. For  
221 this, the number of organisms in each net was summed together and divided by the sum of  
222 the water filtered by all 5 nets, which would be the equivalent to towing a single net.

223 The data were not normally distributed. Hence Kruskal-Wallis tests (KW) were performed to  
224 investigate if total zooplankton abundance and biovolume, and size diversity changed  
225 between cruises and “on/off” the seamount. Spearman’s coefficients ( $r_s$ ) were used to  
226 investigate correlations between variables. All stations were considered for the comparison  
227 between cruises but only La Pérouse and MAD-Ridge were used to test the possible effect of  
228 the seamount. Analyses of covariance (ANCOVA) were used to compare the slopes and the  
229 intercepts of the NBSS to highlight differences between cruises and stations as well as  
230 between on and off seamount. For a synoptic view of the results, a non-metric  
231 multidimensional scaling (nMDS) ordination was performed on the NBSS parameters  
232 described above (i.e. slope, linear fit, size diversity, intercept) and the biovolumes of the 14  
233 size bins used in the NBSS, using all the stations of the three cruises. The “envfit” function  
234 from R (Vegan package) was used to plot the environmental parameters on the ordination  
235 plot. Depth of the nutricline was found to be correlated both with the temperature at 100m  
236 ( $r_s = 0.88$ ) and the Deep Chl  $a$  Maximum (DCM) depth ( $r_s = 0.94$ ). Amongst these three  
237 variables, the DCM depth was the least correlated with SST ( $r_s = 0.6$ ) and was therefore  
238 selected for the analyses. The other environmental parameters used were integrated Chl  $a$   
239 concentration, MLD, SST and Chl  $a$  concentration at the DCM. All the data analyses were  
240 performed using R (R Core Team, 2018).

241

## 242 3. Results

### 243 3.1. Environmental conditions at the three seamounts

244 The hydrographic conditions at La Pérouse and MAD-Ridge were more similar to each other,  
245 compared to Walters Shoal (Table 1). At the time of sampling, SSTs were 3 to 4 °C warmer at

246 La Pérouse and MAD-Ridge with 23.6°C and 24.5°C respectively, compared to 20.5°C at  
247 Walters Shoal. The two northern seamounts had deep DCMs and nutriclines of more than  
248 100m while the Walters Shoal's DCM was only 37m and the nutricline was at about 53m for  
249 the stations sampled around the seamount. The integrated Chl *a* and the Chl *a*  
250 concentration at the DCM were in the same range at all three seamounts. Walters Shoal's  
251 integrated Chl *a* was only slightly higher by ~3 mg m<sup>-3</sup> (23 mg m<sup>-3</sup>) compared to the other  
252 two seamounts (~ 20 mg m<sup>-3</sup>).

253 The main surface current at La Pérouse was orientated north-westwards for the first part of  
254 the cruise but changed to southwards after 26 September shortly before the last two  
255 stations, 23 and 24, were sampled. Stations 3 and 6 were therefore in the lee of the  
256 seamount at the time of sampling (see Marsac et al., this issue, for more details). At MAD-  
257 Ridge, a dipole was present during sampling (Fig. 2), and the west-east transect crossed  
258 both the cyclonic and anticyclonic eddies. Station 2 was located in the cyclonic eddy while  
259 stations 8 to 12 were in the anticyclonic eddy (altimetry and in situ measurements used to  
260 classify these stations are presented in Annasawmy et al., this issue). The stations located  
261 along the south-north transect were mostly in the anticyclonic eddy (stations 16 to 25). The  
262 other stations may have been influenced by the eddies but did not fulfil all the physical  
263 criteria to qualify as part of either the cyclone or anticyclone and were therefore named  
264 "transition". These stations were located either between the two eddies (station 6) or on  
265 the outside edges of the anticyclone (stations 14, 15 and 26 to 28). Stations 29 to 31, the  
266 closest to the Madagascar shelf were classified as "shelf", as described earlier, due to the  
267 filament of high Chl *a* concentration flowing from the South-East tip of the Madagascar  
268 shelf. At Walters Shoal, surface currents were not strong and highly variable, changing  
269 sporadically during the cruise (Demarcq et al., this issue).

270 The three seamounts are located at different latitudes. Bi-monthly averages of SST followed  
271 this latitudinal gradient from the warmer La Pérouse in the North, to the cooler Walters  
272 Shoal in the South, with temperatures varying by 4 to almost 6°C depending on the month  
273 (Fig. 3). The climatology of surface Chl *a* concentration shows that La Pérouse had the  
274 lowest surface Chl *a* concentration of the three seamounts all year round, while Walters  
275 Shoal had a higher Chl *a* concentration than MAD-Ridge during austral winter and spring  
276 (May to December). The strongest seasonality was observed at Walters Shoal followed by La

277 Pérouse and then MAD-Ridge, as highlighted by the coefficient of variation for surface Chl *a*  
278 concentration (Fig. 1). Sampling at these three locations occurred during different months of  
279 the year. The climatologies of SST and Chl *a* indicate that La Pérouse and MAD-Ridge were  
280 sampled towards the end of the productive season while Walters Shoal was sampled at the  
281 beginning (Fig. 3). Despite this difference, the levels of SST and Chl *a* from remote sensing,  
282 at the time of the cruises, are similar at all three seamounts, agreeing with the *in situ*  
283 observations described above.

### 284 3.2. Comparison of the three seamount zooplankton communities

#### 285 3.2.1. Total abundance and biovolume

286 Total zooplankton abundance varied between the seamounts with significantly higher  
287 values at La Pérouse and MAD-Ridge ( $201.2 \pm 98.2 \text{ ind m}^{-3}$  and  $204.6 \pm 90.0 \text{ ind m}^{-3}$ ,  
288 respectively) compared to Walters Shoal ( $60.8 \pm 53.4 \text{ ind m}^{-3}$ , KW test  $p < 0.001$ , Table 2).  
289 Similarly, the averaged total biovolume at La Pérouse ( $42.81 \pm 15.14 \text{ mm}^3 \text{ m}^{-3}$ ) and MAD-  
290 Ridge ( $45.64 \pm 20.92 \text{ mm}^3 \text{ m}^{-3}$ ) were significantly higher than at Walters Shoal ( $12.69 \pm 8.27$   
291  $\text{mm}^3 \text{ m}^{-3}$ , KW test  $p < 0.001$ ).

#### 292 3.2.2. Size Spectrum and diversity

293 The NBSS also differed between the three seamounts with the steepest slope at MAD-Ridge,  
294 followed by La Pérouse and Walters Shoal (Table 2 and Fig. 4). It is worth noting that the  
295 difference between La Pérouse and MAD-Ridge was only due to station 23 at La Pérouse,  
296 which had a very flat slope of -0.57. Once this station was removed, the NBSS slopes at La  
297 Pérouse and MAD-Ridge were similar, being  $-0.95 \pm 0.10$  and  $-1.00 \pm 0.09$ , respectively  
298 (ANCOVA,  $p = 0.094$ ). Walters Shoal had a flatter slope of  $-0.79 \pm 0.09$  compared to the  
299 other two seamounts. The NBSS intercepts were higher at La Pérouse and MAD-Ridge  
300 compared to Walters Shoal, with averages of 0.59, 0.50 and -0.20, respectively. Over the  
301 whole size range, Walters Shoal biovolumes were lower than at the other two seamounts  
302 (Fig. 5a). The NBSS linear fit ( $R^2$ ) was high at La Pérouse and MAD-Ridge (0.93 and 0.94,  
303 respectively) while it dropped to 0.78 at Walters Shoal. The size diversity indices were  
304 significantly different at each seamount with averaged values of, in decreasing order, 2.34 at  
305 MAD-Ridge, 2.27 at La Pérouse and 2.18 at Walters Shoal (KW test,  $p < 0.001$ ).

#### 306 3.2.3. Zooplankton taxonomic composition

307 Overall, copepods comprised about 70% of the total zooplankton abundance with Calanoida  
308 being the most abundant group and Oithonidae second (Table 3). Appendicularia and  
309 Chaetognatha were the next most abundant taxa.

310 Calanoida and Chaetognatha together represented around 50% of the total zooplankton  
311 biovolume at all three seamounts but their proportions varied between seamounts (Table  
312 4). Total biovolume at La Pérouse and MAD-Ridge comprised about 30% Calanoida and 20%  
313 Chaetognatha while at Walters Shoals only 13% was comprised by Calanoida with 40% being  
314 Chaetognatha. This was largely due to the low biovolume overall of Calanoida at Walters  
315 Shoal (only  $\sim 2 \text{ mm}^3 \text{ m}^{-3}$ ) compared to the other two seamounts ( $\sim 15 \text{ mm}^3 \text{ m}^{-3}$ ). Low  
316 biovolume here was clearly visible for Calanoida, especially for size bins of 0.6 mm ESD ( $\sim$   
317  $0.110 \text{ mm}^3$ ) and larger, and for chaetognatha (Figs. 5 b and c) but was also evident for  
318 amphipoda, appendicularia, other copepoda and other crustacea (data not shown).

### 319 3.3. La Pérouse

320 There were no significant differences between the stations on and off the La Pérouse  
321 seamount for any of the zooplankton related parameters measured (*i.e.* total abundance  
322 and biovolume, NBSS parameters, size diversity, KW test,  $p > 0.05$ ). Zooplankton abundance  
323 and biovolume varied between stations, but no major differences in size composition were  
324 observed between on and off seamount stations (Figs. 6 and 7).

325 On the seamount, the two stations downstream (west) of the seamount had the highest  
326 abundance and biovolume, with  $424 \text{ ind m}^{-3}$  and  $66 \text{ mm}^3 \text{ m}^{-3}$  at station 6, and  $231 \text{ ind m}^{-3}$   
327 and  $65 \text{ mm}^3 \text{ m}^{-3}$  at station 3. On the upstream side of the seamount, stations 4 and 9 had  
328 low abundance ( $184$  and  $145 \text{ ind m}^{-3}$  respectively). The biovolume at station 4 was low  
329 compared to the other stations ( $29 \text{ mm}^3 \text{ m}^{-3}$ ) while station 9 biovolume was almost as high  
330 as at station 6 and 3 ( $53 \text{ mm}^3 \text{ m}^{-3}$ ). However, this was mainly due to one trachymedusa  
331 scanned, which was larger than 4mm, and so should perhaps be considered a  
332 methodological bias (Fig. 7). Stations 23 and 24 are described separately from the other  
333 stations as they were sampled at the end of the cruise, after the main surface current had  
334 changed direction. Station 23 had a very low abundance but a high biovolume ( $85 \text{ ind m}^{-3}$   
335 and  $41 \text{ mm}^3 \text{ m}^{-3}$ ) while station 24 had both a low abundance and biovolume ( $130 \text{ ind m}^{-3}$   
336 and  $17 \text{ mm}^3 \text{ m}^{-3}$ ). The total abundance of zooplankton off the La Pérouse seamount  
337 (stations 1, 2, 8 and 10) was relatively similar with an average of  $170 \text{ ind m}^{-3}$  except for

338 station 10 which had 302 ind  $m^{-3}$ . The biovolume was similar at all four stations with an  
339 average of 39  $mm^3 m^{-3}$ .

340 Abundance and biovolume were not correlated at La Pérouse ( $r_s = 0.36$ , Table 5). Each  
341 station sampled at La Pérouse differ significantly from each other in their NBSS slope and  
342 intercept (ANCOVA,  $p < 0.001$ ,  $n = 10$ ). Station 23 had the flattest slope (-0.57) due to the  
343 quasi absence of smaller organisms between 0.3 and 0.5mm ESD, mostly Calanoida, *Oithona*  
344 and *Oncaea* (Fig. 5d, e, f and 7) but a high biovolume of larger Calanoida  $\sim 0.5$  to 1.2 mm  
345 ESD, with station 6 exhibiting the highest total zooplankton abundance at La Pérouse (Fig.  
346 5e). The highest size diversity index at La Pérouse was also found at station 23 (2.370)  
347 indicating a more even distribution of zooplankton sizes across the spectrum sampled  
348 compared to the other stations. Station 3 differed significantly from the others with a slope  
349 of -0.74 and an intercept of 0.87. This station had biovolumes of Calanoida in all size bins  
350 which were similar to the other stations, but had a higher proportion of Chaetognaths,  
351 euphausiids and amphipods larger than 0.5 mm ESD, especially between  $\sim 1.2$  and 2.5 mm  
352 ESD (Figs 5 d, e, f and 7). The slopes and intercepts of the other stations did not differ  
353 significantly from each other ( $n=8$ , ANCOVA,  $p < 0.001$ ). The slope of these 8 stations  
354 combined was -0.94 with an intercept of 0.56. Station 6, which had the highest abundance  
355 and biovolume of zooplankton at La Pérouse, had one of the highest NBSS intercepts (0.82)  
356 and the steepest slope, owing to the high biovolume of small Calanoida of  $\sim 0.3$ -1.2 mm ESD  
357 (Fig. 5e). The linear fit coefficient was stable throughout the stations at La Pérouse being  $\sim$ -  
358 0.99 except for stations 1 and 2 where it was slightly lower (-0.96 and -0.98 respectively).  
359 Overall, the biovolume at La Pérouse was correlated with the NBSS intercept ( $r_s = 0.89$ ), and  
360 the size diversity index was correlated with the slope ( $r_s = 0.79$ , Table 5).

361 The integrated Chl  $a$  concentration was variable amongst the La Pérouse stations, but the  
362 lowest values were found at stations 3 and 6 with 14.3 and 16.9  $mg m^{-2}$  respectively, which  
363 also had the highest zooplankton biovolumes. The other 4 stations on the seamount had an  
364 average of 23.6  $mg m^{-2}$ . Integrated Chl  $a$  was indeed negatively correlated with total  
365 abundance ( $r_s = -0.72$ ), biovolume ( $r_s = -0.68$ ) and the intercept ( $r_s = -0.68$ ) at La Pérouse.  
366 The vertical distribution of the Chl  $a$  varied, with a relatively shallow DCM at 85 m for  
367 stations 6 and 23, and a DCM of 65m at station 9. The other stations off the seamount had  
368 DCMs deeper than 100m. The deeper the DCM was at La Pérouse, the steeper the slope of

369 the NBSS was ( $r_s = -0.72$ ). The temperature and Chl *a* profiles at the four stations off the  
370 seamount were very similar. They all had deep DCMs at about 100m or deeper, and the  
371 integrated Chl *a* concentration averaged  $19.1 \text{ mg m}^{-2}$ .

### 372 3.4. MAD-Ridge

373 At MAD-Ridge, the stations on the seamount (slopes and summit) had a mean zooplankton  
374 abundance of  $157 \pm 26 \text{ ind m}^{-3}$  ( $n=6$ ) and a mean biovolume of  $32.8 \pm 4.9 \text{ mm}^3 \text{ m}^{-3}$  but were  
375 not significantly different from the stations off the seamount ( $199 \pm 77 \text{ ind m}^{-3}$  and  $45.7 \pm$   
376  $22.1 \text{ mm}^3 \text{ m}^{-3}$ , respectively, KW test  $p > 0.05$ ).

377 On the East-West transect, stations 2, 6, 14 and 15, located in the cyclonic eddy and the  
378 edges of the anticyclone (transition zone), showed high integrated abundance and  
379 biovolume ( $240 \text{ ind m}^{-3}$  and  $49.9 \text{ mm}^3 \text{ m}^{-3}$ , Figs 7 and 8). Stations 8, 9, 10 and 12, classified  
380 as anticyclone, were similar with low abundance and biovolume, except for station 12 which  
381 had a greater biovolume due to the size class  $> 4\text{mm}$  containing a few large individuals ( $15.8$   
382  $\text{mm m}^{-3}$ ,  $0.18 \text{ ind m}^{-3}$ ). On the North-South transect, station 18, south of the seamount, had  
383 a greater abundance and biovolume compared to the other stations sampled in the  
384 anticyclone. Considering all the stations within the anticyclone, with the exception of station  
385 18, the average total abundance was  $147 \pm 21 \text{ ind m}^{-3}$  and the biovolume  $33.3 \pm 6.1 \text{ mm}^3 \text{ m}^{-3}$   
386 ( $n = 12$ ), both relatively low compared to the other stations sampled at MAD-Ridge. Out of  
387 the three stations classified as shelf, only stations 29 and 30 had a high abundance of about  
388  $400 \text{ ind m}^{-3}$  and a high biovolume of  $75 \text{ mm}^3 \text{ m}^{-3}$ . Station 31 had average abundance and  
389 biovolume, similar to the other stations.

390 The zooplankton was concentrated in the upper 100m with very low abundance between  
391 100 and 200m, and the highest densities were often found in the upper 30 to 50 m of the  
392 water column (Fig. 9). It seems that on the West-East transect, from stations 6 to 15, the  
393 highest concentrations were restricted to the upper net. Stations 2 and 18 had the highest  
394 concentrations that extended all the way down to about 100m, while the high  
395 concentrations at the two stations closer to the shelf, 29 and 30, were restricted to the  
396 upper 50m. The layer from 50 to 75m depth at station 21 showed a small but intense patch  
397 of all the taxa. Multivariate analysis was performed on the taxonomic composition of each  
398 net at MAD-Ridge (not shown) and only the deepest nets grouped together. We can see  
399 however that, unlike the small Calanoida ( $<1 \text{ mm ESD}$ ), larger zooplankton such as

400 Chaetognaths and other large organisms (>2.7mm ESD) have a patchy distribution, not  
401 always following the general patterns of total abundance and biovolume (Fig. 9). Hence the  
402 proportion of each taxon in terms of abundance and biovolume were not necessarily similar  
403 at all the MAD-Ridge stations within the upper 100m of the water column, but also did not  
404 form any clusters.

405 The NBSS slopes at the MAD-Ridge stations were similar to each other except for station 30  
406 which had a significantly steeper slope of -1.34 (Fig. 8, ANCOVA,  $p < 0.001$ ). This station had  
407 the highest abundance of Calanoida ( $252 \text{ ind m}^{-3}$ ) within the size range of  $\sim 0.68$  to  $1.76 \text{ mm}$   
408 ESD of all the stations sampled, with peaks at  $\sim 0.4 \text{ mm}$  and  $1.3 \text{ mm}$  (Fig. 5h). Station 29,  
409 which had a steep slope (-0.95), also had a high abundance of Calanoida ( $174 \text{ ind m}^{-3}$ ) with  
410 only one peak at about  $1.2 \text{ mm}$  ESD. The biovolume of Calanoida at station 29 was higher  
411 than at station 30, however (Fig. 5h). Stations 29 and 30 had a higher proportion of  
412 Calanoida copepods (45 and 51 %) than all the other stations on this transect (avg. 35%).  
413 Another difference between these two stations was the low biovolume of Chaetognaths at  
414 station 29 compared to 30 (Figs 5i and 9). The flattest slope of MAD-Ridge was at station 28  
415 (-0.87) but it was not significantly different from the others. Stations 2 and 18, which had  
416 amongst the highest abundance and biovolume of zooplankton at MAD-Ridge, had steep  
417 slopes,  $-0.97$  and  $-1.01$  respectively, but these were not significantly different from the  
418 other stations with lower abundance and biovolume. Both stations had a high biovolume of  
419 Calanoida of  $\sim 0.4$  to  $2.4 \text{ mm}$  ESD with a peak at  $\sim 2.2 \text{ mm}$  ESD, slightly larger than what was  
420 observed at stations 29 and 30 (Fig. 5h). The biovolume spectra of Calanoida and  
421 Chaetognatha at the other stations were very similar, as shown in Figs 5 k and 5 l.

422 The slopes varied irregularly with depth (*i.e.* within each net) with an overall average of -  
423  $0.89 \pm 0.1$  ( $n = 115$ , Fig. 9). For instance, the flattest slope was found at station 28 between  
424 25 and 50m depth (-0.6) while the steepest slopes were at station 14 at 50-70 m depth (-  
425 1.18) and station 26 in the upper 30m of the water column (-1.16).

426 The intercept was positively correlated with both abundance ( $r_s = 0.83$ ) and biovolume ( $r_s =$   
427  $0.91$ ) showing high values at stations 2 (0.81), 18 (0.89) and 29 (0.89). The size diversity  
428 index changed sporadically with depth and station and was not correlated with the slope at  
429 MAD-Ridge. The linear fit was weakly correlated with size diversity ( $r_s = 0.44$ ) indicating that  
430 the stronger the linear fit is (*i.e.* the closest to -1), the lower the size diversity is.

431 No relationships were found between Integrated Chl *a* or Chl *a* concentration profiles and  
432 the horizontal or vertical distribution of zooplankton or any of the NBSS parameters  
433 described above.

### 434 3.5. Walters Shoal

435 At Walters Shoal, stations 1 and 14 had a greater abundance compared to the other stations  
436 at this seamount, with 136.4 and 195.6 ind m<sup>-3</sup>, respectively (Figs 7 and 10). These values  
437 are in the same range as the lowest values found at La Pérouse and MAD-Ridge. No pattern  
438 was found between any of the zooplankton parameters measured and the bottom depth at  
439 Walters Shoals. The size fraction 0.3 to 0.5 mm was the most abundant at all stations. The  
440 biovolumes at stations 1 and 14 to the south-west, 3 and 6 to the south-east, and 8 to the  
441 north west were higher compared to the other stations at Walters Shoal, with an average of  
442 21.74 mm<sup>3</sup> m<sup>-3</sup> compared to 7.03 mm<sup>3</sup> m<sup>-3</sup> for the other stations. Many of these stations  
443 showed a substantial amount of biovolume in the size classes larger than 4mm, which was  
444 also the case at MAD-Ridge, but not at La Pérouse where it was evident at only one station.  
445 Abundance and biovolume were correlated at Walters Shoals ( $r_s = 0.88$ , Table 5). The  
446 proportion of each taxon was similar amongst stations in terms of abundance only. The  
447 proportion of biovolume for each taxon showed greater variability between stations with  
448 more than 50% of the total biovolume comprised of euphausiids at stations 1, 8 and 12, and  
449 of chaetognaths at stations 3, 5, 7, 10, 13 and 14.

450 The NBSS slopes did not differ significantly between stations (ANCOVA,  $p = 0.67$ ). Stations  
451 14 and 1, which had the highest abundance, had slopes of -0.9 and -0.84 respectively, not  
452 different from the other stations. The size distribution of Calanoida at station 14 revealed  
453 greater biovolumes than at the other Walters Shoal stations with a peak at 0.4 mm, but very  
454 little biovolume between 0.4 and 1mm ESD, which is where high biovolumes were  
455 measured at the other two seamounts (Fig. 5n). The biovolume of Chaetognaths at this  
456 station was very high and amongst the highest for all three seamounts (Fig. 5o). Station 1  
457 had a high abundance of Oithonidae and other copepods (48 ind m<sup>-3</sup>) as well as a high  
458 biovolume of euphausiids (13.6 mm<sup>3</sup> m<sup>-3</sup>), two groups that are not shown in Figure 5. The  
459 slopes were negatively correlated with abundance ( $r_s = -0.64$ ) and positively correlated with  
460 size diversity ( $r_s = 0.59$ ) but there was no correlation between size diversity and linear fit.

461 None of the environmental parameters tested showed any significant relationship with the  
462 zooplankton abundance, biovolume nor NBSS parameters.

### 463 *3.6. Overview of all three seamounts and relationship with environmental parameters*

464 The nMDS performed on the biovolume of each bin of the NBSS (14 bins) and the NBSS  
465 parameters clearly discriminates Walters Shoal from La Pérouse and MAD-Ridge (Fig. 11).  
466 The stations with high abundance or biovolume stand out on the left hand-side of the  
467 ordination, especially stations 2, 18 and 29 from MAD-Ridge associated with the bin sizes  
468 0.68 to 1.76 mm ESD. Stations 3 and 6 from La Pérouse are closely related to these three  
469 stations too, but station 3 has more larger organisms (closer to bin 2.23) than station 6  
470 (close to 0.53). Station 30 from MAD-Ridge and station 10 from La Pérouse had high total  
471 biovolume and are grouped together for having a greater biovolume in the small bins 0.33  
472 and 0.42 mm ESD compared to the other stations. La Pérouse station 23 is separated from  
473 the other stations and its closest size bin is 2.23 mm ESD. This station had a low abundance,  
474 an intermediate biovolume and a flat slope compared to the other stations at La Pérouse.  
475 We can also distinguish that all the stations sampled inside the anticyclone at MAD-Ridge  
476 are very similar to each other, except for station 18 as described earlier. Most of the  
477 stations classified as “transition” at MAD-Ridge are grouped together (6, 14, 15, 27) with the  
478 exception of 26 and 28. Station 26 was closest to the anticyclone and its northern edge had  
479 a zooplankton size composition similar to that inside the anticyclone. Station 28 differs due  
480 to a greater biovolume in the bin 2.23 mm ESD. Amongst the Walters Shoals stations, the  
481 total biovolume increases from the stations at the bottom right corners (5, 7 and 10)  
482 towards stations 1 and 14. Stations 1 and 14 have a greater biovolume in bin 3.6 mm ESD  
483 compared to the other stations. All the other stations at Walters Shoal have a lower  
484 biovolume than at the other two seamounts. They are characterised by a flat slope (less  
485 negative), a low size diversity index and a low linear fit. These three parameters are close to  
486 each other on the nMDS plot despite relatively low correlation coefficients between them  
487 ( $r_s$  (diversity  $\sim$  slope) = -0.43;  $r_s$  (diversity  $\sim$  linear fit) = -0.31;  $r_s$  (slope  $\sim$  linear fit) = 0.43).

488 Out of the 5 environmental parameters used in the Envfit (SST, depth of the DCM, Chl  $a$   
489 concentration at the DCM, MLD and integrated Chl  $a$ ), SST had the highest correlation with  
490 the ordination ( $r^2 = 0.65$ ,  $p = 0.001$ ), followed by depth of the DCM ( $r^2 = 0.34$ ,  $p = 0.001$ )  
491 which were slightly correlated ( $r_s = 0.6$ ). Integrated Chl  $a$ , MLD and Chl  $a$  concentration at

492 the DCM were not significant and are not represented on the ordination. Hence in this  
493 study, overall, high (warm) SST and deep DCM were associated with the steepest slopes and  
494 the highest total biovolumes.

495

#### 496 **4. Discussion**

##### 497 *4.1. Comparison of the three seamount ecosystems*

498 The three study sites are located at different latitudes in the oligotrophic SWIO. Despite  
499 having clear differences in temperature and Chl *a* climatologies, the Longhurst (2007)  
500 classification, based on oceanographic features and Chl *a* profiles, places La Pérouse and  
501 Walters Shoals in the same bioregion, the Indian South Subtropical Gyre Province (ISSG),  
502 while MAD-Ridge belongs to the Eastern Africa Coastal Province (EAFCR). What particularly  
503 distinguishes MAD-Ridge from the other two seamounts is the high meso-scale activity in  
504 the region due to the East Madagascar Current producing eddies over the Madagascan  
505 Ridge (de Ruijter et al., 2004b; Halo et al., 2014; Quartly et al., 2006). This seamount is also  
506 in the proximity of the Madagascar continental shelf (160 km approximately) which can  
507 influence biological material contained within eddies (e.g. Muhling et al., 2007; Noyon et al.,  
508 2019; Sabarros et al., 2009; Strzelecki et al., 2007; Thompson et al., 2007). Furthermore,  
509 body size of ectotherms tends to increase with latitude, known as Bergmann's rule (1847),  
510 mostly driven by temperature, season length and food availability although the underlying  
511 mechanisms are not fully understood (Blackburn et al., 1999; Watt et al., 2010). Considering  
512 the above and the fact that temperature and Chl *a* are important drivers of zooplankton  
513 distribution (Hirst and Bunker, 2003), one might have expected the zooplankton  
514 communities to differ at the three seamounts. However, the zooplankton communities at La  
515 Pérouse and MAD-Ridge were similar to each other, whereas Walters Shoal, the  
516 southernmost seamount, had very low biovolumes and abundances. The abundance of  
517 zooplankton observed during this study were in the same range as those observed  
518 previously in the Indian Ocean although the concentration at Walters Shoal was amongst  
519 the lowest recorded (Huggett, 2014; Madhupratap, 1983; Noyon et al., 2019; Sävström et  
520 al., 2014).

521 Sea surface temperature was slightly cooler (3 to 4°C) and integrated Chl *a* slightly higher by  
522 2 to 3 mg m<sup>-3</sup> at Walters Shoals compared to the other two seamounts. Cooler temperature

523 induces a decrease in metabolic rates of organisms while increased food availability (*i.e.* Chl  
524 *a*) enhances metabolic rates (e.g. Hirst and Bunker, 2003). Given the low abundance at  
525 Walter Shoals, it seems that the temperature effect may have outweighed the food  
526 availability effect, or alternatively the food quality was poorer although we did not assess this  
527 during this cruise. The NBSS slope at Walters Shoal was flatter than at the other two  
528 seamounts, mostly due to the very low biovolume of Calanoida in the size range of 0.6 to  
529 1.9 mm ESD (equivalent to biovolume of  $-0.95$  to  $0.60 \log \text{mm}^3$ ). The linear fit of the slope  
530 was also low, a sign of irregularities in the size spectra. Some studies have emphasised the  
531 importance of NBSS diverging from linearity, when the size spectra show “domes” or “dips”  
532 due to instabilities or propagation of energy pulses through the system (García-Comas et al.,  
533 2014; Quinones et al., 2003; Rodriguez and Mullin, 1986; Sourisseau and Carlotti, 2006;  
534 Zhou, 2006). Sampling at Walters Shoal may have occurred during one such event while La  
535 Pérouse and MAD-Ridge, which both had a high linear fit, were in a steady state at the time  
536 of sampling. The three seamounts were sampled at different times of the year: La Pérouse  
537 in September, Austral spring, MAD-Ridge in November, Austral summer and Walters Shoal  
538 in May, Austral fall. According to the climatology at each location, Walters Shoals was  
539 sampled at the start of the annual productive season while La Pérouse and MAD-Ridge were  
540 sampled closer to the end. The increased productivity in winter in oligotrophic  
541 environments is often induced by a decrease in heat (*i.e.* solar radiation) and an increase in  
542 wind which breaks the stratification and leads to an increase of nutrients in the euphotic  
543 zone. Hence, we hypothesise that the mismatch observed here between Chl *a* and  
544 zooplankton at Walters Shoal could be due to the phenology of events: primary production  
545 had increased, yielding an increased Chl *a* concentration, yet a delay of a week to a month is  
546 needed to see any accumulation of zooplankton biovolume. The biovolume in the first few  
547 bins of the size spectra (which are not used in the calculation of the slope) were similar at all  
548 three seamounts. This can either highlight the presence of small copepods that are  
549 abundant in oligotrophic systems and not food limited (Hirst and Bunker, 2003), or that  
550 some of these copepods were juvenile stages of larger Calanoida copepods, hence mirroring  
551 an increase in reproduction rates. These irregularities in the size spectrum must be  
552 interpreted with caution, however, as they may also be due to other factors including  
553 methodological bias such as net avoidance, or large swimmers entering and leaving the  
554 system sampled (Quinones et al., 2003; Sourisseau and Carlotti, 2006; Zhou, 2006). The

555 lower abundance of Calanoida could also be due to increased predation pressure. Both  
556 amphipods and chaetognaths, strong copepod carnivores, were in the same proportions at  
557 all three seamounts (abundance  $\sim$  5% of the total), but there were relatively more large  
558 chaetognaths at the Walters Shoals stations with greatest total zooplankton total  
559 abundance.

560 Overall, slopes were flatter when size diversity decreased which is contrary to the theory  
561 that flatter slopes suggest a more even distribution of organisms throughout all size classes.  
562 The fact that Walters Shoal had the flattest slope and the lowest diversity index may  
563 support the fact that the size spectrum was skewed towards large organisms with only few  
564 small organisms which concurred with the low linear fit measured there.

565 At most stations at La Pérouse and MAD-Ridge, the NBSS slopes were similar and relatively  
566 steep, close to -1, with a high linear fit. This is the same as what Sheldon et al (1972)  
567 observed and slightly less than a slope of -1.22 which has been associated with typical  
568 steady-state open-ocean communities (Platt and Denman, 1977). A steep slope concurs also  
569 with the fact that temperature influences metabolic activity, hence low latitude  
570 environments are usually associated with smaller organisms with faster metabolic rates  
571 (Brown et al., 2004; Gillooly et al., 2001; Huntley and Lopez, 1992). The high linear fit is  
572 consistent with oligotrophic ecosystems in a steady-state, with few perturbations or bursts  
573 of production, thus not creating any domes or dips in the size spectrum (e.g. Barber and  
574 Hiscock, 2006; Dai et al., 2016; García-Comas et al., 2014; Lebourges-Dhaussy et al., 2014).  
575 The strong similarity between La Pérouse and MAD-Ridge was not expected considering that  
576 these two seamounts belong to different bioregions, and that MAD-Ridge is influenced by  
577 meso-scale activity as well as being located close to the productive Madagascan shelf.  
578 However, the fact that none of these factors appeared to influence the average values at  
579 MAD-Ridge might be because out of a total of 23 stations, only one station was sampled  
580 inside the cyclonic eddy and three were influenced by the shelf. Some differences in  
581 zooplankton communities were observed for these specific stations, however, and are  
582 discussed later on.

583 Flat slopes are the consequence of a higher proportion of large organisms compared to  
584 small ones and this is often interpreted as an increase in energy available in food webs (e.g.  
585 Brown et al., 2004; García-Comas et al., 2014; Zhou, 2006). Nevertheless, an increase in

586 nutrients will stimulate primary production which will lead to an increase in secondary  
587 production and therefore an increase in small zooplankton (*i.e.* juveniles), translating into a  
588 steeper NBSS slope (García-Comas et al., 2014; Giering et al., 2018; Zhou, 2006; Zhou and  
589 Huntley, 1997). Observations have shown that trophic transfer efficiency increases in food  
590 limited environments and that fast turn-over rates of small primary producers enables a  
591 higher biomass of predators to be supported (Calbet, 2001; García-Comas Carmen et al.,  
592 2016; Gasol et al., 1997; Irigoien et al., 2014; San Martin et al., 2006). Using the NBSS slope  
593 on its own seems too limited to provide an adequate understanding of the system and  
594 several NBSS parameters should be considered simultaneously to better understand the  
595 dynamics of a system at a particular moment. For instance, at Walters Shoal, the flat slopes  
596 interpreted together with the low linear fit and the size diversity probably reflect a low  
597 energy transfer towards higher trophic levels. This kind of conclusion should be taken with  
598 caution though as this study focused only on a limited size spectrum (200  $\mu\text{m}$  to  $\sim 4\text{cm}$ ).

#### 599 *4.2. Meso- and small-scale variability at each seamount and possible seamount effect*

##### 600 *4.2.1. MAD-Ridge*

601 Zooplankton abundance and size structure at MAD-Ridge was influenced more by mesoscale  
602 variability than by any seamount effect. At the time of sampling, the MAD-Ridge sampling  
603 area was influenced by a young dipole eddy, formed a few weeks and days prior to the  
604 cruise (1 Nov for the cyclone and 12 Nov for the anticyclone, Vianello et al. (this issue)). The  
605 region south of Madagascar is well-known for its eddy field, formed by the interaction  
606 between the East Madagascar Current and the land mass of Madagascar (de Ruijter et al.,  
607 2004a). The zooplankton abundance and biovolume in the cyclonic eddy were higher than in  
608 the anticyclone (excluding station 18). This agrees with previous observations where the  
609 cores of cyclonic eddies, in their spinning up phase as in this study, often contain higher  
610 zooplankton concentrations than their surrounding waters due to the upwelling taking place  
611 (e.g. Huggett, 2014; Landry et al., 2008; Lebourges-Dhaussy et al., 2014; Noyon et al., 2019;  
612 Riandey et al., 2005). Cores of anticyclonic eddies usually have less plankton due to  
613 downwelling occurring during the spinning up phase. Yet other factors influence eddy  
614 productivity such as the state of the eddy (spinning up or down), as well as the origin of the  
615 eddy and its interaction with surrounding water masses, especially coastal waters which are  
616 enriched in biological material, more than offshore waters (e. g. Gaube et al., 2014; Huggett,

617 2014; Landry et al., 2008; Mackas et al., 2005; Sabarros et al., 2009; Strzelecki et al., 2007).  
618 It is difficult to characterise the limits of eddies as edges are more a gradient than a clear  
619 boundary. The stations classified as “transition” (6, 14 and 15) were located at the border of  
620 the anticyclone and revealed intermediate concentrations of zooplankton, slightly higher  
621 than inside the anticyclone itself. This matches previous observations showing anticyclone  
622 edges being richer than their core due to either upwelling occurring on the edges or  
623 transient filaments of enriched waters wrapping themselves around eddies (Bakun, 2006;  
624 Holliday et al., 2011; Sabarros et al., 2009).

625 Station 18 which was in the anticyclone was sampled at dusk due to a sampling delay, thus  
626 the high abundance and biovolume, visible in the upper 100m, could be partly attributable  
627 to diel vertical migration (DVM). Previous work revealed that mesozooplankton DVM is  
628 limited in the SWIO (Huggett, 2014; Noyon et al., 2019). Despite a slight increase in  
629 euphausiid biovolume between 25 and 75m depth, the slopes at station 18 were similar to  
630 the average suggesting that all taxa were present in the water column and not only large  
631 diel vertical migrators. Hence, we cannot exclude that the high biovolume of zooplankton  
632 could also be due to natural patchiness. This station was 27 km south of the seamount, so it  
633 is difficult to conclude whether the seamount had an impact here. It is most likely not due to  
634 local enrichment as none was detected at MAD-Ridge (Demarcq et al., this issue) and there  
635 were no retention mechanisms over the seamount. High concentrations of zooplankton  
636 could be due to reduced predation pressure but considering that all the other stations had  
637 lower concentrations than at station 18, this would suggest that the water mass sampled at  
638 station 18 would have been the only one to not suffer from excessive predation pressure  
639 linked to the seamount. Gaps in zooplankton abundance have more often observed around  
640 seamounts (Genin et al., 1994; Hauray et al., 2000).

641 Most stations at MAD-Ridge were located within an anticyclone and showed low  
642 zooplankton biovolume and similar size spectra, with the exception of four stations. These  
643 four stations had similar total abundance, biovolume and taxonomic composition, but  
644 showed differences in their size spectra with stations 29 and 30 having a peak of biovolume  
645 in the small sized organisms (0.7 to 1.5 mm) while stations 2 and 18 had a peak in the larger  
646 ones (1.5 to 3 mm ESD). The influence on zooplankton composition by cross-shelf transport  
647 and offshore flowing filaments that may interact with eddies has already been reported for

648 this region (Noyon et al., 2019). In the latter study, microscope analysis showed that the  
649 shelf was dominated by *Paracalanus* spp and small Calanoid copepodites, both of which are  
650 small sized copepods which could be what was observed at these northern stations. Station  
651 30 showed an even stronger proportion of small organisms (*Oithona* spp and small  
652 calanoids) with the steepest of all slopes measured. The ocean colour images of 20-22  
653 November, just prior to sampling, show this station being in the middle of a filament of high  
654 productivity which may explain the difference with station 29. The offshore stations were  
655 characterised by different zooplankton communities with larger copepods, due to either a  
656 different species composition or an older cohort comprised of older and larger Calanoid  
657 stages, compared to the shelf.

658 Zooplankton was concentrated in the upper 100m of the water column and sometimes even  
659 more so in the upper 30m. The lack of correlation between Chl *a* and zooplankton  
660 concentration at any depth, however, suggests that the zooplankton are most likely not only  
661 feeding on phytoplankton (Calbet, 2001), or that the turn-over in these waters is high  
662 enough that the phytoplankton is grazed as soon it is produced, preventing biomass from  
663 accumulating.

664 Somewhat surprisingly, the NBSS slopes at MAD-Ridge were highly variable with depth and  
665 did not show any correlation with the distribution of Chl *a*. Few studies have explored the  
666 relationship between zooplankton NBSS and depth, but Suthers et al. (2006) observed  
667 steeper slopes around the thermocline (30 or 60m). In Lebourges-Dhaussy et al. (2014),  
668 although they do not show the NBSS at different depths, they did notice an increase in the  
669 small size classes 0.4 to 1 mm and > 2 mm ESD in proximity to the DCM in cyclonic eddies in  
670 the Mozambique Channel. We observed steeper NBSS slopes at the depth of the DCM  
671 within the cyclonic eddy (at station 2 and the adjacent station 6), whereas in the anticyclone  
672 most of the steepest slopes were located in the shallowest net of the Multinet (~25 to 30m).  
673 The variability of the slopes in our study could also be a consequence of the rarity and  
674 patchiness of large migrating zooplankton which are able to enter and leave the system  
675 (Rodriguez and Mullin, 1986). NBSS slopes might be impacted strongly by the occurrence of  
676 these rare large specimens.

677           4.2.2.       *La Pérouse*

678 The zooplankton at La Pérouse was highly variable in terms of abundance and biovolume  
679 and seemed very patchy. This could be due to natural patchiness or a topographic effect,  
680 but was also likely influenced by the change in circulation during the cruise. The detailed  
681 vertical current profiles (Marsac et al., this issue) revealed a prevalent surface current in a  
682 north-north-west direction but a change of direction towards the south at the end of the  
683 cruise when stations 23 and 24 were sampled. Hence stations 4 and 9 (without the one  
684 trachymedusa) were upstream of the seamount at the time of sampling and had low  
685 zooplankton abundance, while stations 3 and 6 were located downstream of the seamount  
686 and had high zooplankton abundance, suggesting a possible retention or aggregation effect  
687 in the lee of the seamount. Previous observations of greater abundance of zooplankton  
688 downstream from seamounts are hypothesised to be due to stronger currents above the  
689 seamount “pushing” the zooplankton downstream (Genin, 2004; Pitcher et al., 2007).  
690 However, due to the small sample size in our study, we cannot conclude with any certainty  
691 that this downstream peak in abundance was an actual seamount effect.

#### 692 4.2.3. *Walters Shoal*

693 We could not do an “on versus off seamount” comparison at Walters Shoal, not having any  
694 samples located at some distance from the seamount due to ship time constraints.  
695 Nonetheless, the stations sampled were located all around the seamount and at different  
696 bottom depths. The main flow around Walters Shoal was extremely low and variable  
697 (Demarcq et al., this issue), making it impossible to identify one side as being the lee of the  
698 seamount. The zooplankton abundance was low everywhere except at station 14 which had  
699 a similar abundance to stations located in the anticyclone at MAD-Ridge, as well as a similar  
700 biovolume size spectrum. Station 1, which was sampled adjacent to station 14 in the same  
701 “canyon” on the south-west of the seamount, also had slightly greater abundance and  
702 biovolume. This deep break in the topography could provide a shelter for organisms which  
703 may explain the slight increase in zooplankton abundance. Unfortunately, no ADCP data  
704 were available to confirm a possible convection cell in this location.

705 We cannot reject the hypothesis that the low zooplankton abundance at all the Walters  
706 Shoal stations could be the result of increased predation pressure linked to the presence of  
707 the seamount. Demarcq et al. (this issue) emphasised that of the three seamounts, Walters  
708 Shoal is the only one with a significant enrichment index. However, backscattering data do

709 not seem to show any major differences in the response at 38 kHz away from or close to the  
710 seamount (unpublished data, G. Roudaut).

#### 711 *4.3. Concluding remarks*

712 Overall the zooplankton communities over the seamounts studied were comparable to  
713 those in the surrounding waters without any clear seamount effect. The classic hypothesis  
714 of enhanced plankton densities around seamounts relies on the presence of a retention  
715 mechanism, induced by the topography, which would retain upwelled or advected biomass  
716 (Rogers, 1994). However, there was no indication of a Taylor column at any of the  
717 seamounts studied here (Annasawmy et al., this issue; Demarcq et al., this issue). Other  
718 hypotheses and observations suggest that seamounts have less zooplankton than the  
719 surrounding waters due to an increased predation pressure (Genin, 2004; Martin and  
720 Christiansen, 2009; Pitcher et al., 2007; Rogers, 1994). At MAD-Ridge, a high acoustic  
721 density was measured on the flanks of the seamount during the cruise, suggesting fish  
722 aggregation (Annasawmy et al., this issue), but the amount of zooplankton was not  
723 significantly different close to or distant from the seamount. Here, the cyclonic eddy and the  
724 influence of the shelf had a greater impact on the zooplankton communities than the  
725 seamount itself. At La Pérouse, as discussed above and in Marsac et al (this issue), the  
726 seamount might have had a small impact on zooplankton at a localised spatial scale with an  
727 enhanced biomass in the lee side of the seamount, however this conclusion is based on only  
728 two observations and should be investigated further. At Walters Shoal the season most  
729 likely had a stronger effect on the zooplankton community than the seamount itself, but the  
730 lack of samples at some distance from the seamount made it difficult to draw firm  
731 conclusions.

732 In a recent review, Rogers (2018) acknowledged that many studies on zooplankton did not  
733 detect any seamount effect, and that amongst the few studies which did find an effect, a  
734 low zooplankton abundance was measured, mostly due to increased predation and  
735 topography blockage. In theory, migrating organisms can become trapped on top of  
736 seamounts during their descent at dawn. This would either lead to a local accumulation of  
737 zooplankton or attract predators and thus result in reduced zooplankton abundance,  
738 leading to the formation of “gaps” in the zooplankton distribution. This hypothesis is  
739 difficult to test with traditional plankton net as it is too risky to sample very close to the

740 bottom over abrupt topography. With the emergence of new technology, optical or acoustic  
741 tools such as the Underwater Vision Profiler (Picheral et al., 2010), the zooplankton  
742 visualization and imaging system (Bi et al., 2015) or the Acoustic Zooplankton Fish Profiler  
743 (Lemon et al., 2012) could be deployed close to the bottom or moored, to convincingly  
744 detect this kind of phenomenon (Hosegood et al., 2019, pers. comm.). However, it is likely  
745 that only large zooplankton will be impacted by such bottom-trapping in the SWIO, as  
746 smaller ones do not seem to perform strong vertical migrations (Huggett, 2014; Martin and  
747 Christiansen, 2009; Noyon et al., 2019), and only at shallow seamounts with a summit within  
748 the range covered by zooplankton migrations.

749

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760

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1027 **List of figures:**

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1066 the size diversity index, the slope, linear fit and intercept of the NBSS. Stations have different  
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1068 stations: dark triangles for the stations within the anticyclone (AC), white triangles for the others.  
1069 Stations are named according to the cruise (P for La Pérouse, M for MAD-Ridge and W for Walters

1070 Shoal) followed by the numbers as per Figure 1. The bin sizes used (red crosses) are named using the  
1071 abbreviation "BV" for biovolume followed by the middle of the bin size in mm ESD. The red dotted  
1072 line links the bin size in order. Green arrows represent the significant environmental explanatory  
1073 variables ( $p > 0.05$ ), plotted on top of the ordination: Sea Surface Temperature (SST) and depth of  
1074 the Deep Chlorophyll a Maximum (DCM)

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Table 1: Environmental variables measured during the three cruises

	La Pérouse <i>n</i> = 10			MAD-Ridge <i>n</i> = 23			Walters Shoal <i>n</i> = 13		
	<i>avg.</i>	$\pm$	<i>std</i>	<i>avg.</i>	$\pm$	<i>std</i>	<i>avg.</i>	$\pm$	<i>std</i>
<i>Sea Surface Temperature (°C)</i>	23.6	$\pm$	0.7	24.5	$\pm$	0.2	20.5	$\pm$	0.4
<i>Mixed Layer Depth (m)</i>	59	$\pm$	22	51	$\pm$	26	41	$\pm$	17
<i>Deep Chl a Maximum Depth (m)</i>	105	$\pm$	23	106	$\pm$	29	37	$\pm$	10
<i>Integrated Chl a (mg m<sup>-3</sup>)</i>	20.23	$\pm$	3.51	20.76	$\pm$	3.06	23.07	$\pm$	4.56
<i>Chl a at Deep Chl a Max (mg m<sup>-3</sup>)</i>	0.314	$\pm$	0.083	0.300	$\pm$	0.134	0.239	$\pm$	0.039
<i>Nutricline Depth (m)</i>	112	$\pm$	22	119	$\pm$	34	53	$\pm$	11

Table 2: Abundance and biovolume of zooplankton collected during the three cruises and Normalised Biovolume Size Spectrum (NBSS) parameters. The last three lines ('all') correspond to the parameters of the global NBSS calculated for each seamount using all the stations together.

	<b>La Pérouse</b>			<b>MAD-Ridge</b>			<b>Walters Shoal</b>		
	<i>n = 10</i>			<i>n = 23</i>			<i>n = 13</i>		
	<i>avg.</i>	$\pm$	<i>std</i>	<i>avg.</i>	$\pm$	<i>std</i>	<i>avg.</i>	$\pm$	<i>std</i>
<i>Abundance (ind m<sup>-3</sup>)</i>	201.2	$\pm$	98.2	204.6	$\pm$	90.0	60.8	$\pm$	53.4
<i>Biovolume (mm<sup>3</sup> m<sup>-3</sup>)</i>	42.81	$\pm$	15.14	45.64	$\pm$	20.92	12.69	$\pm$	8.27
<i>NBSS slope</i>	-0.89	$\pm$	0.15	-1.00	$\pm$	0.09	-0.79	$\pm$	0.09
<i>NBSS intercept</i>	0.59	$\pm$	0.18	0.50	$\pm$	0.17	-0.20	$\pm$	0.32
<i>Size diversity Index</i>	2.27	$\pm$	0.05	2.34	$\pm$	0.05	2.18	$\pm$	0.05
<i>NBSS slope - all</i>			-0.93			-1.00			-0.78
<i>NBSS intercept - all</i>			0.57			0.50			-0.18
<i>NBSS linear fit - all</i>			0.93			0.94			0.78

Table 3: Abundance (ind m<sup>-3</sup>) of all taxa for all the stations at each studied seamount: average  $\pm$  standard deviation (avg  $\pm$  std) and percentage

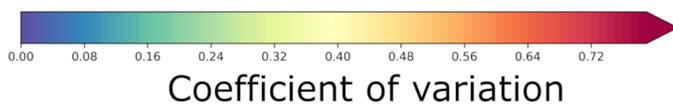
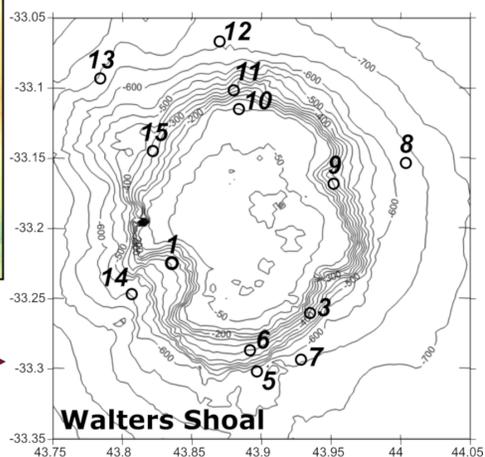
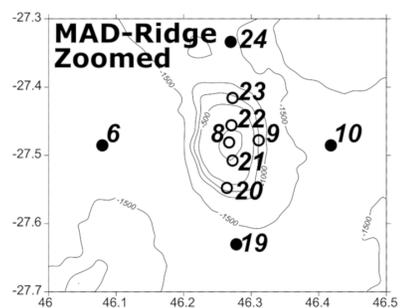
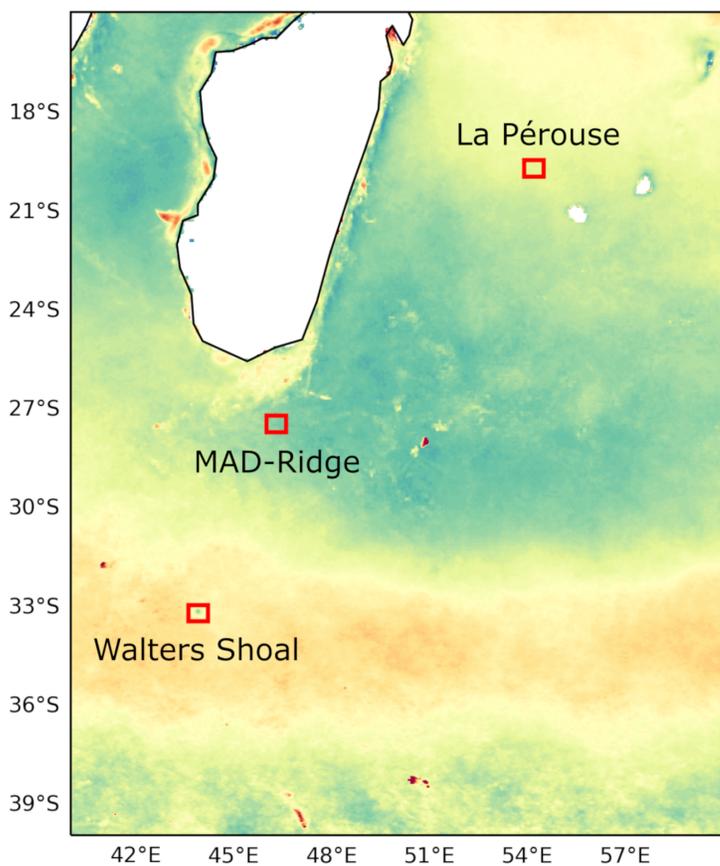
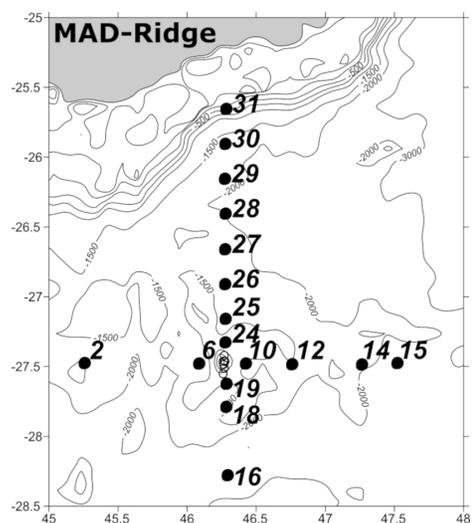
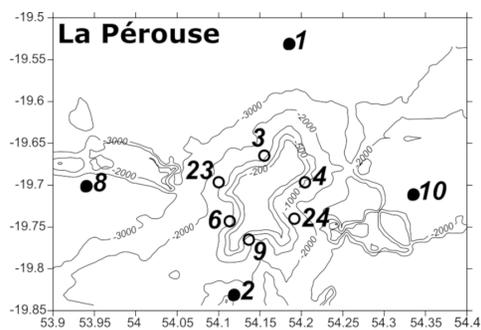
	La Pérouse			MAD-Ridge			Walters Shoal		
	<i>n</i> = 10			<i>n</i> = 23			<i>n</i> = 13		
	avg.	$\pm$ std	%	avg.	$\pm$ std	%	avg.	$\pm$ std	%
<i>Calanoida</i>	86.5	$\pm$ 46.1	42.7	83.1	$\pm$ 49.7	39.1	31.6	$\pm$ 34.0	46.5
<i>Oithonidae</i>	21.7	$\pm$ 12.9	10.3	17.7	$\pm$ 5.8	9.1	7.4	$\pm$ 7.3	12.6
<i>Oncaeidae</i>	19.4	$\pm$ 12.0	9.1	17.7	$\pm$ 10.1	8.4	1.7	$\pm$ 5.7	1.1
<i>Other copepoda</i>	20.5	$\pm$ 7.8	10.5	25.2	$\pm$ 8.0	13.0	5.0	$\pm$ 4.9	8.8
<i>Appendicularia</i>	8.7	$\pm$ 3.8	4.8	10.9	$\pm$ 5.9	5.2	2.4	$\pm$ 1.6	5.0
<i>Chaetognatha</i>	11.5	$\pm$ 4.0	6.2	9.3	$\pm$ 2.2	4.9	2.4	$\pm$ 1.3	5.8
<i>Amphipoda</i>	0.8	$\pm$ 0.8	0.5	1.0	$\pm$ 0.4	0.5	0.1	$\pm$ 0.1	0.2
<i>Euphausiacea</i>	1.3	$\pm$ 0.9	0.7	1.2	$\pm$ 0.8	0.6	0.1	$\pm$ 0.1	0.2
<i>Decapoda larvae</i>	0.5	$\pm$ 0.7	0.2	0.4	$\pm$ 0.2	0.2	0.3	$\pm$ 0.4	0.4
<i>Other crustaceans</i>	12.6	$\pm$ 8.5	6.1	13.2	$\pm$ 6.5	6.4	1.8	$\pm$ 2.9	2.8
<i>Gelatinous zooplankton</i>	1.6	$\pm$ 0.6	0.9	2.7	$\pm$ 1.2	1.4	0.3	$\pm$ 0.4	0.5
<i>Harosa</i>	5.2	$\pm$ 4.0	2.5	10.5	$\pm$ 5.0	5.4	1.9	$\pm$ 1.0	4.6
<i>Other zooplankton</i>	10.9	$\pm$ 8.5	5.3	11.8	$\pm$ 6.5	5.7	5.8	$\pm$ 4.2	11.4

Table 4: Biovolume ( $\text{mm}^3 \text{m}^{-3}$ ) of all the taxa for all the stations at all three seamounts: average  $\pm$  standard deviation (avg  $\pm$  std) and percentage

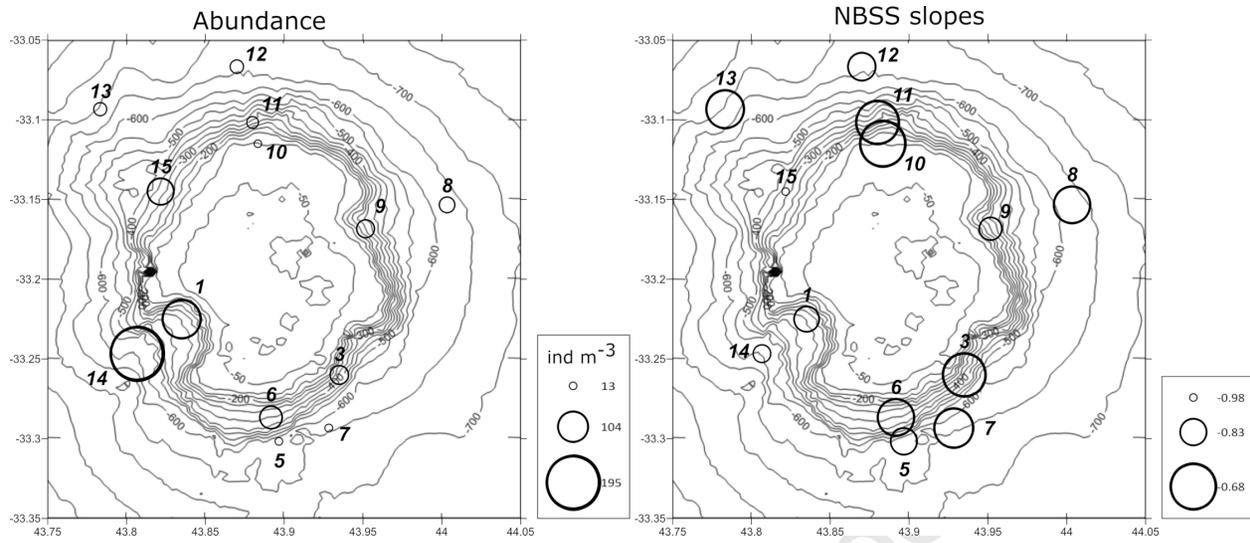
	La Pérouse				MAD-Ridge				Walters Shoal			
	avg.	$\pm$	std	%	avg.	$\pm$	std	%	avg.	$\pm$	std	%
<i>Calanoida</i>	13.94	$\pm$	5.43	33.8	15.18	$\pm$	12.52	30.4	1.96	$\pm$	2.46	13.6
<i>Oithonidae</i>	0.85	$\pm$	0.47	2.1	0.64	$\pm$	0.21	1.5	0.16	$\pm$	0.14	1.3
<i>Oncaeidae</i>	0.87	$\pm$	0.51	2.1	0.83	$\pm$	0.57	1.8	0.05	$\pm$	0.17	0.2
<i>Other copepoda</i>	2.21	$\pm$	1.62	5.0	2.31	$\pm$	1.02	5.4	0.20	$\pm$	0.17	2.1
<i>Appendicularia</i>	0.60	$\pm$	0.29	1.7	0.82	$\pm$	0.66	1.7	0.29	$\pm$	0.59	0.9
<i>Chaetognatha</i>	10.04	$\pm$	3.93	23.6	7.93	$\pm$	3.79	18.6	4.40	$\pm$	3.97	40.2
<i>Amphipoda</i>	1.11	$\pm$	1.50	2.4	1.74	$\pm$	1.48	4.2	0.29	$\pm$	0.59	2.0
<i>Euphausiacea</i>	3.16	$\pm$	3.46	6.7	3.32	$\pm$	3.77	7.1	2.74	$\pm$	4.25	19.6
<i>Decapoda larvae</i>	1.30	$\pm$	1.55	2.8	1.67	$\pm$	2.43	3.6	0.55	$\pm$	0.91	3.9
<i>Other crustaceans</i>	1.23	$\pm$	0.76	2.7	1.52	$\pm$	1.10	3.3	0.11	$\pm$	0.18	0.9
<i>Gelatinous zooplankton</i>	3.65	$\pm$	2.93	8.3	5.92	$\pm$	4.02	14.1	0.71	$\pm$	1.27	4.7
<i>Harosa</i>	0.19	$\pm$	0.13	0.4	0.54	$\pm$	0.21	1.3	0.08	$\pm$	0.03	0.9
<i>Other zooplankton</i>	3.66	$\pm$	3.64	8.2	3.23	$\pm$	2.51	7.2	1.34	$\pm$	2.20	9.7

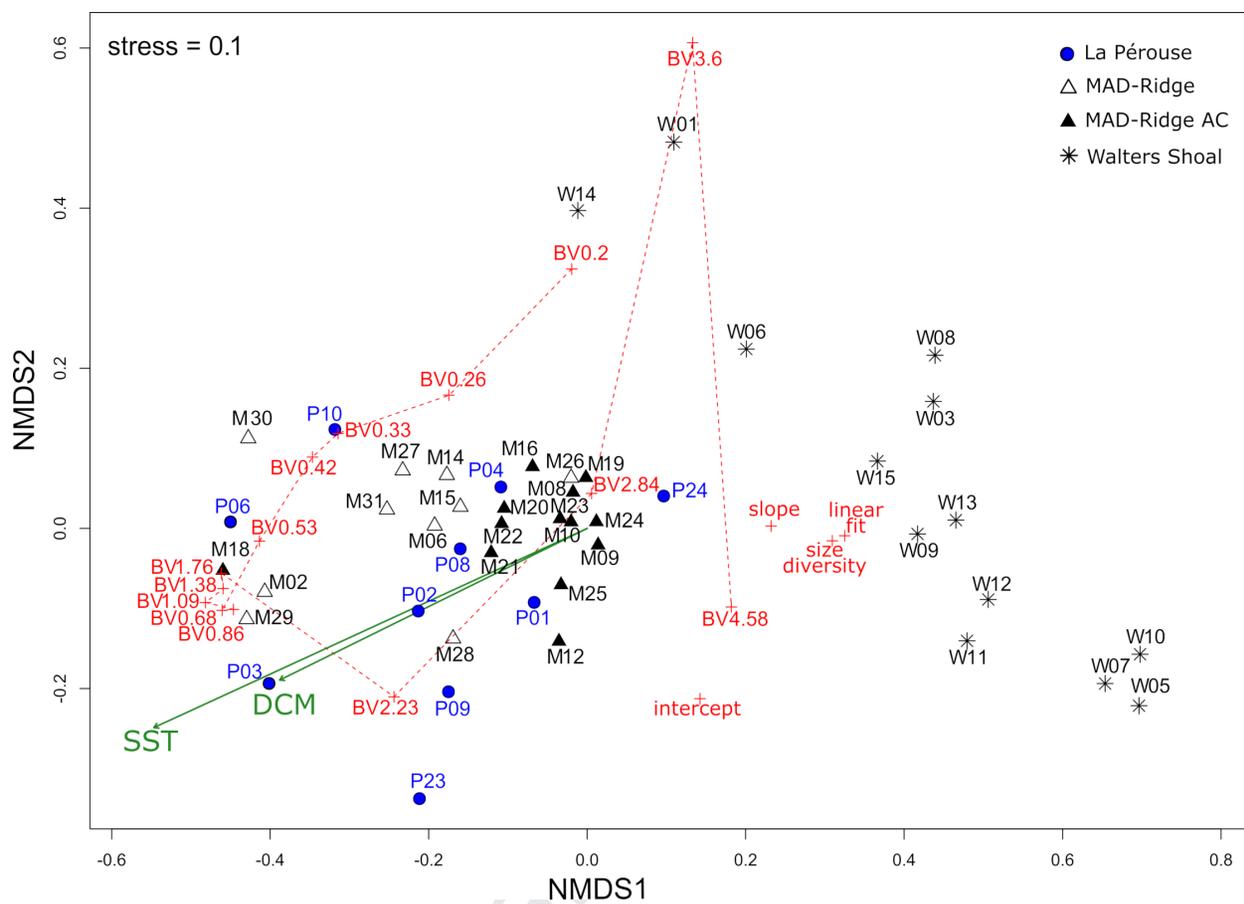
Table 5: Spearman coefficients of some biological parameters measured during all three cruises and for all the stations together. The “\*” symbol corresponds to the level of significance with \* for  $p < 0.05$ , \*\* for  $p < 0.01$ , \*\*\* for  $p < 0.001$ . No star means that no significant relationship was found between the two parameters tested

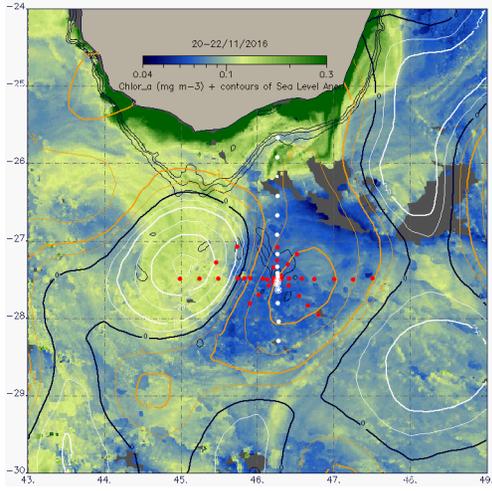
	La Pérouse <i>n</i> = 10	MAD-Ridge <i>n</i> = 23	Walters Shoal <i>n</i> = 13	All <i>n</i> = 46
Abundance ~ Biovolume	0.36	0.77***	0.88***	0.84***
Abundance ~ NBSS slope	-0.29	-0.36	-0.64*	-0.61***
Biovolume ~ NBSS intercept	0.89***	0.91***	-0.65*	0.65***
Diversity index ~ NBSS slope	0.79*	0.00	0.59*	-0.43**
Diversity index ~ NBSS linear fit	0.49	0.44*	-0.48	0.31*



Coefficient of variation







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